Limited ant co-occurrence and defensive mutualism in Acacia plants in a West African savanna

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Abstract

Our understanding of the role of fire and effect of ant species composition, beyond their diversity and abundance, on the effectiveness of mutualism defence is limited. Most of our knowledge of ant–plant defence in tropical Africa is biased towards East African savannas which have richer soil, higher primary productivity and a more diverse arthropod and mammal community than West African savannas. We assessed the diversity of ant species associated with Acacia species in the Pendjari Biosphere Reserve in the Dahomey Gap, and their impacts on elephant damage. Elephant damage, ant diversity and abundance were measured in stands of five Acacia species. Eleven ant species were identified in the Acacia stands. The composition of these ant communities varied across Acacia species. Pair of ant species co-occurred in only 2 % of sampled trees, suggesting a strong competitive exclusion. Within this annually burnt environment, ants were rare on small trees. The intensity of elephant-caused branch breaking did not vary between trees with ants and trees without ants, suggesting limited Acacia–ant mutualism. Such limited biotic defence may mask strong physical and chemical defence mechanisms of Acacia trees against elephant damage. Ant assemblages in West Africa, unlike those in the more productive East Africa, are particularly species-poor. However, there is a convergence between these two regions in low rate of ant co-occurrence which might indicate strong competitive exclusion. Our study suggests that such low ant species richness while limiting the efficacy of mutualism in controlling mega-herbivore damage may mask a strong defence syndrome.

Keywords: Acacia species; ants; Dahomey Gap; defensive mutualism; elephant damage; plant–animal interactions; West African savanna.

Introduction

In African savannas, elephants (Loxodonta africana) confined to protected areas are a major driver of savanna dynamics, impacting trees through browsing, bark stripping and uprooting (hereafter called ‘elephant damage’) (Asner and Levick 2012; Kassa et al. 2014; Morrison et al. 2016; Salako et al. 2016). Elephants disproportionately damaged certain tree species relative to their availability on the landscape as it is the case for Adansonia digitata, Borassus aethiopum (Salako et al. 2016).
A. drepanolobium

For example, many trees lost their ant colonies – Acacia ecosystems, and ultimately contribute to the loss of the rare and Vasconcelos 2014). Fire destroys many ant populations Ratchford human disturbance. In savannas, the species composition of underlying the defensive effects of ants against elephants also Crematogaster sjostedti defending trees against elephants, African acacia ants were of ant defence mutualism in this region is still limited.

2015; Wargui colony mortality was greatest for small trees (Kimuyu 2013; Kimuyu et al. 2014; Morrison et al. 2016). Recent work focussed on the role of weaver ant Oecophylla longinoda as biological control in orchards in Benin (Ouagoussouonon et al. 2013; Vayssières et al. 2015; Wargui et al. 2015; Wetterer 2017) but our understanding of ant defence mutualism in this region is still limited.

According to their aggressiveness and efficiency in defending trees against elephants, African acacia ants were classified into dominant (Crematogaster sjoestedi), intermediate (C. mimosae and C. nigricaps) and subordinate (Tetraponera penzigi) species (Palmer et al. 2013). The aggressiveness that underlies the defensive effects of ants against elephants also enables them to outcompete other ants (Heil 2013). The role played by ants in terrestrial ecosystems is always altered after human disturbance. In savannas, the species composition of ant communities varies across fire regimes (Parr et al. 2004; Ratchford et al. 2005; Vasconcelos et al. 2008, 2017; Maravalhas and Vasconcelos 2014). Fire destroys many ant populations and can reduce ant diversity and abundance in terrestrial ecosystems, and ultimately contribute to the loss of the rare ant species and or limit their aggressiveness. In some Acacia–ant systems, fire management can shift plant–ant occupancy. For example, many A. drepanolobium trees lost their ant colonies after burns (Kimuyu et al. 2014; Pringle et al. 2015). Fire-induced colony mortality was greatest for small trees (Kimuyu et al. 2014). Contrary to arboreal ants, fire increased the mean number of ant species on the ground within neotropical savannas (Frizzo et al. 2012). Without their ant colonies, individuals of the myrmecophyte A. drepanolobium were equally browsed as the typically non-myrmecophyte Acacia mellifera trees which experience catastrophic elephant herbivory (Goheen and Palmer 2010). Such tree vulnerability to elephant damages, due to increased fire, may have profound implications for population viability because Acacia adult trees have relatively low resprouting capacity (Morrison et al. 2016). Individuals of A. mellifera remain non-myrmecophyte even when surrounded by individuals of the myrmecophyte A. drepanolobium (Goheen and Palmer 2010) indicating that not all Acacia species engage in mutualistic defence.

Understanding the ecological interactions between ant communities and Acacia damage by elephants is important for the sustainable management of these savanna ecosystems. In West Africa, the Biosphere Reserve of Pendjari is an ideal area for investigating Acacia–ant mutualism against elephant herbivory because the geomorphology of the reserve does not create natural refuge for tree species to escape elephant damage (Kassa et al. 2014). Unlike East African protected areas, large extensions of the savannas in the Pendjari are annually burnt (Azihou et al. 2013) and dominated by species belonging to the Combretaceae family (Assédé et al. 2012). Early fires are used yearly by the management of the Biosphere reserve to promote grass resprout which attracts wildlife closer to roads for viewing tourism while limiting higher rate of topkill for the woody species. Eleven Acacia species occur in the reserve including Acacia sieberiana, Acacia seyal, Acacia gourmaensis, Acacia hockii and Acacia dudgeoni which have been reported to be highly browsed by elephants (Azihou 2008; Assédé et al. 2012). The Pendjari Biosphere Reserve supports 869 elephants with a density of 1 individual per 6 km² (Bouche et al. 2011).

In this study, we assessed how the composition and diversity of ant species associated with Acacia trees in the Biosphere Reserve of Pendjari impact elephant damage. Because all management units of the reserve experience the same fire regime, we hypothesize that ant community will be similar across management units. We expect annual management fires to favour the richness of ground-dwelling ant species while hindering the establishment of arboreal ants on Acacia trees especially on smaller individuals. Following the competitive exclusion hypothesis, we expect a single ant species to be abundant on myrmecophyte Acacia individuals leading to rare co-occurrence of Acacia ants on the same tree. As observed in East African savannas, we finally predict individuals of non-myrmecophyte Acacia species to suffer higher attack rates from elephants than would ant-inhabiting Acacia species. Testing such hypotheses in the Biosphere Reserve of Pendjari will provide new evidence on the effect of fire on Acacia–ant mutualism while filling the knowledge gap between Eastern and Western Africa on the trirophic interaction between elephants, ants and Acacia species.

Materials and Methods

Study site

The Pendjari Biosphere Reserve is the uppermost north-west Benin in the Sudanian region of the Dahomey Gap (Adomou et al. 2006; Assédé et al. 2012) between the latitudes 10°30′ and 11°30′ N and the longitudes 0°50′ and 2°00′ E. The reserve covers an area of 4661.4 km² and includes the National Park of Pendjari or core zone (2660.4 km²) and the hunting zones (hunting zone of Pendjari: 1750 km² and hunting zone of Konkombi: 251 km²). The core zone is a strictly protected area where the vegetation is less disturbed by anthropogenic activities; only ecotourism is allowed. The core zone and the hunting zones are surrounded by a buffer zone where human activities are under control (Assédé et al. 2012). These management units experience early vegetation fire on a yearly basis. Hunting elephants is prohibited in these management units. The climate of the Biosphere Reserve of Pendjari is characterized by one rainy season (April/ May to October) and one dry season (November to March). The total annual rainfall averages 1000 mm with 60 % falling between July and September. During the rainy season, large parts of the reserve are flooded. The mean annual temperature is 27 °C. In addition, the relative humidity varies between 17 and 99 % over the year (Azihou 2013). The eastern part of the reserve is bordered by the Atacora mountain chain (400–513 m above sea level). Large isolated hills and floodplains are also present. The reserve is mainly characterized by tropical ferruginous soils except on hills (rock outcrops) and in flooded zones (clayey soil and silty soil) (Willaine and Volkoff 1967). The Pendjari is the only important river in the reserve that carries water throughout the year. It runs through the National Park of Pendjari and the Pendjari hunting zone. The vegetation of the Biosphere Reserve of Pendjari is dominated by savannas (tree, shrub and grass
savannas) with islands of woodlands, dry forests and gallery forests along rivers (Azihou 2013).

**Sampling of the diversity and abundance of ants**

We measured the diversity and abundance of ants once during the dry season after the annual vegetation fire in stands of *A. sieberiana*, *A. seyal*, *A. gourmaensis*, *A. hockii* and *A. dudgeonii* in the Pendjari Biosphere Reserve. Data on ants’ abundance were collected on Acacia trees sampled in 28 plots of 100 m × 100 m each. We sampled ants in eight plots for *A. sieberiana* sites and in five plots for each of the other *Acacia* species because *A. sieberiana* was more represented in the Pendjari Biosphere reserve. To evaluate the abundance and diversity of the ants, we used attractive traps consisting of 30 × 30 cm white ceramic tiles, each with a 4 cm spot of bait composed of honey mixed with canned tuna at its centre. These attractive traps designed to evaluate the abundance and diversity of ants were placed under the Acacia trees and deployed for 30 min before the ants were counted and collected with a mouth aspirator. Ant counting was perfected in digital photographs of the samples (Dassou et al. 2015, 2016). Bait traps were placed under 10 randomly chosen Acacia trees in each plot. To reinforce the collection of the diversity and abundance of ants, after collecting all the ant taxa in the bait trap we captured with an aspirator all ants that move on the Acacia tree stem above the trap to a height of 2 m. These ant taxa collected on the tree stem were counted at the lab. In plots with less than 10 Acacia trees, all individuals were sampled. All samples were obtained in the morning between 8:00 a.m. and 12:00 p.m. Ants caught were preserved in 70 % ethanol solution. Ant species collected in the Acacia ecosystems were identified at the Entomological Museum of the International Institute for Tropical Agriculture, Benin Station.

**Measurements of the intensity of elephant damage**

We measured the intensity of elephant damage on the same *Acacia* trees on which ant diversity and abundance data were collected. On each sampled tree we measured the diameter at breast height (dbh), diameter of crown, total and trunk heights. The intensity of elephant damages was scored following the classification of Rignos et al. (2015). Two types of elephant damages were observed in the field: barking and branch breaking. The intensity of branch breaking was measured on a 1–5 scale: 1 for light or no damage (branch tips exhibit slight browsing); 2 for mild damage (branches browsed and broken); 3 for medium damage (20–50 % of canopy was destroyed); 4 for substantial damage (50–99 % of canopy was destroyed); and 5 for catastrophic damage (tree completely pushed over or 100 % canopy destroyed). We used experienced field guides to distinguish tree damaged by elephants from damages due to abiotic factors such as wind or storm. Bark damage was scored on a seven-level scale, from the lowest to the highest intensity (Ihwagi et al. 2012; Kassa et al. 2014): score 0 for undamaged, 1 for tusked, 2 for 1–25 % debarked, 3 for 26–74 % debarked, 4 for 75 % debarked, 5 for 76–99 % debarked and 6 for ring debarked.

**Data analysis**

All statistical analyses were performed in R (R Core Team 2019). A permutational multivariate analysis of variance using distance matrices (ADONIS) was performed on the data on ant communities associated with *Acacia* species using the package vegan (Oksanen et al. 2015). The source of variation introduced in the analysis included the intensity of elephant damages, *Acacia* species (*A. dudgeonii*, *A. gourmaensis*, *A. hockii*, *A. seyal* and *A. sieberiana*) and ant sampling location (tree versus ground). For each ant species, indicator value (IndVal) scores were calculated from samples grouped according to *Acacia* species and ant sampling location (see Dufrene and Legendre 1997 for details on IndVal calculations). The IndVal computed using the package labsao (Roberts 2015) estimates the association of each ant species to each group (*Acacia* species or ant sampling location). IndVal is scaled from 0 to 100 % with a value of 100 % indicating that the ant species was collected in every sample within a group and not in any other group.

Co-occurrence patterns of ant species under *Acacia* trees and on *Acacia* trees were assessed by computing the frequency of observations where each species pair is jointly recorded. The results were presented using a correlogram, an advanced graphical tool (Zuur et al. 2010; Azihou et al. 2013). A general linear model was used to test for difference in the intensity of elephant damages among *Acacia* species. The Student-Newman–Keulh (SNK) test was performed using the package agricolae (De Mendiburu 2014) for pairwise means comparison. We performed a χ² test to assess the independence between *Acacia* species and ant occurrence on trees. For each *Acacia* species, we used a Student's t-test to compare the height and the intensity of elephant damages between trees with ants and trees without ants. A beta regression was performed using the package betareg (Cribari-Neto and Zeileis 2010) to test the effect of ant abundance and species richness under *Acacia* trees and on *Acacia* trees on the intensity of elephant damage. There was

**Table 1.** Outputs of the permutational multivariate analysis of variance using distance matrices (ADONIS) on ant communities associated with *Acacia* species in the Biosphere Reserve of Pendjari. SS = sums of squares, MS = mean square, DF = degree of freedom.

| Source of variation               | DF | SS     | MS     | F     | R²    | P     |
|----------------------------------|----|--------|--------|-------|-------|-------|
| Intensity of damages             | 1  | 0.481  | 0.481  | 1.346 | 0.006 | 0.196 |
| *Acacia* species                 | 4  | 5.168  | 1.292  | 3.612 | 0.063 | 0.001 |
| Ant location                     | 1  | 2.057  | 2.057  | 5.751 | 0.025 | 0.182 |
| Intensity of damages × *Acacia* species | 4  | 1.435  | 0.359  | 1.003 | 0.018 | 0.416 |
| Intensity of damages × ant location | 1  | 0.485  | 0.485  | 1.355 | 0.006 | 0.182 |
| *Acacia* species × ant location  | 2  | 0.804  | 0.402  | 1.123 | 0.010 | 0.318 |
| Intensity of damages × *Acacia* species × ant location | 2  | 0.286  | 0.143  | 0.400 | 0.003 | 0.986 |
| Residuals                        | 199| 71.189 | 0.358  | 0.869 |       |       |
| Total                            | 214| 81.904 |        |       |       |       |
a significant correlation between ant abundance and species richness for observations made on Acacia trees. Therefore, we ran the analysis separately for each response variable.

Results

Abundance and diversity of ant species associated with Acacia trees

At total 8772 ants including 11 ant species were associated with Acacia trees namely Monomorium bicolor (3584 individuals), Pheidole megacephala (3412 individuals), Pheidole rugaticeps (852 individuals), Camponotus sericeus (372 individuals), Trichomyrmex oscaris (230 individuals), Camponotus carbo (147 individuals), Plagiolepis alluaudi (102 individuals), Crematogaster coelestis (29 individuals), Myrmicaria opaciventris (21 individuals), Brachyponera sennaarensis (20 individuals) and Camponotus maculatus (3 individuals). Most of these ant species are generalist with widespread distribution. Abundance and diversity of ant species did not vary across the intensity of elephant damages ($F_1 = 1.346, P = 0.196$) contrary to Acacia species ($F_2 = 3.612, P = 0.001$) and location of ant sampling ($F_1 = 5.751, P = 0.001$) (Table 1). The interaction between the intensity of damages and Acacia species was not significant ($F_2 = 1.003, P = 0.416$), suggesting that the abundance and diversity of ant species associated with an Acacia species did not vary according to the intensity of elephant damages. Similarly, the interaction between the intensity of damages and location of ant sampling was not significant ($F_1 = 1.355, P = 0.182$). Thus, the abundance and diversity of ant species associated recorded under or on Acacia trees did not vary according to the intensity of elephant damages. The interaction between Acacia species and location of ant sampling was not significant ($F_2 = 1.123, P = 0.318$) indicating that the assemblage of ants recorded under or on trees did not vary across Acacia species.

Five ant species were identified as indicator of Acacia species and location of ant sampling (Table 2). Camponotus sericeus (IndVal = 0.414, $P = 0.028$) and C. coelestis (IndVal = 0.088, $P = 0.008$) showed a substantial fidelity with the arboreal habitat. Monomorium bicolor (IndVal = 0.259, $P = 0.003$) and P. rugaticeps (IndVal = 0.200, $P = 0.001$) were most associated with A. gourmaensis trees while C. carbo (IndVal = 0.166, $P = 0.008$) showed a significant fidelity with A. dudgeonii individuals.

Co-occurrence among ant species under Acacia trees and on host plants

All ant species were recorded under the 261 sampled Acacia trees (Fig. 1A). Except C. sericeus (36 %) and M. bicolor (19 %), C. carbo (13 %) and P. megacephala (12 %), ant species were successfully sampled under less than 5 % of Acacia trees. Camponotus maculatus, B. sennaarensis and M. opaciventris did not

Table 2. Indicator species analysis on significant factors identified through ADONIS

| Parameter | Ant species | Indicator value | P-value |
|-----------|-------------|----------------|---------|
| Ant location = on tree | Camponotus sericeus | 0.414 | 0.028 |
| Ant location = on tree | Crematogaster coelestis | 0.088 | 0.008 |
| Acacia species = Acacia gourmaensis | Monomorium bicolor | 0.259 | 0.003 |
| Acacia species = Acacia gourmaensis | Pheidole rugaticeps | 0.200 | 0.001 |
| Acacia species = Acacia dudgeonii | Camponotus carbo | 0.166 | 0.008 |

Figure 1. Corrgram showing the frequency with which pairs of ant species both occurred (A) under the same Acacia tree and (B) on the same Acacia tree. The colour and the amount that a circle has been filled correspond to the proportion of joint presence observations. The diagonal running from the bottom left to the top right represents the percentage of trees where each ant species was observed. Eight-letter acronyms represent the different tree species. Full species names: Monobico = Monomorium bicolor, Pheimega = Pheidole rugaticeps, Tricosca = Trichomyrmex oscaris, Pheimega = Pheidole megacephala, Campseri = Camponotus sericeus, Campcarb = Camponotus carbo, Campsenn = Crematogaster coelestis, Plagalu = Plagiolepis alluaudi, Campmacu = Camponotus maculatus, Bracserin = Brachyponera sennaarensis, Myrmopac = Myrmicaria opaciventris. The legend bar relates the colours in the graph to the proportion of the observations.
co-occur with any ant species. For the remaining species, the highest co-occurrence frequency equalled 7 % and was observed between M. bicolor and C. sericeus mainly under A. dudgeonii and A. seyal individuals. These species, respectively, co-occurred with six and five other ant species.

Only seven ant species were recorded on 12.64 % of the sampled Acacia trees (Fig. 1B) namely M. bicolor, P. megacephala, C. sericeus, C. carbo, C. coelestis, C. maculatus and M. opaciventris. These species occurred on less than 2 % of sampled Acacia trees except C. sericeus (9 %). Monomorium bicolor, P. megacephala and M. opaciventris were not jointly recorded on any Acacia trees with any other ant species. Co-occurrence of ant species pair was rare and included only C. coelestis–C. carbo (0.8 %), C. coelestis–C. sericeus (0.4 %), C. carbo–C. sericeus (0.4 %) and C. carbo–C. maculatus (0.4 %).

**Ant species and elephant damage on Acacia trees**

Across Acacia tree species, branch breaking was the main elephant damage observed on 94–100 % of sampled individuals (Table 3). The intensity of elephant-driven branch breaking significantly varied among Acacia tree species (F4,315 = 2.849, P = 0.025). Individuals of A. sieberiana experienced the highest damage (19 % of branch broken) contrary to A. dudgeonii (10 % of branches broken). Ant species were absent on A. dudgeonii and A. hockii trees. Observation of ants on trees was 2-fold higher for A. sieberiana (29 % of sampled trees) than A. gourmaensis and A. seyal (14 %). However, this variation was not significant (χ² = 4.655, P = 0.098). Acacia gourmaensis trees without ants were significantly smaller than their congener with ants (mean total height equals to 6.36 and 7.62 m, respectively; t45 = −2.050, P = 0.046). Individuals of A. seyal showed a similar but not significant trend (5.72 and 6.65 m, respectively; t45 = −1.862, P = 0.069). The total height did not vary between A. sieberiana trees without and with ants (11.79 and 11.26 m, respectively; t45 = 0.767, P = 0.446). The mean total height within the two Acacia species (A. dudgeonii and A. hockii) whose trees have no ants was statistically equalled to that of A. gourmaensis individuals without ants (5.74, 6.23 and 6.36 m, respectively; F1,30 = 1.985, P = 0.149).

The abundance of each ant species per tree varied between 1 and 8.33 except one observation of 500 individuals of M. bicolor on an A. gourmaensis tree (Table 4). Overall, the intensity of elephant-caused branch breaking did not vary between trees with ants and trees without ants: A. sieberiana (20.68 and 18.28 %, respectively; t63 = −0.654, P = 0.516), A. gourmaensis (12.14 and 15.49 %, respectively; t63 = 0.666, P = 0.509), A. seyal (7.00 and 14.75 %, respectively; t63 = 0.933, P = 0.356). Neither the abundance of ants on Acacia trees, nor their species richness had a significant effect on the intensity of elephant-caused branch breaking across the five Acacia species (Table 5). A similar trend was observed for ants recorded under Acacia trees except A. dudgeonii where the abundance of ants under trees significantly reduced branch breaking by elephants (Z = −3.029, P = 0.002).

**Discussion**

Within the annually burnt reserve, ants were more diverse and frequent beneath than on Acacia trees, consistent with the contrasting effects of fire on arboreal and ground-dwelling ant communities. Fire can reduce the number of ant species

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**Table 3.** Elephant damages on Acacia tree species within the Biosphere Reserve of Pendjari. Numbers followed by the same letter are not different at 5 % level.

| Acacia species       | N  | Elephant damages (%) | Branch breaking |
|----------------------|----|----------------------|-----------------|
|                      |    | Barking             | Branch breaking |
|                      |    | Frequency | Intensity | Frequency | Intensity | Host plants (%) |
| Acacia sieberiana    | 65 | 0               | NA         | 100       | 18.98 ± 1.66a | 29.23 |
| Acacia gourmaensis   | 49 | 6.12             | 23.33 ± 3.33 | 93.88     | 14.98 ± 1.79ab | 14.29 |
| Acacia hockii        | 48 | 0               | NA         | 100       | 14.77 ± 2.67ab | 0.00 |
| Acacia seyal         | 49 | 4.08             | 45.00 ± 5.00 | 95.92     | 13.60 ± 2.95ab | 14.29 |
| Acacia dudgeonii     | 50 | 0               | NA         | 100       | 9.74 ± 0.83b  | 0.00 |

**Table 4.** Abundance (mean ± SE) of each ant species on Acacia trees within the Biosphere Reserve of Pendjari.

| Ant species           | Acacia sieberiana | Acacia gourmaensis | Acacia seyal |
|-----------------------|-------------------|-------------------|-------------|
|                       | Frequency | Abundance (mean ± SE) | Frequency | Abundance (mean ± SE) | Frequency | Abundance (mean ± SE) |
| Pheidole megacephala  | 1         | 5.00               | 0          | NA                   | 0         | NA                   |
| Monomorium bicolor    | 0         | NA                 | 1          | 500.00               | 0         | NA                   |
| Camponotus sericeus   | 12        | 3.50 ± 0.925       | 6          | 4.67 ± 0.558         | 5          | 1.60 ± 0.245         |
| Camponotus carbo      | 4         | 6.00 ± 3.674       | 0          | NA                   | 2          | 1.50 ± 0.500         |
| Myrmica opaciventris  | 2         | 5.50 ± 0.500       | 0          | NA                   | 0         | NA                   |
| Crematogaster coelestis| 3          | 8.33 ± 3.333       | 0          | NA                   | 0         | NA                   |
| Camponotus maculatus  | 1         | 1.00               | 0          | NA                   | 0         | NA                   |
Table 5. Estimates of the beta regression models on the variation of the intensity of elephant-caused branch breaking according to the abundance and species richness of ants on host trees and under host trees.

| Tree species          | Model 1 |       | Model 2 |       | Model 3 |       |
|----------------------|---------|-------|---------|-------|---------|-------|
|                      | Coef    | z     | P       |       | Coef    | z     |
| Acacia sieberiana    | -0.010  | -0.365| 0.715   | -0.013| -0.214  | 0.830 |
|                      | -0.001  | -0.002| -0.490  | -0.003| 0.010   | 0.713 |
|                      | -0.001  | -0.024| -0.680  | -0.003| 0.010   | 0.713 |
|                      | -0.003  | -0.126| 0.207   | 0.002 | -0.002  | -0.118|
|                      | -0.003  | -0.441| 0.659   | 0.008 | -0.008  | 0.246 |
|                      | -0.002  | -1.208| 0.227   | -0.002| -0.369  | 0.720 |

| Variables            | Abundance | richness | Abundance | richness | Abundance | richness |
|----------------------|-----------|----------|-----------|----------|-----------|----------|
|                      | NA        | -0.597   | NA        | -0.597   | NA        | -0.597   |
|                      | 0.556     | 0.556    | 0.507     | 0.507    | 0.507     | 0.507    |
|                      | 0.002     | 0.003    | 0.002     | 0.008    | 0.011     | 0.011    |
|                      | 0.003     | 0.003    | 0.003     | 0.003    | 0.003     | 0.003    |
|                      | 0.003     | 0.003    | 0.003     | 0.003    | 0.003     | 0.003    |
|                      | 0.003     | 0.003    | 0.003     | 0.003    | 0.003     | 0.003    |

As expected, the intensity of elephant damage varies among Acacia species with A. sieberiana as the most damaged species. This is congruent with our predictions that individuals of non-myrmecophyte Acacia species suffer higher attack from elephants. With no record of ants on trees, A. dudgeonii was the least damaged species. This species may be less palatable. Similar trends were observed in Serengeti National Park where elephant highly damaged A. senegal compare to Acacia robusta, Acacia tortilis, Acacia gerradii and A. drepanolobium (Morrison et al. 2016). Ant assemblage, abundance or richness did not limit the intensity of elephant damage on trees in the Biosphere Reserve of Pendjari. The low density of ants observed on trees in our study region may explain this pattern. Indeed, high density of ants on host plants (up to 90 000 workers on some trees) is an important component of their defensive efficacy (Goheen and Palmer 2010). The ecology and behaviour of ant species caught on trees may also explain the observed trends. For instance, C. sericeus, the most frequent species observed on Acacia trees is a ground-nesting and a non-aggressive ant species that regularly visit extra-floral nectaries of savanna trees (Mody and Linssenmair 2003). Similarly, C. maculatus (Blard et al. 2003), P. megacephala (Seguni et al. 2011; Visitacao 2011) and M. opaciventris (Kenne and Dejean 1999) are ground-nesting ant species. Moreover, P. megacephala is an invasive ant (Wetterer 2012) that increases elephant damage to Acacia trees through the disruption of protective ant–plant mutualism (Riginos et al. 2015). Ant species falling to protect Acacia trees from elephant damage on trees and increases species richness on the ground (Frizzo et al. 2012). Moreover, there were few trees with ants and for some species (A. gourmaensis and A. seyal), empty trees were significantly smaller on average than trees with ants. This is in line with the greatest fire-induced ant colony mortality observed on A. drepanolobium (Kimuyu et al. 2014). The absence of ants on individuals of A. dudgeonii and A. hockii, which are the smallest Acacia species in our study area, may be a legacy of such fire-induced tree ant mortality in this annually burnt habitat. This effect was not observed for A. sieberiana which had the taller individuals, indicating that tree height can mediate the effect of fire on ant colonies in frequently burnt habitats. Studies on plant–ant mutualism are rare in West Africa (but see Adenuga 1975; Majer 1976; Belshaw and Bolton 1994) and our understanding of the limitation of ant–Acacia association in this part of the world is limited. Perhaps, the low ant residency on Acacia species in our study system, which is frequently burned, is related to potential disruptive effect of frequent fire in the Pendjari Biosphere Reserve. Fire may kill or weaken host trees and thereby indirectly limit ant colonization (Janzen 1967). Fire may also directly limit ant occupancy (Cochard and Agosti 2008). For example, in the Kenya Long-term Exclosure Experiment, survival of arboreal ant colonies was directly affected by fire with colonies on taller trees, which are out of reach of fire, surviving better (Kimuyu et al. 2014).
damage is not typical of the Biosphere Reserve of Pendjari. Even in East Africa where obligate Acacia–ant mutualism is prevalent (Palmer and Brody 2013), many ant species (e.g. Crematogaster nigricaps and T. penzigi) provide low protection against mega-herbivores (Martins 2010; Palmer et al. 2013). Some Acacia trees are inhabited by non-defending exploiter ants (Heil 2013). Myrmecophytes may be able to persist even in the absence of their mutualistic ant in habitats with limited herbivory and competition (Janzen 1973) or potentially in rich habitats where the cost of biomass reconstruction is limited (Coley et al. 1985; Endara and Coley 2011). However, even in the absence of such direct defence role, ants may indirectly influence myrmecophytes. Several ant species tend hemipterans which exert biological control influence on plant herbivores (Martins 2013), provide additional dry season food supplement that maintains ant colonies (Prior and Palmer 2018) or by developing beneficial association with fungi and microbes (Baker et al. 2017).

All in all, annual vegetation fire hinders the establishment of ants on small Acacia species (A. gourmaensis, A. seyal, A. dudgeonii and A. hockii). The taller species (A. sieberiana) that escape such firetrap falls to attract ant colonies while experiencing high elephant damages. This species may be qualified as non-myrmecophyte. Acacia species that do not engage in ant mutualism respond to browsing by large African herbivores with physical and chemical defences. In Game Ranching Ltd (central Kenya), individual A. seyal exposed to intensive browser utilization was observed to lose shoot tips, produce long thorns and have relatively few flowers and fruits (Milewski and Madden 2006). Similarly, A. sieberiana trees with high browsing intensity had significantly longer spines, smaller leaves and higher total cyanide (prussic acid) concentrations than trees with low browsing intensity (Zinn et al. 2007). Further investigations are required to quantify such defence mechanisms and their effectiveness to protect Acacia trees against elephant damage in the Biosphere Reserve of Pendjari.

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Contributions by the Authors
O.G.G. and A.E.A. conceived and designed the study. A.D. performed the experiments and collected the data with assistance from A.F.A., A.G.D., B.K. and A.G.D. O.G.G. analysed the data. A.F.A., A.G.D., A.D. and O.G.G. wrote the manuscript with revisions from A.E.A. and B.K.

Conflict of Interest
None declared.

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Data Availability
The data and scripts used for the analyses in this paper are published online on Dryad Digital Repository at https://doi.org/10.5061/dryad.0000003t (Gaoue et al. 2021).

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