JEE
ISSN: 2288-1220
https://doi.org/10.5141/jee.25.036
Journal of Ecology and Environment (2025) 49:21

RESEARCH

Disturbances shape the tree community in Ghana's Mole National Park

Collins Ayine Nsor[1]*, Vincent Kusi-Kyei[1], Emelia Anawhyne[1], Micheal Asigbaase[2], Peggy Somuah[1], Patrick Opoku[1], Daniel Dompreh[3] and Osei Owusu Antobre[1]

[1]Department of Forest Resource Technology, Kwame Nkrumah University of Science and Technology, Kumasi 233, Ghana
[2]Department of Forest Science, University of Energy and Natural Resources (UENR), Sunyani 233, Ghana
[3]Department of Silviculture, Kwame Nkrumah University of Science and Technology, Kumasi 233, Ghana

ARTICLE INFO
Received April 29, 2025
Revised September 15, 2025
Accepted September 16, 2025
Published on October 20, 2025

***Corresponding author**
Collins Ayine Nsor
E-mail cansor.canr@knust.edu.gh

Background: The ability of protected areas worldwide to sustain biodiversity is often severely limited due to their vulnerability to persistent and intense disturbance-related drivers, such as agricultural expansion and the exploitation of ecosystem services by humans. Understanding how trees in these protected areas respond to disturbance-related drivers is crucial for determining effective conservation measures that utilize their role in ecosystem functioning. This study examined the primary disturbance-related drivers affecting the tree community assemblages and structural characteristics across five vegetation types (i.e., woodland, shrubland, savannah forest, riparian forest, and boval vegetation) in Mole National Park.

Results: A total of 125 plots measuring 10 × 10 m were established in each of the five vegetation types. In total, 1,023 individuals belonging to 44 species and 19 families were sampled. Community assemblages did not differ significantly across the five vegetation types, contradicting the hypothesis of this study. Canonical correspondence analysis results showed that fire regimes, animal trampling, tree felling, and erosion were the major drivers explaining 83.02% (axes I = 46.8% and II = 36.2%) of the variability in tree community assemblages. Four species - *Detarium microcarpum* (10.56%), *Mitragyna inermis* (8.01%), *Uapaca togoensis* (6.8%), and *Combretum adenogonium* (5.6%) - were the most important taxa contributing to the dissimilarity in the tree community profile. The lower impact of fire regimes, animal trampling, and tree felling contributed to significantly higher diversity, larger stem diameter, and basal area (e.g., *Tamirandus indica*, 180 cm, 2.54 m^2 h^{-2}; *Daniellia olivera*, 140 cm, 1.54 m^2 h^{-2}; and *Vitex doniana*, 120 cm, 1.13 m^2 h^{-2}) in the savannah forest, while severe driver effects led to low diversity and smaller tree DBH of < 10 cm in the boval vegetation.

Conclusions: The findings suggest that different vegetation types respond uniquely to various disturbance-related drivers. Therefore, the park's vegetation types should inform the design of conservation measures.

Keywords: canonical correspondence analysis, Hill numbers, Mole National Park, rarefaction, species composition, structural attributes

Introduction

The ability of protected areas worldwide to sustain biodiversity is often severely limited because of their susceptibility to constant and severe disturbance-related drivers, such as urbanization, agricultural expansion, human exploitation of ecosystem services (tourism, recreation, and the sustainable extraction of resources) (Angulu et al. 2016; Martinuzzi et al. 2015). A key component of biodiversity that is mainly impacted as a result of disturbance-related drivers includes vegetation. The Millennium Ecosystem Assessment defines a driver as any natural or human-induced factor that directly (physical and biological) or indirectly causes a change in an ecosystem (Carpenter et al. 2006; Nelson et al. 2006). A direct driver influences ecosystem processes, while an indirect driver operates in a more diffused form by altering one or more direct drivers (Nelson et al. 2006).

Studies have shown that plant communities in many National Parks in Africa, have undergone a significant transformation, largely due to anthropogenic impact, such as changes in historical fire regimes (Holdo 2007; Shackleton and Scholes 2000), high or uneven foraging pressure (Ashiagbor and Danquah 2017; Brits et al. 2002; Fullman and Bunting 2014; Rutina et al. 2005), deforestation and tree felling (Janssen et al. 2018; Keenan et al. 2015), herbivory (Bond 2008; Holdo 2007) and the occurrence of wind and water erosion associated with these disturbances (Beugler-Bell and Buch 1997).

Despite the importance of fire in maintaining savannas (Bond 2008), the increased occurrence of wildfires beyond historical fire intervals can cause damage to plant community structure or reduce their populations in parks and game reserves (Balfour and Howison 2001; Foster et al. 2017; van Wilgen et al. 2007). Fires sweep annually and uncontrollably into Mole National Park (MNP) from surrounding communities, especially during land preparation for farming, burning to attract game for hunting, and charcoal production. Therefore, fire regimes in MNP may have modified the plant community structure, which serves as forage, shelter, and breeding ground for wildlife and the overall integrity of the ecosystem. In addition to the occurrence of wildfires in the National Park, managers of MNP have also observed illegal tree felling and cutting by members of the surrounding communities (e.g., Murugu, Mognori, and Larabanga), alongside admitted settlements in the park and other distant rural communities for domestic use and export. Of particular importance is the illegal felling of African rosewood (*Pterocarpus erinaceus*) (Bosu 2013; Saibu 2016). These disturbances can have far-reaching impacts on vegetation by modifying the dominant woodland community, reducing and homogenizing species richness and abundance, and consequently affecting faunal biodiversity and abundance. As the regional population continues to increase, human pressures coupled with climate cascades are likely to impact the ecological integrity of the park, which is located in the fragile savannah landscape. Already, there is evidence of an emerging threat to similar protected areas in neighbouring Togo's savanna region, where Fousseni et al. (2012) found significant transformations of the woodland community into grassland and a reduction in the area of specific plant communities following illegal tree felling for charcoal and wood fuel production.

There is no known Scientific study that examined the response of the tree community structure to different disturbance-related drivers in MNP. MNP is the largest park in Ghana and, by far, the most visited tourism destination. It substantially contributes to income generation for the government of Ghana and the surrounding communities. Thus, to understand how the tree community structure in the park responds to effects of disturbance-related drivers like fire regimes, animal trampling, tree felling, erosion, and bare ground is critical in determining the suitable conservation measures necessary, since the survival of the wildlife is inextricably linked to the park's ecosystem well-being. This study aimed to determine the key disturbance-related drivers impacting tree community structure in MNP. To achieve this, we asked the following questions: (1) Is there any difference in tree community assemblages (i.e., abundance, richness, and diversity) among the five vegetation types, with varying levels of disturbances? (2) Will the structural attributes of the tree population be similar across the five types? We hypothesized that the impact of fire, animal trampling, tree felling, soil erosion, and bare ground on the structure of tree community assemblages and their attributes will vary among the five vegetation types, as individual species respond differently to identical drivers (Salk and McMahon 2011) and that (2) each vegetation type exhibits distinct signs of disturbance (for instance, shrubland and Boval vegetation are characterized by high levels of fire, while woodland shows significant signs of animal trampling).

Materials and Methods

Study area

MNP is the largest savanna woodland (Torello-Raventos et al. 2013) and the most developed protected area for eco-tourism in Ghana. The different vegetation types serve as a major source of forage, cover against predation, and nesting/breeding site for ungulates and birds (Ashiagbor and Danquah 2017; Nsor et al. 2018) and the protection of rivers and their tributaries from reduced erosion and the moderation of flooding. The Park is situated in an area of high conservation concern, where recent cascading climatic factors may have contributed to transforming the vegetation of the park (Armah et al. 2010; Jung and Kunstmann 2007; Laube et al. 2012).

MNP is state-owned and managed by the Wildlife Division of the Forestry Commission and was gazetted in the year 1971. It covers an area of 4,577 km^2 and lies within geographic coordinates of 9°12′-10°06′ North and 1°25′-2°17′ West with an elevation of 120 to 490 meters above sea level (Fig. 1). The mean annual temperature is 28°C, which varies from 26°C in December to 31°C in March. The average annual rainfall is about 1,100 mm, decreasing to 1,000 mm in the north of the park (Mole National Park Management Plan 2005-2010). The Park has a fairly undisturbed savannah vegetation, with dominant open savanna woodland interspersed with grasses (Schmitt and Adu-Nsiah 1993). Short grasslands are found around shallow soils and iron pans and may reach 3 m high in the wet season. Narrow bands of riverine forest also grow along most of the streams, swamps and floodplains grasslands (Schmitt and Adu-Nsiah 1993). The Park also has a narrow escarpment running north-south. Soils are mostly plinthic ferrasols in the south and rhodic nitisols in the north, with the ferra-

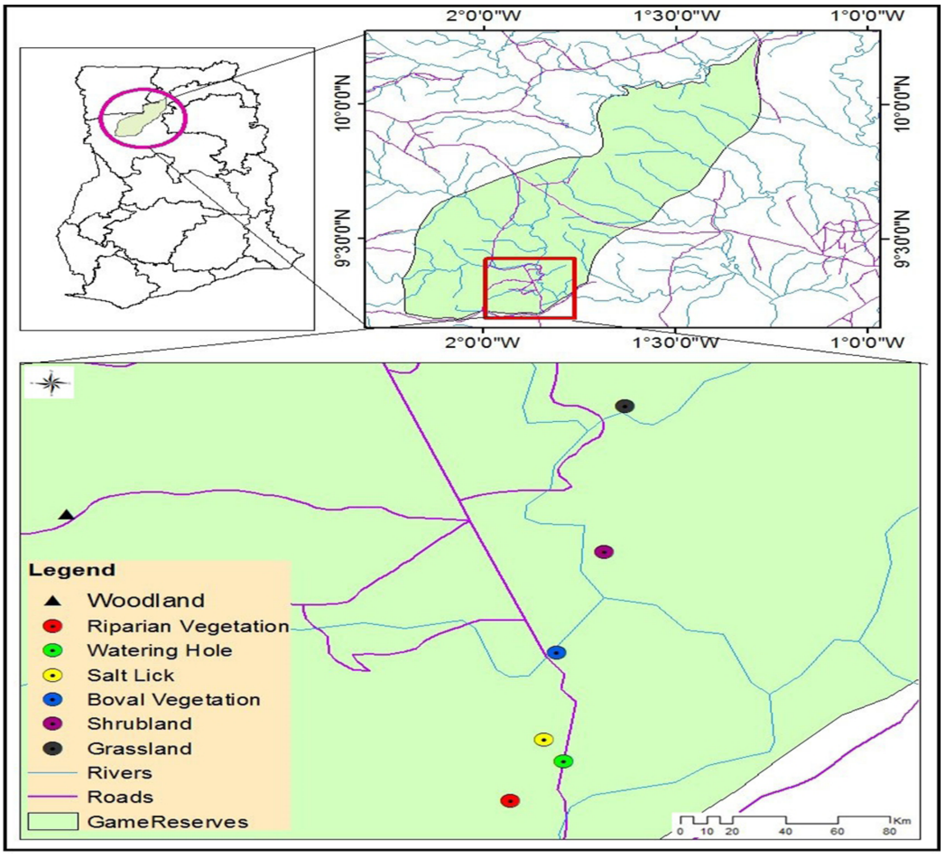

Fig. 1 Map of Ghana, showing the five vegetation types in Mole National Park. Northern Region.

sols often developing a hardened layer of iron pan (Mole National Park Management Plan 2005-2010). See Table S1 for the summary description of the five vegetation types (after Schmitt and Adu-Nsiah 1993).

Data collection

Vegetation sampling procedure

We initially conducted a ground validation survey to identify and mark out the different vegetation types identified on the topographic map of the park, using a Garmin Etrex GPS. The vegetation types included: woodland, shrubland, savanna forest, riparian forest and Boval vegetation (see Table S1). A stratified random sampling method (e.g., Hirzel and Guisan 2002) was used to assess plant species in each of the five vegetation types (referred to as dominant plant cover or plant community, in a designated geographical unit). A total of 25 plots of 10 m × 10 m (100 m^2) were randomly laid in each of the five vegetation types, bringing the total to 125 sampled plots. A random sampling technique was used to ensure that species from the sampled population were fairly represented in all five vegetation types and to maximize species heterogeneity. The sampling period spanned from January – June and November – December 2023, which is the long dry season in the Northern Region of Ghana. Sampling was done twice, covering seven months, and only new species that were detected in the repeated sampling were recorded. The vegetation parameters that we measured included species presence/absence, cover abundance, stem diameter and basal area (BA). Cover abundance was estimated and expressed in %, using the Domin-Krajina cover-abundance scale (see Mueller-Dombois and Ellenberg 1974). Next, we measured the BA and diameter at breast height (*DBH*) of the woody species that were ≥ 5 cm and height of 1.4 m above ground level, using a standard diameter tape. The *BA* expressed in m^2/ha was calculated as $0.00007854 \times D^2$ (D = diameter at breast height). For plant identification up to the species level, we referred to the Trees, shrubs and lianas of West African dry zones keys provided by Arbonier (2004). Specimens whose taxonomy was in doubt were placed in a plant press and taken to the Forest Research Institute of Ghana Herbarium for identification by a plant taxonomist.

Assessment of disturbance-related drivers of change

Drivers such as fire, animal trampling, tree felling, and responses to drivers like erosion and bare ground were measured based on their scope and severity in each of the five vegetation types, by adopting the categorical approach provided by Salafsky et al. (2008) and Battisti et al. (2009). We assessed these disturbance-related drivers to determine the extent of their influence on the woody community structure across each of the five vegetation types. A score ranging from 1 to 4 (with 1 indicating the least impact and 4 indicating the highest impact) was used to assess the scope and severity of each disturbance-related driver. For "scope", we referred to the percentage ratio of the sample plot affected by a specific disturbance-related driver in the last 5 years (Battisti et al. 2009) in each of the five vegetation types. Here, we conducted a focus group discussion with park managers to ascertain whether each of the identified disturbance-related drivers persisted in the last 5 years. Following confirmation of the occurrence of these disturbance-related drivers, sample plots were subsequently laid in all identified disturbance types between the five vegetation types. The scores for disturbance-related drivers were assigned as follows: 4 the disturbance is found throughout (50%) the plot; 3 the disturbance is spread across 15%–50% per plot; 2 the disturbance is scattered (5%–15%); and 1the disturbance is very localized (< 5%).

For "severity" we referred to the degree to which a driver has an impact on the viability and integrity of the plant community across the five vegetation types within the last 5 years. A score of 4 was assigned if the direct driver led to serious damage or loss of the plant community; 3 if it had induced serious damage; 2 if moderate damage was induced; 1 for little or no damage. Finally, for each driver per plot, we calculated their "magnitude" which is the sum of values for scope and severity. The summed values for each driver per plot per vegetation type were then averaged and ranked from highest to lowest.

Data analysis

To address the first question, we initially performed an Analysis of Similarity with 999 permutations (ANOSIM; Anderson 2003; Clarke and Warwick 2001) to evaluate species composition differences among the five vegetation types. Where significant differences were established among the five vegetation types, we proceeded to compute the similarity percentages (SIMPER) based on Bray-Curtis similarity and unrestricted permutation of the raw data ($N = 9{,}999$; Anderson et al. 2008; Somerfield and Clarke 2013), to look out for the taxon that best determined the dissimilarity among the five vegetation types.

For the second question, the mean *DBH* and *BA* of species were evaluated to determine their significant difference across the vegetation types, using a one-way ANOVA test. We further performed ordinary least squares regression with a 95% bootstrapped confidence interval, to determine the relationship between the *DBH* and *BA* of the woody species. These functional attributes were quantified because we sought to find out how they responded to the identified disturbances. Quantifying woody structural attributes is useful in the sense that it provides information on species-specific resilience to disturbances.

Species richness was quantified using the individual-based rarefaction model (Gotelli and Colwell 2001) was performed to quantify species richness. Rarefaction curves are generated by randomly resampling the pool of N samples and then plotting the mean number of species identified in each sample (1, 2... N) (Gotelli and Colwell 2001). Rarefaction curves are intended to permit quantitative analyses of species richness for comparison between methods or between sites (King and Porter 2005).

Hill numbers or the effective number of species (Chao et al. 2014; Hill 1973; Jost 2007) were applied to quantify and compare the status of plant and ungulate species diversity among the five vegetation types. Hill numbers are a mathematically unified family of diversity indices that differs from three-diversity metrics by an exponent q (where $q = 0$, represents the number of species in the sample richness index, $q = 1$, represents the exponential of the Shannon-Weiner index, and $q = 2$, is the reciprocal of the Simpson's index). This diversity measure weighs species in proportion to their frequency and can be interpreted as the number of "typical species" in the assemblage (Tóthmérész 1995).

One-way ANOVA was used for the number of individual plants and ungulates that significantly differed among the five vegetation types. Mean stem diameter and BA of plant species were also subjected to a one-way ANOVA test to evaluate their significant difference. PERMANOVA (Anderson 2001) was used to test the null hypothesis that (a) plant community assemblages' response to the disturbance-related drivers will not be similar in the five vegetation types. PERMANOVA facilitates the analysis of *beta diversity* (variation in community structure) across multiple spatial or temporal scales, which is quantified directly by such components of variation (Anderson et al. 2011).

Canonical correspondence analysis (CCA) (ter Braak 1986) was then performed to determine the relationship between plant species assemblages and disturbance-related drivers. CCA is a direct ordination method, with the resulting product being the variability of the environmental data, as well as the variability of species data (Kent and Coker 1992). The Spearman rank correlation test evaluated the significant relationship among the disturbance-related drivers. All analyses were performed using the PAST version. 3.06 software package (Hammer et al. 2001).

Results

Species composition and abundance across the five vegetation types

A total of 1,023 individuals, belonging to 44 species and 19 families, were sampled among the five vegetation types (Table 1). Despite the substantial compositional differences in the five vegetation types (ANOSIM: global R = 0.73, $p < 0.01$), individual abundances did not differ significantly ($df = 4$, *F-statistic* = 0.608, $p = 0.66$, one-way ANOVA test). Species from the family Fabaceae were the most dominant, followed by Combretaceae (See Table S2). The Boval vegetation type registered the highest number of individuals ($n =$

Table 1 Summary of the number of plant individuals sampled in 125 quadrats, across the five vegetation types in Mole National Park

Vegetation types	Number of individuals per vegetation type	Mean ± standard error of plant individuals per plot	Number of species observed per vegetation type
Woodland	227	5.16 ± 1.3	24
Shrubland	163	5.39 ± 2.1	13
Savannah forest	193	4.42 ± 1.3	14
Riparian forest	203	4.11 ± 1.4	28
Boval vegetation	237	5.39 ± 2.1	20
Total number	*1,023*		

Number of species = 44.

237 per 0.01 ha, 5.39 ± S.E. 2.1 per plot), followed by woodland (*n* = 227 per 0.01 ha, 5.16 ± 1.3 per plot). The least was shrubland (*n* = 163 per 0.01 ha, 5.39 ± 2.1 per plot) (Table 1).

Of the 44 species, two species (*Terminalia avicennoides* and *Burkea africana*) were widely distributed in all the vegetation types and constituted 40% (Table S2). SIMPER analysis revealed the overall average dissimilarity to be 70.6% among the five vegetation types. However, the contribution of individual species showed *Detarium microcarpum* (10.56%, av. dissim = 7.5), *Mitragyna inermis* (8.01%, av. dissim = 5.7), *Uapaca togoensis* (6.8%, av. dissim = 4.8) and *Combretum adenogonium* (5.6%, av. dissim = 4.0) to be the most important taxa that contributed to the dissimilarity in the woody community profile across the four vegetation types (Table 2). *Detarium microcarpum* was the single most abundant species (*n* = 126 per 0.01 ha, cumulative abundance), and dominant in the boval vegetation (*n* = 86). *Mitragyna inermis* was the second most abundant species (*n* = 63 per 0.01 ha) and was only found along the fringes of the riparian forest and Boval vegetation. Rarer species, which included *Maytenus senegalensis*, *Strychnos innocua*, *Lannea acida* and *Terminalia mollis* from the families Celastraceae, Fabaceae, Anacardiaceae and Combretaceae, respectively, were found only in the woodland and shrubland vegetation types and represented 15.9% of the total individuals sampled (Table S2).

Variations in woody structural attributes in the five vegetation types

The *DBH* (*df* = 4, *F-test* = 2.414, *p* = 0.09) and the *BA* (*df* = 4, *F-test* = 0.391, *p* = 0.76) of the tree species did not differ substantially among the five vegetation types (Fig. 2). The insignificant differences in their structural attributes contrast with one of the hypotheses in this study, which states that the structural attributes of the woody species would vary across the five vegetation types. The *DBH* classes ranged between 4–10 and 100–180 cm across the five vegetation types across the two sites (Fig. 2A). About 97% of trees with a *DBH* larger than 20 cm (e.g., *Daniella olivera, Diospyros mespiliformis,* and *Isoberlina doka*) were found in the savanna, riparian and woodland types, while most of the smaller trees (*DBH* < 10 cm) were found in the Boval vegetation (*Terminalia avicennioides* and *C. adenogonium*) (Fig. 2A, Table S2). The BA also ranged from 0.001–1.9 m^2 h^{-1}. Species with a larger *BA* of 1.0–1.9 m^2 h^{-1} (e.g., *Khaya senegalensis, Vitex doniana,* and *Afzelia africana*) were found in all but the boval vegetation type (Fig. 2B, Table S2). On the part of the relationship between the stem diameter and the BA, ordinary least squares regression showed an overall strong positive correlation coefficient in all five vegetation types ($r = 0.39$ to 0.95, $p < 0.0001$) (Fig. 3). This was evident in the general asymptotic growth attributes of the tree stands (*DBH*:*BA* relationship).

Trends in tree richness, diversity profile and functional attributes among the five vegetation types

Tree richness (individual-based rarefaction) did not vary significantly across the five vegetation types (*df* = 4, *F-statistic* = 0.287, *p* = 0.88, one-way ANOVA test) (Fig. 4A). Even though species richness did not differ significantly in all five vegetation types, there were some marginal variations in their richness indices (e.g., the woodland, *n* = 30, shrubland, *n* = 25, and the Boval, *n* = 19 vegetation types) (Fig. 4A). Similar to what was observed individual abundance and richness, tree diversity equally showed no significant difference among the five vegetation types (*df* = 4, *F-statistic* = 0.375, *p* = 0.95, one-way ANOVA test) (Fig. 4B). This contrasted with our hypothesis, that community assemblages will vary in the five vegetation types since individual species will react to identical drivers in different ways. The insignificant differences in Hill's diversity are reflected in their low evenness distribution across the five vegetation types. The annual occurrence of wildfires, animal trampling activities and tree felling, particularly in the boval vegetation type, tended to influence the dominance and even distribution of saplings, with a *DBH* range of 4 cm–10 cm (Fig. 2A).

Influence of disturbance-related drivers on tree community assemblages and structural attributes across the five vegetation types

Overall, axes I = (46.82%) and II = (36.21%) jointly accounted for 83.02% of the variability in tree community assemblages and structural attributes among the five vegetation types (Fig. 5, Table 3). The metrices generated by the

Table 2 Dominant species contribution to similarity (based on SIMPER analysis) within the five vegetation types

Taxon	Av. dissim	Contrib. %	Cum %	Mean woodland	Mean shrubland	Mean savannah forest	Mean riparian forest	Mean boval vegetation
Detarium microcarpum	7.481	10.56	10.56	8.37	8.59	4.66	0	35.4
Mitragyna inermis	5.672	8.005	18.56	0	0	0	25.6	5.49
Uapaca togoensis	4.843	6.835	25.4	0	4.91	21.8	0	0
Combretum denogoniium	3.987	5.628	31.03	7.49	17.2	0	1.97	5.49
Anogeissus leiocarpus	3.696	5.216	36.24	14.5	0	0	7.88	0
Monodora tenuifolia	3.646	5.146	41.39	0	1.23	17.6	0	0.422
Terminalia avicennioides	3.433	4.846	46.23	12.8	13.5	5.18	0.493	13.5
Combretum nigricans	3.321	4.687	50.92	6.61	0	6.22	13.3	0
Vitellaria paradoxa	3.154	4.451	55.37	14.5	0	0	2.46	0.844
Acacia sebrienna	3.114	4.394	59.76	0	5.52	0	12.8	0
Nauclea latifolia	2.782	3.926	63.69	3.08	12.3	0.518	0	3.8
Combretum moll	2.528	3.568	67.26	0.441	11.7	0	1.97	0
Annona senegalensis	1.784	2.518	69.78	0.441	0	5.18	0	6.33
Parkia africana	1.651	2.33	72.11	1.32	0	0	0.493	7.59
Kyaha senegalensis	1.418	2.001	74.11	4.85	0	0.518	4.93	3.8
Diospyros mespiliformis	1.333	1.882	75.99	0.881	0.613	3.11	5.42	0
Kigelia africana	1.288	1.817	77.81	0.441	0	6.22	0	0
Allophylus americana	1.244	1.756	79.56	0	0	2.59	4.93	0
Burkea africana	1.188	1.677	81.24	2.64	1.23	6.22	4.43	2.53
Daniellia oliveri	0.9964	1.406	82.65	0	3.07	0.518	3.45	0
Pilostigma thonningii	0.948	1.338	83.98	0.441	0.613	0	4.43	0
Strychnous innocua	0.9424	1.33	85.31	4.41	0.613	0	0	0.422
Ximenia americana	0.8981	1.268	86.58	2.2	1.84	4.15	0	2.53
Parinari curatellifolia	0.8726	1.231	87.81	0.441	3.07	2.59	0	0
Diospyros ellioti	0.8672	1.224	89.04	0	2.45	3.11	0	0
Lannea kerstingii	0.855	1.207	90.24	2.64	0	0	0.985	2.95
Pseudocedrela kotshyi	0.8008	1.13	91.37	3.08	1.84	0	0.493	0
Afzelia africa	0.7694	1.086	92.46	0.441	0	3.63	0	0
Securidica pedunculata	0.7136	1.007	93.47	0	0	2.07	0	2.53
Pericopsis laxiflora	0.623	0.8792	94.35	1.32	2.45	0	0.985	0
Acacia hockii	0.4833	0.6821	95.03	0	0.613	0	0	2.11
Erythropheleum africana	0.4405	0.6217	95.65	2.2	0	0	0	0
Vitex donina	0.4375	0.6174	96.27	0	0.613	1.55	0	1.27
Gardenia aqualla	0.4122	0.5817	96.85	0.441	1.84	0	0	0
Tamarindus indica	0.3568	0.5035	97.35	0	0	1.04	0	1.27
Crossoptereyx febrifuga	0.336	0.4742	97.83	1.32	1.23	1.55	1.48	0
Manilkara multinervium	0.3145	0.4439	98.27	0	0.613	0	0	1.27
Grewia mollis	0.2895	0.4085	98.68	0.441	1.23	0	0	0
Ziziphus mauritiana	0.197	0.2781	98.96	0	0	0	0.985	0
Isoberlinia doka	0.1762	0.2487	99.21	0.881	0	0	0	0
Lannea acida	0.1668	0.2353	99.44	0.441	0.613	0	0	0
Terminalia mollis	0.1426	0.2012	99.64	0.441	0	0	0.493	0
Pterocarpus erinaceous	0.1303	0.1839	99.83	0.441	0	0	0	0.422
Maytenus senegalensis	0.1227	0.1732	100	0	0.613	0	0	0

Overall average dissimilarity = 91.32.
Contrib. %: species contribution percentage; Cum %: cumulative percentage.

CCA ordination revealed that animal trampling ($r = 0.55$, $p < 0.05$) on axis I, soil erosion ($r = -0.68$, $p < 0.05$), bare ground ($r = -0.60$, $p < 0.05$) and tree felling ($r = 0.58$, $p < 0.05$) on axis II, explained the variance in tree community assemblages and driver relationship across the five vegetation types (Fig. 5, Tables 3, 4). The magnitude of these disturbance-related drivers (i.e., the combination of the mean scores of the scope and severity of the impact) varied substantially across the 125 plots ($df = 4$, $F\text{-}ratio = 3.765$, $p < 0.02$, PERMANOVA test) (Table 4). Variations on the tree community assemblages and structural attribute responses were observed between woodland and shrubland ($p < 0.02$), woodland and savanna forest ($p < 0.09$) and woodland and boval vegetation types ($p < 0.04$). Generally, fire regimes, soil erosion and animal trampling were moderate or milder in about 17 of the 25 plots in the savanna forest (Table 4). Species with larger *DBH* and *BA*, such as *Tamirandus indica* (180 cm, 2.54 m^2 h^{-2}), *D. olivera* (140 cm, 1.54 m^2 h^{-2}), *K.*

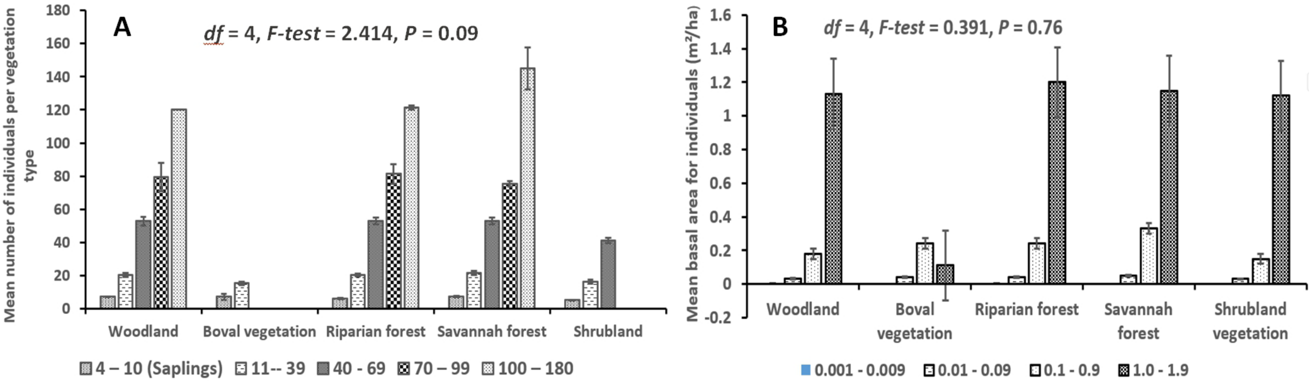

Fig. 2 Comparison of mean (± S.E.) tree diameter at breast height (*DBH* cm) and basal area (*BA* $m^2 h^{-1}$) across the five vegetation types. (A) denotes variations in the *DBH* and (B) *BA* of woody species among the five vegetation types. Notice the general steady increase in *DBH* class range in each of the five vegetation types, with the Boval vegetation registering the least *DBH* class range.

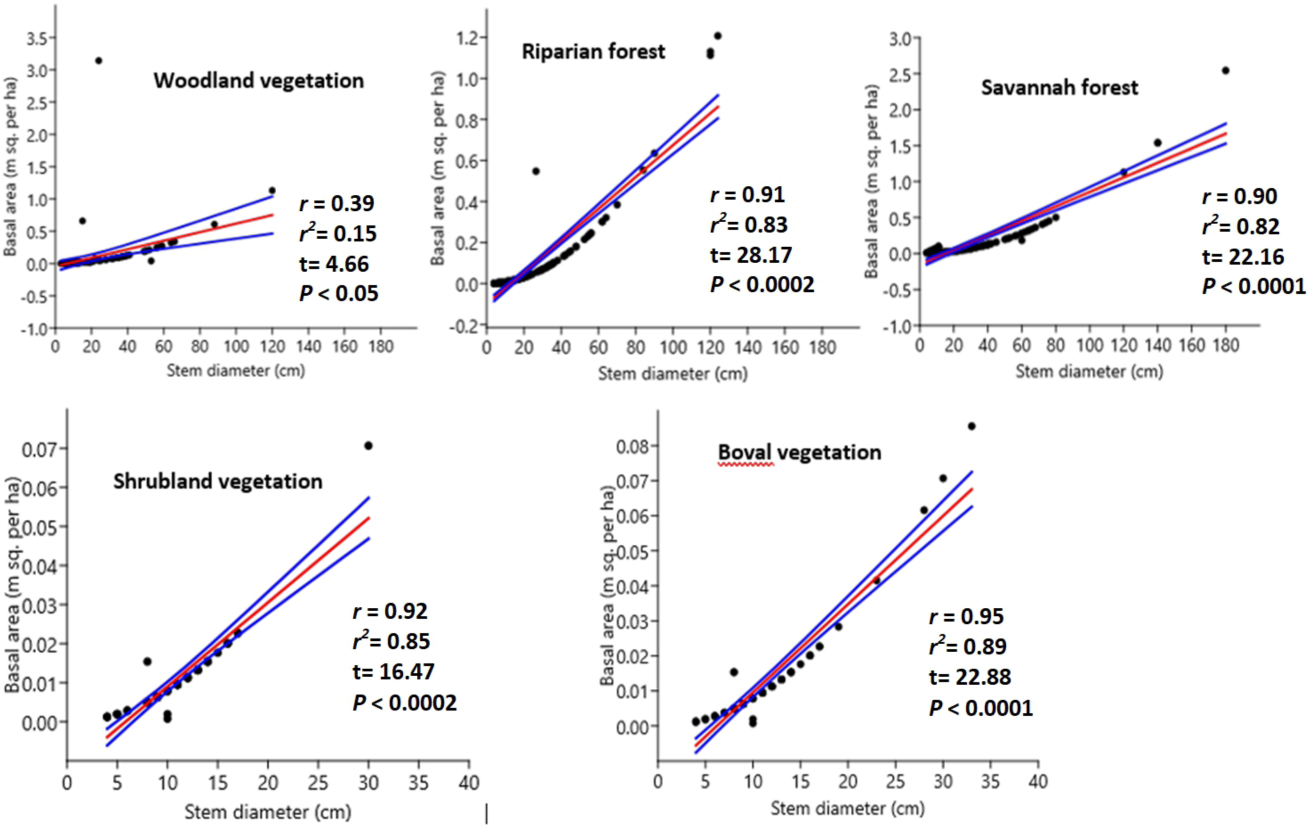

Fig. 3 Ordinary least squares regression, displaying the relationship between stem diameter (*DBH*) and the basal area (*BA*), across the five vegetation types. Every dot represents a record, with a 95% bootstrapped confidence interval (*N* = 1,999).

senegalensis (140 cm), and *V. doniana* (120 cm, 1.13 $m^2 h^{-2}$), were largely dominant in this vegetation type. We also observed that the broad dominance of the African nutmeg tree, *Monodora tenuifolia* (n = 34), occurred in plots that were characterized by tree felling ($r = 0.58$, $p = 0.05$, axis I) in the same vegetation type. About 12% of the 25 plots (located at the foothills in the savannah forest) where tree felling occurred showed a strong correlation with animal trampling activities, mostly caused by elephants ($r_s = 0.811$, $p < 0.0001$) (Fig. 5, Tables 4, 5).

The majority of plots affected by wildfires exhibit a strong negative correlation with ground ($r_s = -0.623$, $p < 0.001$) in the Boval vegetation type (Fig. 5, Table 5). Nevertheless, individuals of the Sweet Dattock tree (*D. microcarpum*) were the most dominant (n = 84) and widely distributed within this vegetation type. The Violet tree - *Securidica longpedunculate* and *Manilkara bidentata* were among the species with the lowest abundances, and constituted 2.5% and 0.001%, respectively, of the total number of individuals sampled. Species with a smaller *DBH* of < 10 cm and *BA* = 0.0013 $m^2 h^{-1}$ (e.g., *T. avicennioides and C. adenogonium*) were also found in the Boval vegetation. In the woodland

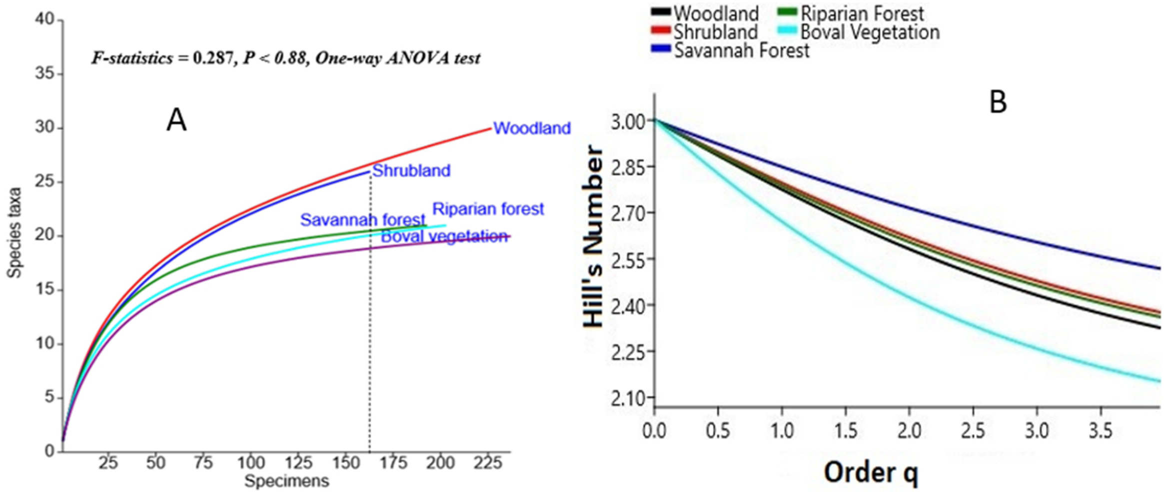

Fig. 4 Comparison of species richness (individual-based rarefaction) and Hill's diversity numbers among the five vegetation types. The data represent summary counts of trees that were recorded from the five vegetation types in Mole National Park. (A) The dotted vertical line illustrates a species richness comparison standardised to 163 individuals, representing the least abundant species in the shrubland. Notice that the woodland (the upper curve in red colour) was the most species-rich, while the boval vegetation type (the bottom curve in turquoise colour) was the most species-poor. (B) A shallower shape in the diversity profiles indicates a high diversity of a vegetation type, while a steeper shape indicates less diversity. Notice that the Savannah forest (the upper shallowest curve in purple colour) was the most diverse, while the boval vegetation type (the steepest bottom curve in light blue colour) was the least diverse.

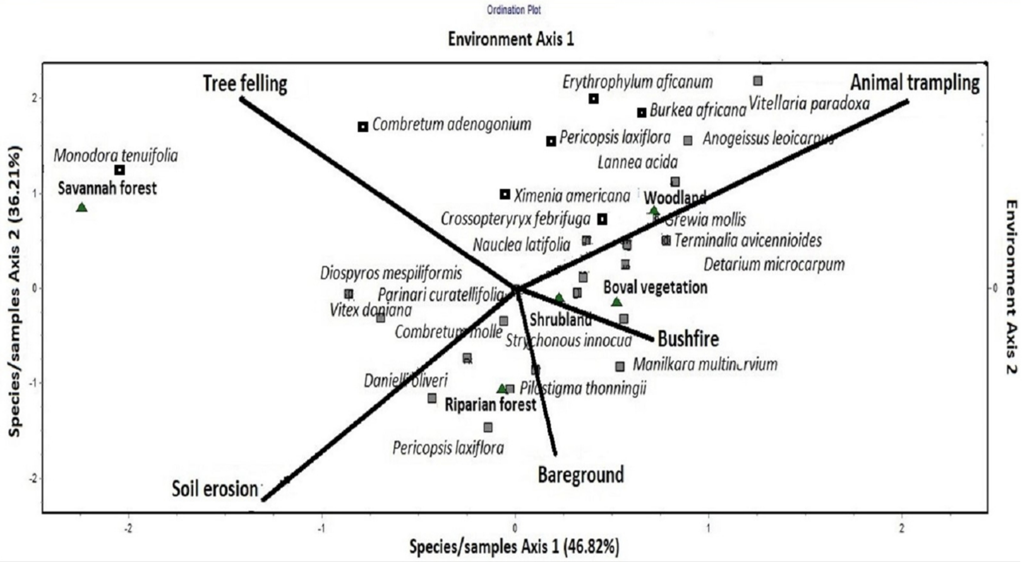

Fig. 5 Canonical correspondence analysis ordination diagram, showing the relationship between anthropogenic drivers of change and plant species across five vegetation types (woodland, shrubland, savannah forest, riparian forest and boval vegetation). The triangles represent vegetation communities, the squares represent plant species, and the arrows represent each of the drivers of change pointed in the direction of maximum change of explanatory variables across the five vegetation types. Disturbance-related drivers accounted for 83.02% (Axes I = 46.82% and II = 36.21%) variability in tree community assemblages.

vegetation type, we found that the lower abundance of individuals from species such as the African Walnut (*L. acida*, n = 1), African teak (*Pericopsis laxiflora*, $n = 3$), and Common crown-berry (*Crossoptereyx febrifuga*, $n = 3$) occurred in < 50% of the 25 plots, where animal trampling and tree felling on axis I ($r_s = 0.81$, $p < 0.0001$) were evident (Fig. 5, Tables 3, 5). Patches of erosion and background ($r_s = 0.56$, $p = 0.01$, Table 5) occurred in the same plots where animal trampling and tree felling were observed. Similar observations were made in the riparian forest, where fewer species, such as *P. laxiflora, Daniellia oliveri,* and *Combretum molle*, persisted in the severely eroded riverbank fringes.

Discussion

Influence of disturbance-related drivers on the tree species composition and abundance of individuals across the five vegetation types

The findings in this study revealed that variations in tree species diversity were attributed to differences in the severity of disturbance-related drivers such as fire, animal trampling, soil erosion, bare ground and tree felling, in the five vegetation types. Studies in several National Parks in Africa have found that anthropogenic drivers like fire (Holdo 2007; Shackleton and Scholes 2000), foraging pressure (Ashiagbor and Danquah 2017; Brits et al. 2002; Fullman and Bunting 2014; Rutina et al. 2005) and natural drivers (climate change) (Rutherford et al. 1999) as some of the factors contributing to vegetation transformation. Although fire and herbivory are part of the natural processes that shape the savannah vegetation, the current situation, where severe burns on the woody species occur in the park, due to uncontrolled fires from the park-adjacent communities, tends to impact the tree community assemblages negatively. For instance, the low abundance of tree species in the boval vegetation was partly attributed to severe fire regimes and animal trampling activities, caused by elephants and buffalos. The presence of salt licks in the boval vegetation contributed to the presence of large ungulates during the sampling period, which appears to explain why widespread animal trampling activity occurred. These disturbances led to the creation of large contiguous patches of bare ground in several plots that we sampled. The effect of these disturbances, did not only affected the abundance of the individuals like the Violet tree - *S. longpedunculate* and *M. bidentata* in the boval vegetation type, but also contributed to its lowest species richness and diversity compared to the remaining four vegetation types. Similar disturbances like tree felling and widespread animal trampling contributed to the low abundance of *L. acida* ($n = 1$), *P. laxiflora* ($n = 3$) and *C. febrifuga* in the woodland vegetation type. These disturbances not only affect the individual abundance of some species, but also lead to the occurrence of severe erosion and background. As ground cover of a habitat is reduced or decreased, as a result of tree felling and animal trampling, the bare ground is exposed to the direct impact of rainstorms or flash floods, leading to the development of erosion via sediment transport and deposition. This process tends to damage plant species and consequently stalls their growth and survival. We observed that the low abundance of individual species, such as *P. laxiflora*, *D. oliveri*, and *C. molle*, is attributed to the similar impact of severely eroded banks along the riparian forest.

Table 3 Summary of CCA axis length for plant species, showing the levels of correlation between the five vegetation types and the disturbance-related drivers and percentage variance in species assemblages, in 125 plots

	Axis I	*Axis II*
Eigenvalues	1.13	0.87
% Variance explained (83.03)	46.82	36.21
Cumulative variance	46.82	83.02
Pearson correlation for sp./ env'tal scores	0.96	0.66
Correlation		
Bushfire	0.17	–0.16
Animal trampling	0.55^{*}	-0.69^{**}
Soil erosion	–0.31	-0.67^{**}
Bare ground	0.06	-0.60^{**}
Tree felling	0.32	0.58^{*}

CCA: canonical correspondence analysis.
Asterisk (*) = disturbance-related drivers that were significant. The significance of the correlation coefficients is denoted as: $^{*}p < 0.05$, $^{**}p < 0.01$.

Table 4 Summary of the average scores for five drivers (bushfire, animal trampling and tree felling) and responses (erosion and bare ground) assessed in each of the 125 plots among the five vegetation types

Disturbance-related drivers	Woodland scores	Shrubland scores	Savannah scores	Riparian scores	Boval scores
Bushfire	4.2 ± 1.2 (4 plots)	5.3 ± 2.4 (7 plots)	2.5 ± 1.0 (3 plots)	2.0 ± 1.0 (3 plots)	6.2 ± 0.1 (8 plots)
Erosion	1.4 ± 0.3 (3 plots)	4.0 ± 1.5 (4 plots)	2.2 ± 0.6 (4 plots)	5.2 ± 1.7 (12 plots)	5.1 ± 0.02 (2 plots)
Animal trampling	2.1 ± 1.1 (8 plots)	3.3 ± 0.6 (3 plots)	3.7 ± 1.4 (10 plots)	6.3 ± 1.5 (5 plots)	6.5 ± 1.3 (5 plots)
Bare ground	1.3 ± 0.4 (3 plots)	3.2 ± 1.8 (7 plots)	2 ± 0.8 (4 plots)	4.0 ± 1.1 (3 plots)	5.5 ± 1.9 (4 plots)
Tree felling	3.3 ± 1.02 (7 plots)	2.3 ± 1.2 (4 plots)	1.1 ± 0.05 (4 plots)	3.1 ± 0.3 (2 plots)	4.4 ± 0.5 (6 plots)

The mean scores (± S.E.) (i.e., magnitude) are a combination of the scope and severity scores of each disturbance-related driver.

Table 5 Summary of Spearman's rank (r_s) correlation matrix between the anthropogenic drivers in the Mole National Park

	Bushfire	Animal trampling	Soil erosion	Bare ground	Tree felling
Bushfire		0	0.15	0.76^{***}	0.15
Animal trampling			0.25	-0.83^{***}	0.81^{***}
Soil erosion				0.56^{*}	0.65^{**}
Bare ground					0.11
Tree felling					

The significance of the correlation coefficients is denoted as: $^{*}p < 0.05$, $^{**}p < 0.01$, and $^{***}p < 0.001$.

The persistence or broad-based distribution of *D. microcarpum*, *T. avicennioides, B. africana,* and *K. senegalensis* in the woodland and the boval vegetation types, where fire regimes and animal trampling were widespread, was probably because their thick bark and glabrous (e.g., de Jonge et al. 2024) leaves buffered against the impact of the fire regimes by resprouting. The persistence of these species in such fire-prone and climate cascade environments may have, over time, developed these resistant and resilient morphological traits as a survival strategy. According to Chase and Myers (2011) and Maire et al. (2012), at a given point in space and time, the composition of species assemblage is the result of at least two concurrent processes: dispersion and habitat filtering. While dispersion enables individuals to spread through different habitats, habitat filtering (both abiotic and biotic) permits populations to persist. Keeley et al. (2011) stated that plant traits, namely, resprouting, serotiny and germination by heat and smoke, are some of the adaptive strategies that plants use to survive in fire-prone environments. Cunningham (2001), Wilson and Witkowski (2003), and de Jonge et al. (2024) reported that many species of savannah origin are characterized by hooks/larger spines, coarse, thick bark and asperous leaves, which make them withstand fire regimes mostly in the dry season. Measurement of fire severity and plant responses through resistance traits (i.e., thick bark) and resilience traits (i.e., regenerative organs and fire-cued recruitment) across fire-prone landscapes has been extensively conducted by several researchers (e.g., Lawes et al. 2016). It can therefore be stated that the ability for *B. africana*, *D. microcarpum*, *K. senegalensis* and *T. avicennioides* to thrive in the face of fire regimes, animal trampling, and erosion may be attributed to their resistant and resilient traits.

As the savannah ecosystem continues to expand towards the transition through to the forest zones of Ghana (due to the occurrence of similar disturbance-related drivers as observed in the current study area), there is the likelihood that species of the savannah-origin species will begin to take a foothold in this new environment. This is so because if the impact of bushfires, for example, becomes so severe and well beyond the threshold tolerance of the species from the forest or transition zone, it may drive them to extinction, thus paving the way for the savannah species to establish. Studies in Ghana's Kogyae Strict Nature Reserve (KSNR - located in the transitional vegetation zone between the Guinea savanna and Forest regions) found the presence of savanna species (e.g., *Terminalia glaucescens*, *K. senegalensis* and *Hymenocardia acida*, Armani et al. 2018) that are similar to what we found in our study at MNP. Thus, the similarity of the woody species in our findings and that of KSNR suggests the contribution of similar disturbances, leading to the expansion of the savanna vegetation in KSNR. Past studies have already shown much concern over the 'savannization' of tropical forests, primarily due to the loss of trees to clear felling or logging, often followed by fires, across the globe (Barlow and Peres 2008).

Influence of disturbance-related drivers on the woody species richness and diversity

The influence of animal trampling and fires on the structuring of vegetation composition, biomass, and richness across African savannah landscapes has been widely reported by several researchers (e.g., Bond 2008; Bond and Keeley 2005). Our findings also show that fire regimes, animal trampling, erosion, and tree felling not only shape woody composition, abundance, and structural attributes but also influence richness and diversity. The high diversity in the savannah forest (resulting from the high evenness index, see Table 5) is likely due to the relatively mild impact of fire regimes, animal trampling, tree felling, and erosion. The species evenness index (one of the metrics for measuring biodiversity, mostly used in ecosystems - Chao and Ricotta 2019; Ricotta and Avena 2002) is important because species distributed at even spatial scales tend to facilitate equitable resource utilization (e.g., soil nutrients, light, water, and space). When species are evenly distributed in a habitat with relatively mild disturbances, competition for space and resource utilisation may be eliminated, leading to stress reduction and promoting growth for both mature and young recruits or saplings. Similar to our findings, a study by Mishra et al. (2004) on the effect of anthropogenic disturbance on plant diversity and community structure of a sacred grove in northeast India revealed that a mild disturbance regime provides greater opportunities for species turnover, colonization, and persistence of high species richness (Mishra et al. 2004). Besides the relatively high diversity in the savannah forest, we also observed that species with larger *DBH* and *BA*, such as *T. indica* (180 cm, 2.54 m^2 h^{-2}), *D. olivera* (140 cm, 1.54 m^2 h^{-2}), *K. senegalensis* (140 cm), and *V. doniana* (120 cm, 1.13 m^2 h^{-2}), were all found in the same habitat type. This suggests that the mild disturbances barely impacted their growth. The savannah forest vegetation type is located in the hilly areas of the park. This physical feature naturally serves as a "checkerboard" against intense herbivory activities, especially by large-sized ungulates like elephants. The widespread distribution of the African nutmeg tree - *M. tenuifolia,* in fewer plots where tree felling occurred in the savannah forest, may be due to their resilience and resistance to moderate or mild disturbance, through their ability to quickly recover and establish from these persistent disturbances.

The relatively lower tree diversity in the woodland and the boval vegetation could be due to frequent wildfires, animal trampling and tree felling, leading to the uneven distribution of species. The woodland and the boval vegetation types are where herbivory activities were concentrated, as a result of the high ungulate population. Thus, animal trampling activities, particularly elephants, buffalos, bushbucks and kobs, were visibly common. The presence of saplings with an average *DBH* of 5.2–7.4 cm in nearly all plots in the woodland vegetation type was probably due to limited space for recovery following repeated trampling and frequent fires (Sackey and Hale 2008). As the scale of disturbances continues to increase, especially the uncontrolled fire regimes sweeping into the park (from park-adjacent communities), there is a likelihood that the woodland vegetation will transform to a grassland/forb community sooner than anticipated. Evidence of a gradual grassland encroachment was observed in some areas of the woodland and boval vegetation types, where the elephant population was high surrounding waterholes. Studies in the northern savanna region of Botswana have shown that the African elephant (*Loxodonta africana*) is one of the leading sources of landscape shifts (Fullman and Bunting 2014). The near absence of rarer species may also have contributed to the low diversity in the two vegetation types. Nearly 90% of the plots where fire, trampling and tree felling occurred were characterized by patches of bare ground and erosion, at irregular intermediate levels. Such environmental conditions not only lead to uneven distribution of species but also affect the recruitment of pioneer species and the survival of rarer or infrequent species. Hobbs and Yates (2003) argued that an increase in disturbance regimes (e.g., fire, herbivory), especially in fragmented habitats, not only impacts rare and uncommon species but also increases the prevalence of exotic species and increases the risk of local extinction of indigenous species.

Given the ecosystem services role of MNP (i.e., provisioning, regulating and cultural) to the wildlife, and park-adjacent community livelihood, there is the likelihood that the annual wildfire occurrence, particularly from park-adjacent communities, may lead to a decrease in forage availability, destroy nesting/breeding sites and shelter for the wildlife therein. Thus, the location of the park in such a high conservation concern environment requires instituting the following management measures, including (a) intensifying awareness creation among the park-adjacent communities on the dangers of indiscriminate fire hazards in the park; (b) construction of functioning fire belts; (c) checking of illegal tree felling for either domestic fuelwood or commercial purposes; (d) restoration of eroded areas using stone or crop residue bunding techniques; (e) construction of more water holes in each of the five vegetation types, to spatially distribute the ungulates around the park and reduce the impact on the vegetation and soil structure, through animal trampling activities surrounding the few existing waterholes. Our fifth conservation consideration is supported by several studies among national parks in the African landscape. For instance, Tefempa et al. (2008) and Hagwet et al. (2014) suggested increasing the number of artificial water sources for animals in the Serengeti and Waza National Parks, to lessen the impact on the vegetation and soil surrounding the natural sources of water. Owen-Smith (1996) and Smit et al. (2007a, 2007b) also stated that the provision of water is a particularly important wildlife management tool in water-limited savannah ecosystems. Throughout Africa, particularly in water-stressed ecosystems like the savannas, a large number of protected areas have constructed water sources, where water is supplied in pans or filled in ponds via the use of water pumping engines, such as in Hwange National Park (Kamanda et al. 2008). This conservation approach could help offset anthropogenic exploitation of natural water sources (Marshal et al. 2006).

Conclusions

Overall, the plant community in MNP is a complex, heterogeneous community that serves numerous functional roles, including forage, shelter, nesting and breeding sites for mammals, as well as enhancement of the ecological integrity of the park. Fire, animal trampling, tree felling and erosion were the major disturbance-related drivers that contributed to the low diversity in the boval and woodland vegetation types, while the mild or moderately disturbed savannah vegetation type was the most diverse. Also, species with larger *DBH* and *BA* were found in the savannah forest, where disturbances were relatively moderate. Finally, the dominance and broad-based distribution of *D. microcarpum*, *T. avicennioides, B. africana,* and *K. senegalensis* in the woodland and the boval vegetation types, where fire regimes and animal trampling were widespread, was attributed to the development of morphological traits like thick bark and glabrous leaves, which enable them to withstand the cyclical impact of wildfires and other related disturbances.

Supplementary Information

Supplementary information accompanies this paper at https://doi.org/10.5141/jee.25.036.

Table S1. Summary description of the five vegetation types in the Mole National Park. **Table S2.** List of plant species sampled among the five vegetation types in Mole National Park.

Abbreviations

MNP: Mole National Park
BA: Basal area
DBH: Diameter at breast height
CCA: Canonical correspondence analysis
KSNR: Kogyae Strict Nature Reserve

Acknowledgements

The authors are grateful to the staff and management of Mole National Park for their assistance during the field study.

Authors' contributions

All authors conceived the research idea and formulation of the research goals. CAN, VKK, DD, EA, MA, PS and PO developed the study design and field methods. CAN, VKK, DD, EA, MA, PS, OOA and PO conducted the field data collection. CAN, EA, MA, PS and PO undertook data analysis. CAN, EA, MA and PO interpreted the output of the statistical analysis. CAN, MA wrote the manuscript. VKK, EA, MA, PS, OOA and PO edited the original draft. All authors read and approved the final manuscript.

Funding

None.

Availability of data and materials

The code and data used in the analysis of this study will be publicly accessible at Dryad Digital Repository: DOI: 10.5061/dryad.3r2280gtn.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

References

Anderson MJ. Analysis of ecological communities: Bruce McCune and James B. Grace, MjM Software Design, Gleneden Beach, USA, 2002, ISBN 0 9721290 0 6, US$ 35 (Pbk). J Exp Mar Biol Ecol. 2003;289(2):303-5. https://doi.org/10.1016/S0022-0981(03)00091-1.

Anderson MJ. Permutation tests for univariate or multivariate analysis of variance and regression. Can J Fish Aqua Sci. 2001;58:626-39. https://doi.org/10.1139/f01-004.

Anderson MJ, Crist TO, Chase JM, Vellend M, Inouye BD, Freestone AL, et al. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. Ecol Lett. 2011;14(1):19-28. https://doi.org/10.1111/j.1461-0248.2010.01552.x.

Anderson MJ, Gorley RN, Clarke KR. PERMANOVA+for PRIMER: guide to software and statistical methods. Plymouth: PRIMER-E; 2008.

Angulo E, Boulay R, Ruano F, Tinaut A, Cerdá X. Anthropogenic impacts in protected areas: assessing the efficiency of conservation efforts using Mediterranean ant communities. PeerJ. 2016;4:e2773. https://doi.org/10.7717/peerj.2773.

Arbonier M. Trees, shrubs and lianas of West African dry zones. The Netherlands: CIRAD, Margraf Publishers, MNHN; 2004.

Armah FA, Yawson DO, Yengoh GT, Odoi JO, Afrifa EKA. Impact of floods on livelihoods and vulnerability of natural resource dependent communities in Northern Ghana. Water. 2010;2(2):120-39. https://doi.org/10.3390/w2020120.

Armani M, Van Langevelde FV, Tomlinson KW, Adu-Bredu S, Djagbletey GD, Veenendaal EM. Compositional patterns of overstorey and understorey woody communities in a forest-savanna boundary in Ghana. Plant Ecol Divers. 2018;11(4):451-63. https://doi.org/10.1080/17550874.2018.1539133.

Ashiagbor G, Danquah E. Seasonal habitat use by Elephants (*Loxodonta africana*) in the Mole National Park of Ghana. Ecol Evol. 2017;7(11):3784-95. https://doi.org/10.1002/ece3.2962.

Balfour DA, Howison OE. Spatial and temporal variation in a mesic savanna fire regime: responses to variation in annual rainfall. Afr J Range Forage Sci. 2001;19(1):43-53. https://doi.org/10.2989/10220110209485773.

Barlow J, Peres CA. Fire-mediated dieback and compositional cascade in an Amazonian forest. Philos Trans R Soc Lond B Biol Sci. 2008;363(1498):1787-94. https://doi.org/10.1098/rstb.2007.0013.

Battisti C, Luiselli L, Teofili C. Quantifying threats in a Mediterranean wetland: are there any changes in their evaluation during a training course? Biodivers Conserv 2009;18(11):3053-60. https://doi.org/10.1007/s10531-009-9598-2.

Beugler-Bell H, Buch MW. Soils and soil erosion in the Etosha National Park, northern Namibia. Madoqua. 1997;20(1):91-104.

Bond WJ. What limits trees in C_4 grasslands and Savannas? Annu Rev Ecol Evol Syst. 2008;39(1):641-59. https://doi.org/10.1146/annurev.ecolsys.39.110707.173411.

Bond WJ, Keeley JE. Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. Trends Ecol Evol. 2005;20(7):387-94. https://doi.org/10.1016/j.tree.2005.04.025.

Bosu D. 'Operation Halt' chainsaw in Northern Ghana: alarming trends and reactive responses. 2013. https://www.modernghana.com/news/468012/operation-halt-chainsaw-in-northern-ghana.html. Accessed 12 Jan 2025.

Brits J, Van Rooyen MW, Van Rooyen N. Ecological impact of large herbivores on the woody vegetation at selected watering points on the eastern basaltic soils in the Kruger National Park. Afr J Ecol. 2002;40(1):53-60. https://doi.org/10.1046/j.0141-6707.2001.00344.x.

Carpenter SR, Bennett EM, Peterson GD. Editorial: special feature on scenarios for ecosystem services. Ecol Soc 2006;11(2):32. https://doi.org/10.5751/ES-01609-110232.

Chao A, Gotelli NJ, Hsieh TC, Sander EL, Ma KH, Colwell RK, et al. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecol Monograph. 2014;84(1):45-76. https://doi.org/10.1890/13-0133.1.

Chao A, Ricotta C. Quantifying evenness and linking it to diversity, beta diversity, and similarity. Ecology. 2019;100(12):e02852. https://doi.org/10.1002/ecy.2852.

Chase JM, Myers JA. Disentangling the importance of ecological niches from stochastic processes across scales. Philos Trans R Soc Lond B Biol Sci. 2011;366(1576):2351-63. https://doi.org/10.1098/rstb.2011.0063.

Clarke KR, Warwick RM. Change in marine communities: an approach to statistical analysis and interpretation. 2nd ed. Plymouth: PRIMER-E; 2001.

Cunningham AB. Applied ethnobotany: people, wild plant use and conservation. London: Routledge; 2001.

de Jonge IK, Olff H, Mayemba EP, Berger SJ, Veldhuis MP. Understanding woody plant encroachment: a plant functional trait approach. Ecol Monogr. 2024;94(3):e1618. https://doi.org/10.1002/ecm.1618.

Foster CN, Barton PS, Robinson NM, MacGregor CI, Lindenmayer DB. Effects of a large wildfire on vegetation structure in a variable fire mosaic. Ecol Appl. 2017;27(8):2369-81. https://doi.org/10.1002/eap.1614.

Fousseni F, Marra D, Wala K, Batawila K, Zhang CY, Zhao XH, et al. Assessment and impact of anthropogenic disturbances in protected areas of northern Togo. For Stud China. 2012;14(3):216-23. https://doi.org/10.1007/s11632-012-0308-x.

Fullman TJ, Bunting EL. Analyzing vegetation change in an elephant-impacted landscape using the moving standard deviation index. Land. 2014;3(1):74-104. https://doi.org/10.3390/land3010074.

Gotelli NJ, Colwell RK. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol Lett. 2001;4(4):379-91. https://doi.org/10.1046/j.1461-0248.2001.00230.x.

Hagwet MB, Senzota RB, Balakrishnan M, Bekele A. Impacts of grazing ungulates on vegetation and soils in areas closer to water holes in Serengeti plains, Tanzania. J Biodiv Environ Sci. 2014;4(5):296-302.

Hammer Ø, Harper DAT, Ryan PD. PAST: paleontological statistics software package for education and data analysis. Palaeontol Electron. 2001;4(1):9.

Hill MO. Diversity and evenness: a unifying notation and its consequences. Ecology. 1973;54(2):427-32. https://doi.org/10.2307/1934352.

Hirzel A, Guisan A. Which is the optimal sampling strategy for habitat suitability modelling. Ecol Model. 2002;157(2-3):331-41. https://doi.org/10.1016/S0304-3800(02)00203-X.

Hobbs RJ, Yates CJ. Impacts of ecosystem fragmentation on plant populations: generalizing the idiosyncratic. Aust J Bot. 2003;51(5):471-88. https://doi.org/10.1071/BT03037.

Holdo RM. Elephants, fire, and frost can determine community structure and composition in Kalahari Woodlands. Ecol Appl. 2007;17(2):558-68. https://doi.org/10.1890/05-1990.

Janssen TAJ, Ametsitsi GKD, Collins M, Adu-Bredu S, Oliveras I, Mitchard ETA, et al. Extending the baseline of tropical dry forest loss in Ghana (1984–2015) reveals drivers of major deforestation inside a protected area. Biol Conserv. 2018;218:163-72. https://doi.org/10.1016/j.biocon.2017.12.004.

Jost L. Partitioning diversity into independent alpha and beta components. Ecology. 2007;88(10):2427-39. https://doi.org/10.1890/06-1736.1.

Jung G, Kunstmann H. High-resolution regional climate modelling for the Volta Basin of West Africa. J Geophys Res Atmos. 2007;112(D23):17. https://doi.org/10.1029/2006JD007951.

Kamanda M, Ndiweni V, Imbayarwo-Chikosi VE, Muvengwi J, Musakwa A. The impact of tourism on sable antelope (Hippotragus niger) vigilance behaviour at artificial waterholes during the dry season in Hwange National Park. J Sustain Dev Afr. 2008;10(3):299-314.

Keeley JE, Pausas JG, Rundel PW, Bond WJ, Bradstock RA. Fire as an evolutionary pressure shaping plant traits. Trends Plant Sci. 2011;16(8):406-11. https://doi.org/10.1016/j.tplants.2011.04.002.

Keenan RJ, Reams GA, Achard F, de Freitas JV, Grainger A, Lindquist E. Dynamics of global forest area: results from the FAO Global Forest Resources Assessment. Forest Ecol Manage. 2015;352:9-20. https://doi.org/10.1016/j.foreco.2015.06.014.

Kent M, Coker P. Vegetation description and analysis: a practical approach. Boca Raton: CRC-Press; 1992.

King JR, Porter SD. Evaluation of sampling methods and species richness estimators for ants in upland ecosystems in Florida. Environ Entomol. 2005;34(6):1566-78. https://doi.org/10.1603/0046-225X-34.6.1566.

Laube W, Schraven B, Awo M. Smallholder adaptation to climate change: dynamics and limits in Northern Ghana. Climatic Change. 2012;111(3):753-74. https://doi.org/10.1007/s10584-011-0199-1.

Lawes MJ, Keith DA, Bradstock RA. Advances in understanding the influence of fire on the ecology and evolution of plants: a tribute to Peter J. Clarke. Plant Ecol. 2016;217:597-605. https://doi.org/10.1007/s11258-016-0625-6.

Maire V, Gross N, Börger L, Proulx R, Wirth C, Pontes LDS, et al. Habitat filtering and niche differentiation jointly explain species relative abundance within grassland communities along fertility and disturbance gradients. New Phytol. 2012;196(2):497-509. https://doi.org/10.1111/j.1469-8137.2012.04287.x.

Marshal JP, Krausman PR, Bleich VC, Rosenstock SS, Ballard WB. Gradients of forage biomass and ungulate use near wildlife water developments. Wildl Soc Bull. 2006;34(3):620-6. https://doi.org/10.2193/0091-7648(2006)34[620:GOFBAU]2.0.CO;2.

Martinuzzi S, Radeloff VC, Joppa LN, Hamilton CM, Helmers DP, Plantinga AJ, et al. Scenarios of future land use change around the United States' protected areas. Biol Conserv. 2015;184:446-55. https://doi.org/10.1016/j.biocon.2015.02.015.

Mishra BP, Tripathi OP, Tripathi RS, Pandey HN. Effects of anthropogenic disturbance on plant diversity and community structure of a sacred grove in Meghalaya, northeast India. Biodivers Conserv. 2004;13(2):421-36. https://doi.org/10.1023/B:BIOC.0000006509.31571.a0.

Mole National Park Management Plan. 2005-2010. https://papaco.org. Accessed 12 Jul 2023.

Mueller-Dombois D, Ellenberg H. Aims and methods of vegetation ecology. New York: John Wiley and Sons; 1974.

Nelson GC, Bennett E, Berhe AA, Cassman K. DeFries R, Dietz T, et al. Anthropogenic drivers of ecosystem change: an overview. Ecol Soc. 2006;11(2):29. https://doi.org/10.5751/ES-01826-110229.

Nsor CA, Acquah E, Mensah G, Kusi-Kyei V, Boadi S. Avian community structure as a function of season, habitat type, and disturbance, in Mole National Park, Northern Region (Ghana). Int J Ecol. 2018;(1):2045629. https://doi.org/10.1155/2018/2045629.

Ricotta C, Avena GC. On the information-theoretical meaning of Hill's parametric evenness. Acta Biotheor. 2002;50(1):63-71. https://doi.org/10.1023/a:1014717428386.

Rutherford MC, Powrie LW, Schulze RE. Climate change in conservation areas of South Africa and its potential impact on floristic composition: a first assessment. Divers Distrib. 1999;5(6):253-62.

Rutina LP, Moe SR, Swenson JE. Elephant *Loxodonta africana* driven woodland conversion to shrubland improves dry-season browse availability for impalas *Aepyceros melampus*. Wildl Biol. 2005; 11(3):207-13. https://doi.org/10.2981/0909-6396(2005)11[207:E-LADWC]2.0.CO;2.

Sackey I, Hale WHG. Effects of perennial fires on the woody vegetation of Mole National Park, Ghana. J Sci Technol (Ghana). 2008;28(2): 36-47. https://doi.org/10.4314/just.v28i2.33092.

Saibu BN. Illegal rosewood loggers ruin Mole Park; threaten farmers. 2016. Retrieved from https://www.ghanaweb.com/GhanaHomePage/business/Illegal-rosewood-loggers-ruin-Mole-Park-threaten-farmers-430738. Accessed 12 Jul 2023.

Salafsky N, Salzer D, Stattersfield AJ, Hilton-Taylor C, Neugarten R, Butchart SH, et al. A standard lexicon for biodiversity conservation: unified classifications of threats and actions. Conserv Biol. 2008;22(4): 897-911. https://doi.org/10.1111/j.1523-1739.2008.00937.x.

Salk CF, McMahon SM. Ecological and environmental factors constrain sprouting ability in tropical trees. Oecologia. 2011;166(2):485-92. https://doi.org/10.1007/s00442-010-1850-7.

Schmitt K, Adu-Nsiah M. The vegetation of Mole National Park. 1993. https://portals.iucn.org/library/node/11490. Accessed 20 Jul 2023.

Shackleton CM, Scholes RJ. Impact of fire frequency on woody community structure and soil nutrients in the Kruger National Park. Koedoe. 2000;43(1):a210. https://doi.org/10.4102/koedoe.v43i1.210.

Smit IPJ, Grant CC, Devereux BJ. Do artificial waterholes influence the way herbivores use the landscape? Herbivore distribution patterns around rivers and artificial surface water sources in a large African savanna park. Biol Conserv. 2007a;136(1):85-99. https://doi.org/10.1016/j.biocon.2006.11.009.

Smit IPJ, Grant CC, Whyte IJ. Elephants and water provision: what are the management links? Divers Distrib. 2007b;13(6):666-9. https://doi.org/10.1111/j.1472-4642.2007.00403.x.

Somerfield PJ, Clarke KR. Inverse analysis in non-parametric multivariate analyses: distinguishing groups of associated species which covary coherently across samples. J Exp Mar Biol Ecol. 2013;449: 261-73. https://doi.org/10.1016/j.jembe.2013.10.002.

Tefempa HB, Ngassam P, Mapongmetsem PM, Nkongmeneck BA, Gubbuk H. Behaviour of mammals around artificial waterholes in the Waza National Park (Cameroon). Journal of the Faculty of Agriculture of Akdeniz University (Turkey). 2008;21(1):7-13.

ter Braak CJF. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology. 1986; 67(5):1167-79. https://doi.org/10.2307/1938672.

Torello-Raventos M, Feldpausch TR, Veenendaal E, Schrodt, F, Saiz G, Domingues TF, et al. On the delineation of tropical vegetation types with an emphasis on forest/savanna transitions. Plant Ecol Divers. 2013;6(1):101-37. https://doi.org/10.1080/17550874.2012.762812.

Tóthmérész B. Comparison of different methods for diversity ordering. J Veg Sci. 1995;6(2):283-90. https://doi.org/10.2307/3236223.

van Wilgen BW, Govender N, Biggs HC. The contribution of fire research to fire management: a critical review of a long-term experiment in the Kruger National Park, South Africa. Int J Wildland Fire. 2007;16(5):519-30. https://doi.org/10.1071/WF06115.

Wilson BG. Witkowski ETF. Seed banks, bark thickness and change in age and size structure (1978–1999) of the African savanna tree, *Burkea africana*. Plant Ecology. 2003;167:151-62. https://doi.org/10.1023/A:1023999806577.