



Anthropogenic activities affect forest structure and arthropod abundance in a Kenyan biodiversity hotspot

Gladys Nyakeru Kung'u^{1,4} · Laurence Cousseau^{2,4} · Mwangi Githiru^{3,4} · Jan Christian Habel¹ · Mwangi Kinyanjui⁵ · Kennedy Matheka⁶ · Christine B. Schmitt⁷ · Tobias Seifert¹ · Mike Teucher⁸ · Luc Lens² · Beate Apfelbeck^{1,4}

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Abstract

Land-use change remains the main threat to tropical forests and their dependent fauna and flora, and degradation of existing forest remnants will further accelerate species loss. Forest degradation may result directly from human forest use or through spatial effects of land-use change. Understanding the drivers of forest degradation and its effects on biodiversity is pivotal for formulating impactful forest management and monitoring protocols, but such knowledge is lacking for many biodiversity hotspots, such as the Taita Hills in southeast Kenya. Here we first quantify effects of social factors (human activity and presence) at plot and landscape level, forest management (gazetted vs. non-gazetted) and spatial factors (fragment size and distance to forest edge) on the vegetation structure of indigenous Taita forest fragments. Next, we quantify effects of degraded vegetation structure on arthropod abundance and diversity. We show that human presence and activity at both the plot and landscape level explain variation in vegetation structure. We particularly provide evidence that despite a national ban on cutting of indigenous trees, poaching of pole-sized trees for subsistence use may be simplifying vegetation structure, with the strongest effects in edge-dominated, small forest fragments. Furthermore, we found support for a positive effect of vegetation structure on arthropod abundance, although the effect of daily maximum temperature and yearly variation was more pronounced. Maintenance of multi-layered forest vegetation in addition to reforestation may be a key to conservation of the endangered and endemic fauna of the Taita Hills.

Keywords Tropical rainforest · Forest degradation · Land-use · Subsistence activity · Understory insectivores · Forest management

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Extended author information available on the last page of the article

Introduction

Tropical forests are unequivocally recognized for their importance in biodiversity conservation (FAO 2020; Pillay et al. 2022). They hold more than half of the Earth's terrestrial biodiversity, but their rapid loss and deteriorating quality remains a major conservation concern (Barlow et al. 2016; Pillay et al. 2022). The scale of deforestation of the world's tropical forests is highest in Africa and is mostly propagated by the socio-economic demands associated with a rapidly growing human population in the region (FAO 2020; Williams 2013). Unlike in South America and Asia, where the leading driver of tropical forest loss is commodity-driven plantations and timber extraction, forest loss in Africa is primarily due to clearance for small-scale agriculture and selective harvesting for subsistence use (Abernethy et al. 2016; Boudreau et al. 2005; Ordway et al. 2017). Consequently, many African forests are highly fragmented and distributed in a human-dominated agricultural landscape matrix. In addition, weak governance and poor land-use management has led to degradation of the remaining indigenous forests (Christensen et al. 2021; Nzau et al. 2020). The extent and intensity of forest degradation, may be influenced by various landscape factors resulting from deforestation itself [e.g., edge effects (Laurance et al. 1998) and forest size] and social factors such as the density of the consumer community (Shah et al., 2021), accessibility as determined by presence of roads or proximity to human habitation (Laurance et al. 2009) and forest management status. For example, edge-related effects such as extreme climate at the forest edges compared to the interior contribute to changes in forest structure due to tree falls, desiccation of germinating moisture-dependent forest interior plant species and colonization of disturbance-adapted lianas and pioneer species (Campbell et al. 2018; Laurance et al. 1998). At the same time, as forest edges (especially near roads and trails) are the first point of contact to people, they may be subjected to further degradation by human activity (Laurance et al. 2009). Assessing and understanding the drivers of forest degradation and the effects of a degraded forest on biodiversity is critical for developing optimum forest management and conservation systems.

Conversion of tropical forests to land-uses such as agriculture and exotic tree plantations has a considerable impact on the high species richness and endemism that these forests still support (Alroy 2017; Roberts et al. 2021). In addition to the loss and fragmentation of habitat for forest-dependent taxa, degradation of the remaining indigenous forest may jeopardize long-term survival of habitat specialized species (Barlow et al. 2016; FAO 2020). For example, insectivorous birds of the tropical rainforest understorey are particularly vulnerable to forest fragmentation and degradation (Powell et al. 2015) as they often show limited dispersal (Lens et al. 2002), and depend on a distinct vegetation structure for foraging and breeding (Şekercioğlu et al. 2002; Stratford 2015). The persistence of forest species may not only be a direct function of the availability of vegetation structure attributes that provide shelter, breeding sites and protection from predators (Atikah et al. 2021; Melin et al. 2019), but also the availability of sufficient food such as arthropods (Ferber et al. 2014; Peter et al. 2015). Several studies suggest that multi-layered vegetation (henceforth referred to as vertical vegetation heterogeneity) and canopy cover determine species richness and abundance of arthropods (Basset et al. 2015; Dial et al. 2006; Knuff et al. 2020). Alteration of the vertical vegetation heterogeneity and canopy cover e.g., through selective logging, may therefore influence arthropod and population of insectivores directly and indirectly through predator-prey interactions.

An example of an imperilled and highly fragmented tropical forest ecosystem is the Taita Hills located in southeast Kenya, where about 95% of historical montane cloud forest cover has been lost to subsistence agricultural land, human settlements, and exotic tree plantations (Pellikka et al. 2009; Teucher et al. 2020). Despite these losses, the Taita Hills forests house a diverse and unique flora and fauna and, as a part of the greater Eastern Arc Mountains, rank among the world's biodiversity hotspots (Burgess et al. 2007). However, a number of endemic species are currently globally threatened (listed as vulnerable, endangered or critically endangered by the International Union for Conservation of Nature), among them several insectivorous birds, such as the critically endangered Taita Apalis *Apalis fuscigularis* (Birdlife International 2022). While habitat loss is a major threat to the endemic fauna of the Taita Hills, the quality of the remaining forests may also play a major role in their long-term persistence.

Human resource use may contribute to the loss of forest quality in some of the Taita forest fragments as they provide a variety of resources such as woody products for subsistence use and livestock grazing areas to the densely populated local community (KNBS, 2019). Strict forest conservation regulations prohibiting exploitation of indigenous forests exist in Kenya, including the 2010 constitution which prescribes for a maintenance of a tree cover of at least ten per cent of the country's land area (GoK, 2010;2016). Despite these regulatory frameworks, a recent study that evaluated trends in land cover changes between 2003 and 2018 in parts of the Taita Hills ecosystem still detected a notable decrease in the indigenous forest cover (Teucher et al. 2020). A forest cover decline noticeable within such a short span of time demonstrates that anthropogenic activities in the Taita hills are a threat to the persistence of this already fragile ecosystem. In the Taita Hills, some forest fragments are gazetted as protected forests by the National Government and therefore receive more protection from resource extraction (Wekesa et al. 2020). Other fragments are non-gazetted but are managed as community forests by the County Government on behalf of the community. However, in non-gazetted forests, resource exploitation is relatively uncontrolled (Wekesa et al. 2020). Furthermore, the fragments differ greatly in size (1 ha -220 ha; Aerts et al. 2010; Pellikka et al. 2009), are embedded in an agricultural landscape of subsistence farming, human settlements, and exotic plantations and hence easily accessible. While it has been shown that forest loss and degradation are ongoing problems (Teucher et al. 2020) and that they negatively affect biodiversity (Aerts et al. 2010; Obunga et al. 2022; Rosti et al. 2022), it is less clear which factors contribute to the ongoing loss and degradation of forests in the Taita Hills. Furthermore, while all the globally threatened and endemic birds of the Taita Hills are insectivorous (International 2022), the connection between forest degradation and availability of arthropods has received little attention. Such knowledge is important for effective conservation and management of the remaining indigenous forest and, thus, the long-term persistence of endemic flora and fauna.

Therefore, the objectives of this study are two-fold: (i) to examine social, forest management and spatial factors that best explain variation in vegetation structure in the Taita Hills, and (ii) to assess whether variation in vegetation structure affects arthropod abundance and diversity. For this purpose, we determined several vegetation structural features, two social factors (human presence and activity) at the plot and landscape level, the forest management status of each forest fragment (gazetted vs. non-gazetted), and a set of spatial factors (fragment sizes, distance of the survey plots to the forest edge). In addition, we sampled arthropods in the forest understorey using three complementary methods (sweep nets, visual

counts, flight interception traps) to determine whether, and to what extent, a degraded vegetation structure is reflected in shifts in arthropod abundance and diversity.

Materials and methods

Study area and selection of study plots

The Taita Hills are located in the Taita-Taveta county in the southeast of Kenya (3° 20' S, 38° 15' E). Geologically, the Taita Hills are part of the Eastern Arc Mountains, a chain of massifs that run from the southeast of Kenya to the south of Tanzania. However, the Taita Hills are isolated from the rest of the mountains (e.g., West Usambara Mountains, and North Pare) by the expansive semi-arid Tsavo plains (see map in Burgess et al. 2007). The Taita Hills landscape contains two distinct and isolated hills (Mount Sagalla and Mbololo mountain) and the main massif (Dabida). Due to the influence of the Intertropical Convergence Zone (ITCZ), the rainfall pattern is bimodal (long rainy season from March to May and a short one between November and December), but the hilltops maintain mist and cloud precipitation throughout the year. Because of the favourable climate in the Taita Hills compared to the surrounding semi-arid plains, a large part of the forest has been cleared for small-scale mixed agriculture, commercial (railway construction) and subsistence use (fuel wood and building material) and thus, the indigenous forest is mainly found on hilltops (Beentje 1988; Pellikka et al. 2018; Thijs et al. 2015). Mbololo mountain contains the largest indigenous forest remnant (about 200 ha; Aerts et al. 2010), while three other relatively large forest fragments (> 70–120 ha) and around ten small fragments (< 1–20 ha) are found on the Dabida massif at an elevation range spanning between 1400 and 2200 m above sea level (Aerts et al. 2010; Pellikka et al. 2009). Our study covered eight forest fragments within the Dabida massif, including Ngangao (120 ha), Chawia (86.3 ha), Vuria (70.3 ha), Msidunyi (20.9 ha), Ndiwenyi (3 ha), Yale (15.7 ha), Susu (15 ha) and Fururu (8.1 ha; Pellikka et al. 2018; Pellikka et al. 2009). Among these forest fragments, five (Ngangao, Yale, Susu, Ndiwenyi and Fururu) are gazetted as protected areas under the Kenya Forest Service (KFS) while three (Chawia, Msidunyi, and Vuria) are non-gazetted (Pellikka et al. 2009; Wekesa et al. 2020).

General sampling procedure

Study plots were distributed throughout the forest and were radially separated from each other by at least 200 m from the centre (Fig. 1). Vegetation structure sampling took place in two main field sessions. The first field session took place in April/May 2021 and 70 plots were sampled. The second field session took place in September 2021 and a subsample of the 70 plots were sampled (n=41).

Visual count of arthropods overlapped with the first vegetation field session and 51 plots of the 70 vegetation plots were counted for arthropods. FIT sampling took place in September 2021 during the second vegetation field session and in 18 plots sampled for vegetation, FITs were applied. Sweep netting took place from 2016 to 2022 between October and March as part of a longer-term effort to assess arthropod abundance in the Taita Hills. In total 158 sweep net samples were collected in 83 plots. Vegetation structure for most of the plots was assessed during the first vegetation field session in April/May 2021. In April

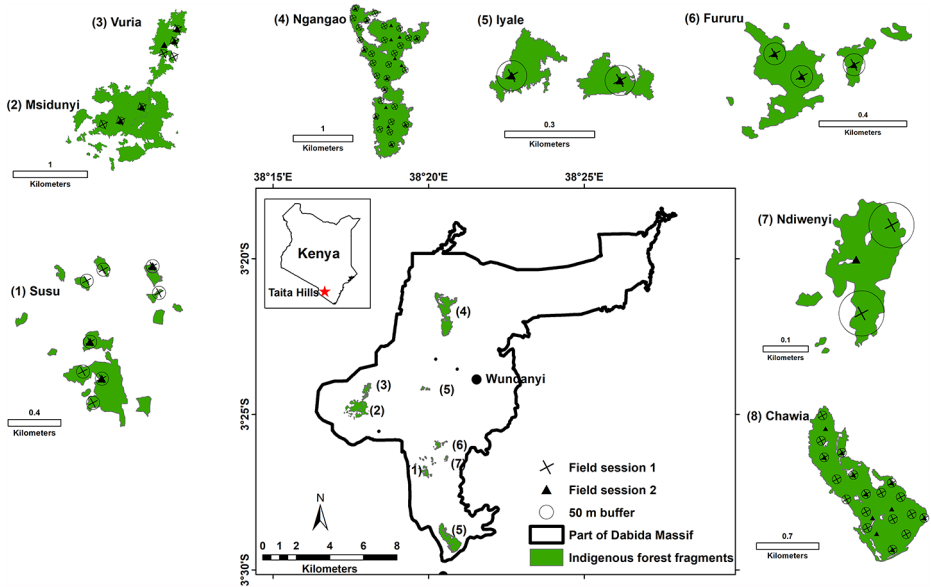


Fig. 1 Location of Taita Hills in southern Kenya (small inset map), and Dabida massif with the remaining cloud forest patches (1–8, central map). The zoomed-out maps show distribution of vegetation structure sampling plots in each forest fragments. The scale differs for each fragment due to the differing sizes. All vegetation structure sampling was done inside the indigenous forest within a 50 m buffer. Whenever a subplot (50 m South, 50 m Northeast, 50 m Northwest from the centre subplot) would fall outside the indigenous forest, we shifted to the opposite cardinal subplot falling inside the indigenous forest

2022 the remaining plots were assessed so that for every sweep net sampling plot vegetation structure data were available. These additional plots were not included in the comparison of vegetation structure between plots because of potential spatial autocorrelation (<200 m apart).

Vegetation structure sampling

We assessed different structural vegetation elements: vertical vegetation heterogeneity (VVH), plant growth form diversity, ground, shrub and canopy cover, diameter at breast height (DBH), tree height, tree species richness and tree species diversity (see a summarized definition of terms in Supplementary Material 1). During the field session in April/ May 2021 as well as April 2022 we assessed VVH, a canopy cover index and diversity of plant growth forms in four subplots per plot that is, a centre subplot, and three additional subplots, 50 m away from the centre subplot (50 m South, 50 m Northeast, 50 m Northwest, n=70 plots). In each subplot, the presence of vegetation within a circle of 0.5 m radius in five height intervals (0–1 m, 1–5 m, 5–9 m, 9–15 m, > 15 m) was recorded at five points, the central point and in all four cardinal directions located 15 m away from the central point (15 m North, 15 m South, 15 m West, 15 m East) leading to a total of 20 vegetation records per sampling plot. We computed VVH as an estimate of the diversity of vegetation layers by calculating the Shannon-Wiener diversity index across the five vegetation height intervals following the computation of foliage height diversity in Erdelen (1984) and an index of

canopy cover by summing all presences of vegetation above 9 m for the 20 sampling points per plot (Bibby et al. 2000). We also assessed the presence of different plant growth forms (herbs, ferns, dracaenas, climbers, tree-ferns, phoenix, shrubs, and trees) in each of the 20 points and five height layers per plot. We calculated the diversity of plant growth forms with the Shannon-Wiener diversity using the proportion of each plant growth form as the number of counts for each plant growth form divided by the total counts of all plant growth forms. During the second field session (September 2021), we assessed additional vegetation structural elements including diameter at breast height (DBH), tree species richness, tree species diversity and tree height of woody plants with DBH > 10 cm within a radius of 15 m in a total of 41 plots, which is a subset of the 70 plots assessed during the first field session. We also estimated the percentage of woody vegetation cover at height intervals of < 1 m (ground cover), 1–5 m (shrub cover) and > 9 m (canopy cover). Trees were identified by an experienced local taxonomist following Beentje (1988), Beentje et al. (1994), and various publications of the Flora of Tropical East Africa (1952–2012). We summarized vegetation data by averaging each plot's DBH and tree height and calculated tree species diversity using the Shannon-Wiener diversity index.

Human presence and activity and spatial factors

To determine the frequency of human activities at the plot level, we recorded the presence of footpaths, forest fires, tree stumps, firewood bundles, wood splitting, debarked trees, water extraction, grazing and garbage in the 20 points within 70 sampling plots where vegetation structural elements were assessed during the first field session (see detailed description of vegetation sampling procedure above). We summarized signs of human presence and activities for each plot ($n=70$) as the proportion of points where either of the aforementioned activities were present. During the second field session, in accordance with the vegetation assessment presence of human activity was scored within a 15 m radius. To characterize landscape variables that reflect human presence and activity and that may predict the forest resource utilization patterns of the local people, we used recent land cover and land-use maps of the Taita-Taveta County, produced from 20 m resolution remote sensing images (Abera et al. 2022). With the knowledge that our study area is densely populated [421 persons per km² (KNBS, 2019)] with small-scale farming households, we assumed that land-use classifications linked to human activities and presence, such as human settlement and agricultural lands (hereafter referred to as the anthropogenic land cover) would give an indication of human pressure on the indigenous forest. Using QGIS v3.22 (QGIS Development Team, 2022), we quantified anthropogenic land cover by calculating its proportion within a 1 km radius surrounding all study plots. Based on the indigenous forest boundaries maps of the Taita Hills created from airborne remote sensing images (Pellikka et al. 2009, 2018), we calculated the Euclidian distance from the forest edge to each study plot using the *raster* and *rgdal* packages in R. Distance to the forest edge and forest fragment sizes were included as spatial predictors. We also included forest management status (gazetted and non-gazetted) as a predictor of variation in vegetation structure.

Arthropod sampling

Because arthropods are a megadiverse animal group occupying a diversity of niches within the tropical forest understorey, employment of multiple sampling methods is recommended to assess arthropod availability and diversity (Basset et al. 2015). Therefore, we estimated the abundance of understorey invertebrates using sweep nets, flight interception traps (FITs) and visual counts. Sweep nets and visual counts mainly assess insects on vegetation, while FITs, capture flying insects. In March/April 2021 during the first vegetation field session, we visually counted arthropods on the underside of leaves of the five most abundant plant growth forms (50 leaves per plant growth form) in 51 plots of the 70 plots assessed for vegetation. Between September and October 2021, during the second vegetation field season, UV LED equipped FITs were operated in 18 of the 41 plots where vegetation was assessed. FITs were hung from tree branches at a height of about 4 m above the ground in the evening and retrieved after 48 h for each location. The FITs used in this study and the sampling procedure are extensively described in (Seifert et al. 2022). Sweep net samples were collected in 83 plots between 08:00 h – 14:00 h from 2016 to 2022 between October and March. At each sampling location, three samples of 8 sweep net strikes were taken at a vegetation height of 1–2 m. Arthropods obtained from sweep nets and FITs were stored in 70% ethanol. Arthropods were counted to obtain arthropod abundance and identified to order level for all three sampling methods. As a measure of order diversity, we calculated each plot's Shannon-Wiener diversity index across orders for data obtained from sweep nets. Order diversity was not calculated for data obtained from visual counting and FITs because of the low sample size for these methods. Arthropod sampling plots for the three sampling methods overlapped with the centre plots of the vegetation structure sampling plots (see map in Supplementary Material 1).

Climate and weather variables

We obtained 4 km by 4 km gridded daily weather data (precipitation, maximum and minimum temperature) from the Kenya Meteorological Department (KMD) until the year 2020. The KMD compiles these weather data by blending ground collected data (from 10 weather stations within Taita-Taveta County) and gridded data from meteorological satellites. Blending and interpolation is done using the Background-Assisted Station Interpolation for Improved Climate Surfaces (BASIICS) tool based on the simple and ordinary kriging concept. To obtain seasonal summaries, we averaged daily temperatures from October to March when the sweep net data was collected. These weather data were only considered for the analysis of sweep net samples as samples from all other methods were obtained after 2020.

Statistical analysis

Modelling the influence of human presence and activity, forest management, and spatial factors on vegetation structure

We used linear mixed models to assess the effects of human presence and activity at the plot (HPA) and landscape level, spatial factors (distance to forest edge and fragment size) and forest management status (gazetted and non-gazetted). To account for potential non-

independence of data points sampled within the same fragment, we included fragment ID as a random factor. To determine the best combination of predictor variables that explain variation in vegetation structure, we developed 13 hypothesis-informed candidate models based on our ecological understanding of the Taita Hills ecosystem (Supplementary Material 2: *Priori candidate models*). We began with a global model, which included the influence of all three sets of predictor categories, that is, (1) the social (human activity at the plot level (HPA) or landscape level (anthropogenic land cover), (2) forest management (gazetted and non-gazetted) and (3) spatial factors (fragment size or distance to the forest edge). Additionally, we built bivariate models containing combinations of two predictor variables. HPA and anthropogenic land cover were not included in the same model since they both represent human influence on vegetation structure but on different spatial scales (plot level and landscape level respectively). Moreover, HPA represents more direct evidence of human exploitation, while anthropogenic land cover represents an indirect influence (a proxy of human density and thus the amount of human pressure that the indigenous forest is potentially subjected to). Spatial factors were also not included in the same model (fragment size or distance to the forest edge) as we expected that changes in vegetation structure attributed to biotic (herbivory and restructured animal and plant species community composition) and abiotic (microclimate fluctuation) processes would be similar in forest edges and edge-dominated small sized forests (Caitano et al. 2020; Campbell et al. 2018; Laurance et al. 1998, 2009; Rossetti et al. 2017) Among these candidate models, we also included the null model (intercept only).

Modelling the influence of vegetation structure on arthropod abundance and diversity

We modelled the effect of vegetation structure and spatial factors on arthropod abundances from sweep nets, FITs and visual counts, and arthropod diversity from sweep nets as separate response variables, using linear mixed models with fragment ID as a random factor. For visual arthropod counts vegetation structure variables obtained in the first field session (i.e., VVH, index of canopy cover, plant growth forms diversity), and spatial factors (fragment size, distance to forest edge) were included as explanatory variables. FITs had been restricted to 18 plots only. Thus, to reduce the number of candidate models we only considered fragment size as a spatial factor. As all of the FIT sites overlapped with vegetation plots assessed during the second field session, we considered ground, shrub and canopy cover, tree height and tree species richness as predictors in the candidate models.

For sweep net samples we ran two different analyses. The first included all data up to 2022. The second was restricted to data obtained up to 2020 as for these weather data were available. For the dataset 2016–2022 we added year to control for variation in weather between years and season (short rains (October, December), hot dry (January – March) to control for variation between months. In the dataset 2016–2020 we added average seasonal maximum temperatures to control for variability introduced by fluctuations in weather conditions between years as a fixed factor. Since ambient temperature has been shown to affect the activity of arthropods and thus their trapping rates (Taylor 1963), we also added maximum daily temperature to account for variation in daily weather conditions. We also added plot ID as random factor to account for non-independence of data points in plots that were sampled multiple times. Furthermore, we considered vegetation structure (VVH, index of

canopy cover, plant growth forms) and spatial factors (fragment size, distance to forest edge) as predictors of variation in sweep net samples.

We built 13 a priori candidate models for arthropod abundance and diversity from sweep nets, 12 models for arthropod abundance from visual counts and 7 models for arthropod abundance from FIT. We outline and describe the a priori models in the supplementary information (Supplementary Material 3: Priori candidate models).

General modelling procedure

Prior to performing multivariate modelling, we tested for collinearity between continuous predictor variables using *corrplot* package (Wei et al., 2017). Predictor sets with a Pearson's r of >0.7 were not included in the same model (Supplementary Material 1). To examine whether the distances between sampling points influenced the linear regressions, we tested for presence of spatial autocorrelation in the residuals using the *gstat* package. An examination of the semi variograms (*variogram* function in *gstat* package) indicated no spatial autocorrelation in the residuals for all the models.

To identify the best combination of predictor variables, we ranked candidate models based on the Akaike Information Criterion, corrected for small sample sizes (ΔAICc) (Burnham et al., 2002) using the *model.sel* function of the *MuMIn* package (Barton 2019). Models with an AICc difference of ≤ 2 units ($\Delta\text{AICc} \leq 2$) from the top ranked model were accepted as equally parsimonious unless they were complex versions of a simpler higher ranked model (Arnold 2010; Richards 2008). We identified the complex models following Arnold (2010) and Richards (2008). Complex models were discarded. When the null model was equally supported in addition to other models, we used the 9% confidence interval of the retained predictor variables to identify the strength of their ecological influence and thus the probability of the model being informative (Anderson 2008). We report the coefficients of retained parsimonious models in the main text (unless otherwise described in the results) and include all model sets (retained models and complex models) in the supplementary materials (Supplementary Material 2 and 3: Model results). Linear mixed models were fitted using the *nlme* package and we specified the maximum likelihood option to allow for model selection. Predictor variables were standardized to a mean of zero and a standard deviation of one before running the models. We log-transformed vegetation at the ground, shrub and canopy level (vegetation structure data) and arthropod abundance data from sweep nets and FITs to improve normality and homoscedasticity of model residuals. All statistical analysis was performed with the R software package 4.1.2 (R Core Team 2022).

Results

The influence of human presence and activity, spatial factors, and forest management on vegetation structure

Vertical vegetation heterogeneity (VVH): when examining variation in VVH, four out of the 13 a priori candidate models were retained within $\Delta\text{AICc} \leq 2$. The first three models included human presence and activity at the plot level (HPA), but the 95% CI overlapped zero suggesting a weak effect. Spatial variables (edge distance and fragment size) and for-

est management also appeared in either of the first three best models and their 95% CI also overlapped zero (Table 1). Marginally included within the most parsimonious models was also the null model (ΔAICc : 1.94).

Index of canopy cover: two competing models ($\Delta\text{AICc} \leq 2$) explained variation in canopy cover index (cumulative AIC weight: 0.59; Table 1). These models included the influence of human presence and activity at plot level (HPA) and spatial variables (distance to the forest edge and fragment size). These models suggested that the index of canopy cover decreased with increasing HPA (Table 1; Fig. 2). However, distance to the forest edge and fragment size showed a weak positive effect as the 95% confidence interval of the slope estimate of both predictors overlapped with zero.

Plant growth forms diversity: three models were retained within the $\Delta\text{AICc} \leq 2$ model set (cumulative AIC weight: 0.89; Table 1). These models suggested that the diversity of plant growth forms increased with increasing distance to the forest edge (included in all top models; Table 1). Human presence and activity at the plot level, forest management status and anthropogenic land cover were also appearing within the four best supported models, however their 95% CIs overlapped considerably with zero suggesting weak ecological effects.

Ground cover: Only one model was retained, which accounted for half of the AIC weight (AIC weight: 0.50; Table 2). According to this model ground cover (woody vegetation below 1 m) increased with increasing anthropogenic land cover within 1 km and non-gazetted fragments had more ground vegetation cover than gazetted ones (Table 2; Fig. 2).

Shrub cover: two models ($\Delta\text{AICc} \leq 2$) explained variation in shrub cover (cumulative AIC weight: 0.83; Table 2). These models suggested that shrub cover decreased with increasing anthropogenic land cover within 1 km and distance to the forest edge (Table 2; Fig. 2). Forest management status was included in the second-best supported models, but its 95% CIs overlapped with zero suggesting weak support for a higher woody vegetation cover within the shrub level in non-gazetted forest fragments than in gazetted ones (Table 2).

Canopy cover: when investigating variation in woody vegetation cover at the canopy level (vegetation cover > 9 m), the null model and a model including the influence of human presence and activity assessed at the plot level (HPA) and distance to the forest edge) were within the $\Delta\text{AICc} \leq 2$ model set (AIC weight: 0.28 and 0.19 respectively; Table 2). As the null model was the top-best model, this suggests a moderate or inconclusive support for a negative effect of HPA on canopy cover.

Diameter at breast height (DBH): when investigating variation in DBH, only the null model was retained and accounted for over half of the AIC model weight (AIC weight: 0.52; Table 2). Thus, support for our alternative hypotheses was weak.

Tree height: Two competing models explained variation in tree height (Table 2). The top model included the combination of HPA, fragment size and forest management status (AIC weight: 0.29; Table 2). This model suggested that tree height decreased with increasing HPA while it increased with increasing fragment size (Fig. 2). Gazetted fragments had taller trees than non-gazetted ones (Fig. 2). The second-best model was the null model (AIC weight: 0.17; Table 2). Although the null model was included within the most parsimonious models, the confidence intervals of all variables in the top model did not overlap zero, suggesting that they are informative.

Tree species richness: We recorded a total of 1464 woody individuals (Supplementary Material 1). These were represented by 61 species belonging to 56 genera and 37 families. The study recorded five globally threatened species, of which two are red-listed as endan-

Table 1 Predictor coefficients of the best supported linear mixed models (with $\Delta AIC_c \leq 2$) for vegetation structure elements sampled during the first field session, where $n=70$ plots

Response variable	Model rank	Intercept	Human presence and activity at plot level	Anthropogenic land cover (1 km)	Edge distance	Fragment size	Forest management status (non-gazetted)	K	L	AICc	ΔAIC_c	weight
VVH	1	1.47 1.41;1.54	-0.02 -0.03;0.00		0.01 -0.01;0.03			5	84.63	-158.30	0.00	0.31
	2	1.49 1.40;1.57	-0.02 -0.04;0.00				-0.03 -0.17;0.11	5	83.82	-156.69	1.61	0.14
	3	1.48 1.40;1.57	-0.02 -0.04;0.00		0.01 -0.06;0.08			5	83.76	-156.56	1.74	0.13
	4	1.46 1.40;1.53						3	81.36	-156.36	1.94	0.12
Index of canopy cover	1	12.60 10.30;14.90	-0.70 -1.27; -0.13		0.42 -0.13;0.97			5	-158.83	328.60	0.00	0.34
	2	13.92 10.99;16.85	-0.75 -1.32; -0.17			1.61 -0.75;3.97		5	-159.14	329.23	0.62	0.25
Plant growth forms	1	1.20 1.08;1.31			0.07 0.03;0.11		0.07 -0.11;0.25	5	30.42	-49.90	0.00	0.27
	2	1.23 1.15;1.32	0.01 -0.02;0.05		0.07 0.04;0.11			5	30.37	-49.81	0.09	0.26
	3	1.24 1.15;1.33		-0.02 -0.08;0.03	0.07 0.03;0.11			5	30.33	-49.73	0.17	0.25

The columns outline predictor variables and rows contain different models. VVH means the vertical vegetation heterogeneity while HPA is human presence and activity at plot level. Blank spaces for each predictor variable mean that the model depicted in the corresponding row did not include this variable. K is the number of fixed effect parameters (including the intercept) estimated in the model, while L is the likelihood of the model given the data. We used Akaike Information Criteria adjusted for small samples (AICc) to select and weigh best performing models. We report model estimates and 95% confidence intervals for each predictor variable

gered and three as vulnerable (Supplementary Material 1). Two models were retained for variation in tree species richness. The top model included HPA and fragment size (AIC weight: 0.34), while the second-best model retained HPA and forest management (AIC weight: 0.17; Table 2). These models suggested that tree species richness decreased with increasing HPA. As the 95% CI of forest management status and fragment size overlapped with zero, this suggested a weak support of a higher tree species richness in gazetted forest fragments and a weak positive influence of fragment size on tree species richness (Table 2).

Tree species diversity: when investigating variation in tree species diversity, three models were retained (cumulative AIC weight: 0.74; Table 2) These models demonstrated that tree species diversity was inversely related with HPA and increased with increasing fragment size. The 95% CI of forest management status overlapped with zero suggesting weak evidence for a higher tree species diversity in gazetted forest fragments than in non-gazetted ones (Table 2).

Influence of vegetation structure and spatial factors on arthropod abundance and diversity in the forest understorey

We recorded 4,979 arthropods belonging to 12 orders using visual counting and 5,885 arthropods from 13 orders using flight interception traps. Using sweep netting, we recorded 15,460 arthropod specimens from 34 orders. Among these specimens, 638 were unidentified individuals.

Arthropod abundance from sweep nets: For the larger dataset 2016–2022, two models were parsimonious models (Table 3). All models contained year and season as important predictors of arthropod abundance, and vegetation structure (VVH and canopy cover index) was included within the top model and the CI did not cross zero (Table 3). Canopy cover index replaced VVH in the second model. In conclusion, these models suggested that there was a negative influence of yearly and seasonal variation in weather and a positive influence of VVH (Fig. 3) and canopy cover on arthropod abundance.

For the dataset 2016–2022, four models were within the $\Delta AIC_c \leq 2$ model set (Table 4). All models included maximum daily temperature, which had a positive effect on arthropod abundance, and maximum seasonal temperature, which showed a negative relationship with arthropod abundance. Vegetation structure variables (VVH and canopy cover index) and distance to forest edge were included within models 2–4 respectively. However, these models (models 2–4) were complex versions of the top model and the 95% CI of the slope estimates of the retained predictors overlapped zero (Table 4).

Arthropod diversity from sweep nets: For the larger dataset 2016–2022, three models were parsimonious (cumulative AIC weight: 0.55). All models contained year and season as important predictors of arthropod diversity as well as fragment size and canopy cover in two of the best-supported models (Table 3). However, 95% CI of the slope estimate for all retained predictors crossed zero, suggesting a weak ecological effect (Table 3).

For reduced dataset (2016–2022) the null model was retained (AIC weight: 0.46; Table 4). This suggested a weak or no support for our alternative priori candidate models (Supplementary Material 3: sweep net).

Arthropod abundance from visual counts: one model explained variation in arthropod abundance sampled using visual counts (AIC weight: 0.35; Table 5). This model included

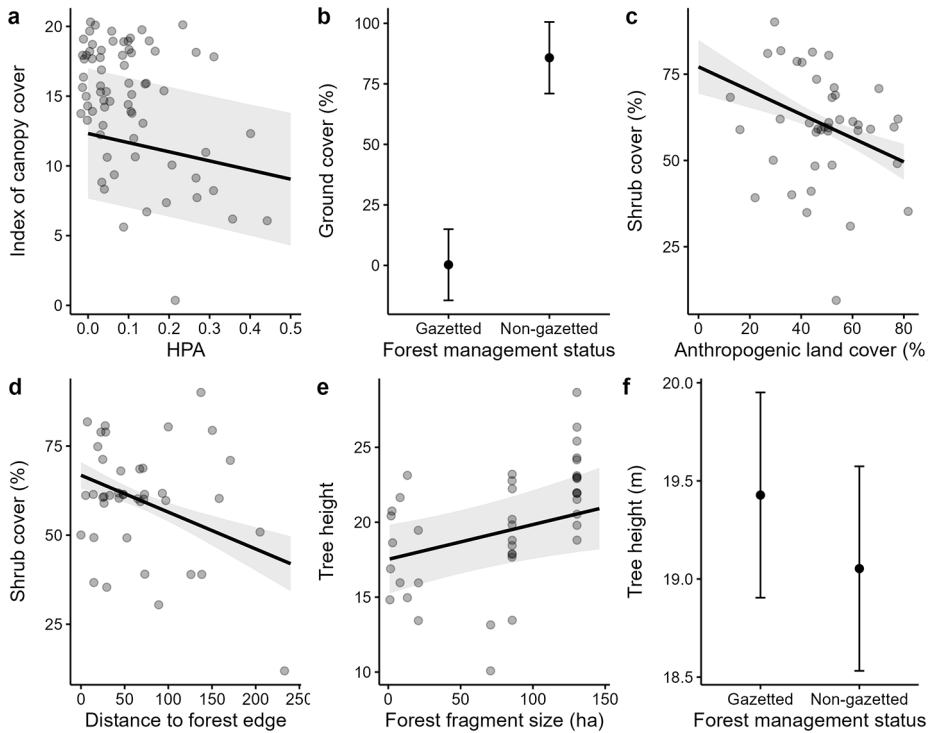


Fig. 2 Maximum likelihood model selection (line and error bars) and raw data (dots) showing the effects of landscape and plot level factors on vegetation structure. We included error structure for both fixed and random effects (fragment ID). **(a)** Negative effect of human presence and activity at plot level (HPA) on index of canopy cover index respectively (n=70 plots). **(b)** Lower vegetation cover at the ground level (woody vegetation <1 m) were found in gazetted forest fragments than non-gazetted ones. **(c)** A negative association between anthropogenic land cover at 1 km radius and vegetation cover at the shrub level (Woody vegetation between 1–5 m) **(d)** Negative relationship of distance to the forest edge and vegetation cover at the shrub layer **(e)** Positive relationship of fragment size and tree height **(f)** Higher trees were found in gazetted forest fragments than non-gazetted ones. In figures b-f, n=41 plots

fragment size as the only important predictor and suggested an inverse relationship with arthropod abundance (Fig. 3).

Arthropod abundance from flight interception traps (FITs): When investigating variation in arthropod abundance sampled using FITs, the null model (AIC weight: 0.36; Table 6) and two more models including the influence of tree species richness and vegetation cover within the shrub level respectively were within the $\Delta AIC_c \leq 2$ model set. As the null model was the top-best model and the 95% CI of slope estimate for tree species richness and vegetation cover within the shrub level overlapped zero (Table 6), this suggested a weak or inconclusive support of influence these predictors on arthropod abundance from FIT.

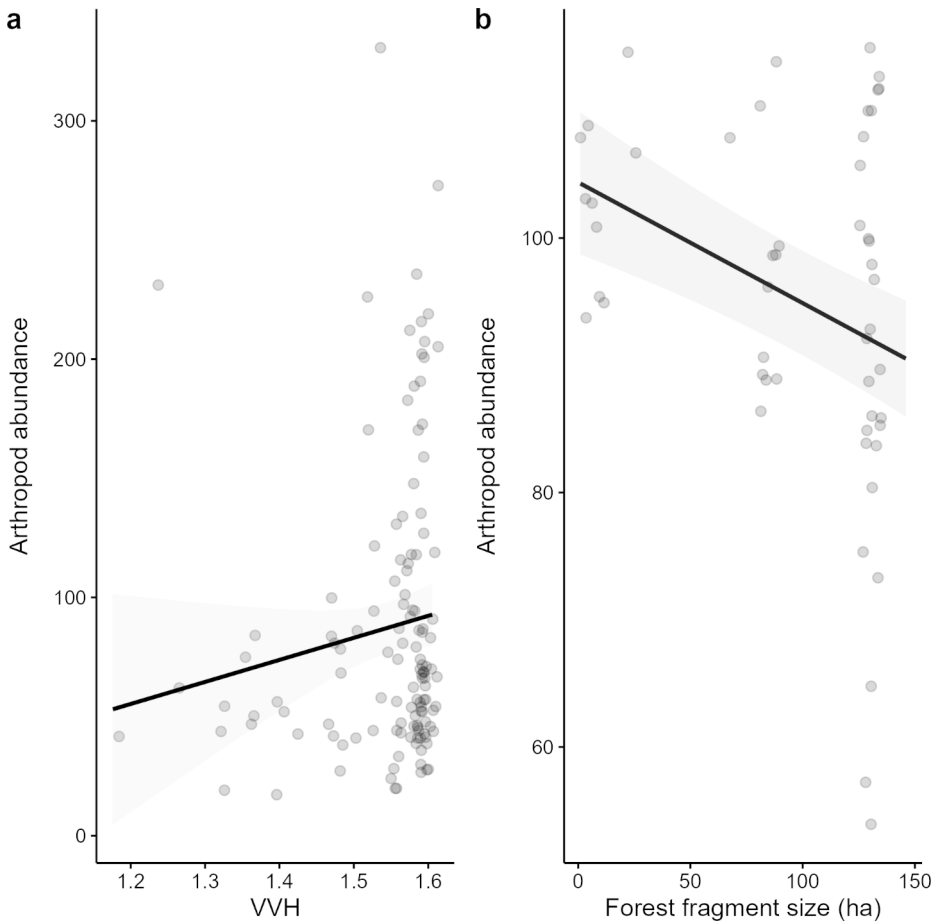


Fig. 3 Maximum likelihood model selection (line and error bars) and raw data (dots) showing the effects of vegetation structure and spatial factors on arthropod abundance and diversity. We included error structure for both fixed and random effects (fragment ID and plot ID). **(a)** and **(b)** Positive effect of vertical vegetation heterogeneity (VVH) and canopy cover index respectively on arthropod abundance from sweep nets, where $n=158$ sweep netting events in 83 plots. **(f)** Negative effect of fragment size on arthropod abundance sampled using visual counting where $n=51$ plots

Discussion

Our data show that human presence and activities at the landscape and plot level were important predictors of variation in vegetation structure. The results suggest negative effects of human presence and activity at the landscape and/or plot level on index of canopy cover, shrub cover, tree height, tree species richness and tree species diversity and a positive effect on the extent of vegetation cover at the ground level. We further found support for a positive effect of fragment size and distance of sampling plots to the forest edge on various components of the vegetation structure (tree height and tree species diversity) and negative effects of distance to the forest edge on vegetation cover at the shrub level. Our study also hints that that state protected forest fragments (gazetted forests) were in better condition.

Table 2 Predictor coefficients of the best supported linear mixed models (with $\Delta AICc \leq 2$) for vegetation structure elements sampled during the second field session, where $n = 41$ plots

Response variable	Model rank	Intercept	Human presence and activity at plot level	Anthro-pogenic land cover (1 km)	Edge distance	Fragment size	Forest manage-ment status (non-gazetted)	K	L	AICc	$\Delta AICc$	weight
Ground cover (Log transformed)												
	1	3.28 2.97;3.58		0.33 0.12;0.53			0.68 0.13;1.23	5	-25.42	62.55	0.00	0.50
Shrub cover (Log transformed)												
	1	4.04 3.93;4.14		-0.13 -0.24; -0.01	-0.18 -0.29; -0.07			5	-11.82	35.36	0.00	0.40
	2	3.94 3.80;4.08			-0.16 -0.27; -0.05		0.22 -0.02;0.47	5	-12.17	36.05	0.69	0.28
Canopy cover (Log transformed)												
	1	3.67 3.47;3.87						3	-14.08	34.82	0.00	0.29
	2	3.71 3.47;3.87	-0.10 -0.21;0.02		0.05 -0.06;0.15			5	-12.11	35.94	1.13	0.16
DBH												
	1	27.81 24.84;30.79						3	-138.32	283.28	0.00	0.52
Tree height												
	1	21.30 20.06;22.55	-0.98 -1.95; -0.02			1.40 0.40;2.40	-3.03 -5.26; -0.79	6	-101.42	217.32	0.00	0.29
	2	18.25 16.03;20.47						3	-106.00	218.64	1.32	0.15
Tree species richness												

Table 2 (continued)

Response variable	Model rank	Intercept	Human presence and activity at plot level	Anthropogenic land cover (1 km)	Edge distance	Fragment size	Forest management status (non-gazetted)	K	L	AICc	ΔAICc	weight
Tree species diversity	1	9.17	-0.89		0.75			5	-95.57	202.85	0.00	0.34
		8.38;9.86	-1.72; -0.06		-0.08;1.58							
	2	9.66	-1.11				-1.11	5	-96.27	204.25	1.40	0.17
		8.58;10.74	-3.00;0.77				-3.00;0.77					
	1	1.70	-0.17		0.13			5	-19.84	51.39	0.00	0.43
		1.57;1.82	-0.31; -0.04		0.00;0.26							
	2	1.77	-0.21				-0.17	5	-20.84	53.39	2.00	0.16
		1.60;1.95	-0.34; -0.08				-0.47;0.13					

The columns outline predictor variables and rows contain different models. HPA means human presence and activity at plot level. Blank spaces for each predictor variable mean that the model depicted in the corresponding row did not include this variable. K is the number of fixed effect parameters (including the intercept) estimated in the model, while L is the likelihood of the model given the data. We used Akaike Information Criteria adjusted for small samples (AICc) to select and weigh best performing models. We report model estimates and 95% confidence intervals for each predictor variable

Table 3 Predictor coefficients of the best supported linear mixed models (with $\Delta AICc \leq 2$) for the affects of vegetation structure and spatial factors (edge distance and fragment size) on forest understorey arthropod abundance and order diversity sampled using sweep nets from 2016 to 2022 (full data set), where $n = 158$ sweep netting events in 83 plots

Model rank	Intercept	VVH	Index of canopy cover	Plant growth forms diversity	Edge distance	Fragment size	Climatic seasons	Sampling year (2017/2018)	K	L	AICc	$\Delta AICc$	weight
Sweep net abundance (log transformed)													
1	4.14	0.12					-0.45	-0.07	11	-122.31	268.43	0.00	0.36
	3.93;4.35	0.03;0.20					-0.70; -0.20	-0.45;0.32					
2	4.15		0.10				-0.45	-0.08	11	-123.24	270.30	1.87	0.14
	3.94;4.36		0.02;0.19				-0.70; -0.20	-0.46;0.31					
Sweep net arthropod order diversity													
1	1.54				-0.04		0.03	0.08	11	1.02	21.77	0.00	0.21
	1.44;1.64				-0.08; 0.00		-0.09;0.15	-0.09;0.26					
2	1.53		-0.04				0.04	0.08	11	0.48	22.84	1.07	0.13
	1.44;1.63		-0.08;0.00				-0.07;0.16	-0.09;0.26					
3	1.56						0.04	0.07	10	-0.69	22.88	1.11	0.12
	1.45;1.66						-0.07; -0.22	-0.04;0.15					

The columns outline predictor variables used in the models and rows contain different models. K is the number of fixed effect parameters (including the intercept) estimated in the model, while L is the likelihood of the model given the data. We used Akaike information Criteria adjusted for small samples (AICc) to select and weigh best performing models. We report model estimates and 95% confidence intervals for each predictor variable

Table 4 Predictor coefficients of the best supported linear mixed models (with $\Delta AICc \leq 2$) for the affects of vegetation structure and spatial factors (edge distance and fragment size) on forest understorey arthropod abundance and order diversity sampled using sweep nets from 2016 to 2020 (reduced data set), where $n = 112$ sweep netting events in 70 plots

	Model rank	Intercept	VVH	Index of canopy cover	Plant growth forms diversity	Edge distance	Fragment size	Daily max temperature	Seasonal max temperature	K	L	AICc	$\Delta AICc$	weight
Sweep net abundance (log transformed)	1	4.31						0.25	-0.21	6	-101.52	215.83	0	0.23
		4.19;4.42						0.11;0.38	-0.34;-0.08					
	2	4.31	0.07					0.24	-0.21	7	-100.78	216.64	0.80	0.15
		4.19;4.42	-0.04;0.18					0.10;0.37	-0.34;-0.08					
Sweep net arthropod order diversity	3	4.31		0.06				0.23	-0.20	7	-101.04	217.16	1.33	0.12
		4.19;4.42		-0.06;0.17				0.10;0.37	-0.33;-0.06					
	4	4.31				0.04		0.25	-0.21	7	-101.24	217.56	1.73	0.10
		4.19;4.42				-0.07;0.16		0.12;0.38	-0.07;0.16					
	1	1.77								4	-12.69	33.76	0	0.46
		1.70;1.84												

The columns outline predictor variables used in the models and rows contain different models. K is the number of fixed effect parameters (including the intercept) estimated in the model, while L is the likelihood of the model given the data. We used Akaike information Criteria adjusted for small samples (AICc) to select and weigh best performing models. We report model estimates and 95% confidence intervals for each predictor variable. Rows in bold indicate the retained models.

Table 5 Predictor coefficients of the best supported linear mixed models (with $\Delta AICc \leq 2$) for the affects of vegetation structure and spatial factors (distance to forest edge and fragment size) on arthropod abundance sampled using visual counts where $n = 51$ plots

Model rank	Intercept	VVH Index of canopy cover	Plant growth forms diversity	Edge distance	Fragment size	K	L	AICc	$\Delta AICc$	weight
1	4.54 4.50;4.59				-0.05 -0.10; -0.01	4	22.71	-36.54	0.00	0.35

The columns outline predictor variables used in the models and rows contain different models. K is the number of fixed effect parameters (including the intercept) estimated in the model, while L is the likelihood of the model given the data. We used Akaike information Criteria adjusted for small samples (AICc) to select and weigh best performing models. We report effective sizes and 95% confidence intervals for each predictor variable.

Table 6 Predictor coefficients of the best supported linear mixed models (with $\Delta AICc \leq 2$) for the affects of vegetation structure and spatial factors (fragment size) on arthropod abundance sampled using Flight interception traps (FIT), where $n = 18$ plots

Model rank	Intercept	Ground cover	Shrub cover	Canopy cover	Tree height	Tree species richness	Fragment size	K	L	AICc	$\Delta AICc$	weight
1	5.45 4.94;5.94							3	-23.10	54.05	0.00	0.36
2	5.45 4.98;5.91					-0.36 -0.84;0.12		4	-21.82	54.96	0.91	0.23
3	5.45 4.97;5.93		-0.29 -0.78;0.21					4	-22.33	56.00	1.94	0.14

The columns outline predictor variables used in the models and rows contain different models. K is the number of fixed effect parameters (including the intercept) estimated in the model, while L is the likelihood of the model given the data. We used Akaike information Criteria adjusted for small samples (AICc) to select and weigh best performing models. We report effective sizes and 95% confidence intervals for each predictor variable

Compared with non-gazetted forest fragments, gazetted fragments were characterized by taller trees and a trend for higher levels of tree species richness and tree species diversity. Non-gazetted forest fragments were also characterized by a higher vegetation within the ground and shrub layer. For sweep net samples we found that daily and seasonal maximum temperature showed a strong influence on arthropod abundance. Nevertheless, vegetation structure also appeared to have a positive influence on arthropod abundance. Furthermore, we found a negative influence of fragment size on arthropod abundance from visual counts.

Influence of human presence and activity and spatial factors on vegetation structure

Although the legal framework in Kenya prohibits the cutting of indigenous trees (GoK, 2016; KMEF, 2018), our study showed that human activity and presence at both the landscape and plot level are influential in explaining the spatial patterns of vegetation structure such as canopy cover index, shrub cover, tree height, tree species richness and tree species diversity that have been widely used to characterize undisturbed natural forests (Şekercioğlu 2002; Wekesa et al. 2019; Wilder et al. 1998). The negative relationship between human activity and presence and vegetation structure suggests that both past and recent human impacts determine forest structure within the Taita Hills. Firstly, the selective large-scale historical exploitation of large trees for commercial purposes before the enactment of forest conservation policies left canopy gaps and reduced tree species richness and diversity (Beentje 1988; Pellikka et al. 2018; Thijs et al. 2015). Secondly, the current and ongoing illegal exploitation, which may be suppressing forest regeneration at the canopy gaps and replacement of old trees through selective cutting of pole-sized trees, which might often be juvenile canopy species. Large-scale exploitation of the Taita Hills forests happened during the construction of the railway between 1898 and 1924, as well as the period before the enactment of the presidential decree in 1977 that prohibited the unlicensed cutting of indigenous forests (Beentje 1988; Hildebrandt 1877; Pellikka et al. 2009). The negative influence of anthropogenic land cover on vegetation cover within the shrub layer (vegetation at a height of 1–5 m), but no effect on DBH of larger trees (> 10 cm), indicates that local communities maybe particularly extracting smaller sized trees (DBH < 10 cm) and shrubs, from the forest fragments. These findings are supported by other studies in African tropical forests, which demonstrate that subsistence harvesting pressure in tropical forests involves the removal of trees with a small DBH (usually < 10 cm) which are used for fencing and building or firewood (Borghesio 2008; Hall et al., 1986; Paul et al. 2004; Schwartz et al., 2003). Moreover, Paul et al. (2004) found that selective logging of immature pole-sized trees exerted pressure on certain tree species thereby decreasing the potential for canopy regeneration and normal forest succession. This might be an explanation for our findings of low values of canopy cover index and shrub cover, and tree species richness and diversity in areas with high human presence and activity. While our findings suggest that human activity maybe contributing to suppression of normal forest development and reduction of tree species diversity, our survey methods did not include the identification of the tree species that local people harvested. Future studies may therefore aim to identify the tree species that are harvested and quantify the harvesting intensity to evaluate their effects on the regeneration of understorey and emergent canopy species.

Edges of forest fragments are susceptible to extreme weather, such as strong winds and high temperatures, which increase the incidences of tree falls and desiccation of roots and seedlings (Laurance et al. 1998; Martinez-Ramos et al. 2016). Consequently, forest edges in fragmented areas are characterized by open canopies and low seedling recruitment, especially for low-light demanding and heat intolerant forest-interior tree species, but may favour the proliferation of light demanding and heat adaptable edge species (Campbell et al. 2018; Laurance et al. 1998; Martinez-Ramos et al. 2016). In line with this our study indicated that shrub cover increased, and canopy cover index decreased at the forest edge. The edge effects were similarly conspicuous in small-sized forest fragments in that index of canopy cover, tree height, tree species richness and tree species diversity decreased with decreasing forest sizes, which echoes the findings of other studies in fragmented tropical forests (Cardelus et al. 2019; Wekesa et al. 2019) and is also in line with another study in the Taita Hills that found that small fragments have lower tree species diversity and are dominated by early-successional tree species (Thijs et al. 2014). The legal framework governing how forest products should be utilized and the administrative status of the forest may determine the rate and level of forest loss and degradation (Krishnadas et al. 2018; Luoga et al. 2002; Nzau et al. 2020; Wekesa et al. 2020). Forest fragments in the Taita Hills have different management statuses: they are either gazetted as protected areas by the national government through the KFS or non-gazetted but managed by the County government as community forests (GoK, 2016; Pellikka et al. 2009; Wekesa et al. 2020). Gazettement status appeared as important predictor of variation for several vegetation variables, albeit often in the second-best model only, in addition to or replacing fragment size or distance to the forest edge (i.e., tree species richness and diversity, shrub cover). Thus, although the effect of fragment size on vegetation structure appeared to be stronger, forest gazettement may contribute to a more intact vegetation structure as well because gazetted forests exhibited better vegetation structure values (taller trees, higher tree species diversity and lower vegetation at the ground and shrub cover) than non-gazetted community forests under the management of the county government. Our findings also agree with previous studies in the Taita Hills by Wekesa et al. (2020), who found that forest cover loss was higher in non-gazetted fragments than in gazetted forests in the period between 1987 and 2016. Wekesa et al. (2020) suggested that the poor status of non-gazetted forests in the Taita Hills may be linked to the lack of enough county government personnel who can monitor forest exploitation within the community forests.

Influence of vegetation structure and spatial factors on forest understorey arthropods

In forested habitats, plant communities and their physical structure influence the distribution and abundance of organisms (e.g., Amorim et al. 2022). In accordance with other studies (Knuff et al. 2020; Muller et al. 2018) we found higher arthropod abundance with an increasing diversity of vegetation layers (VVH). Multi-layered vegetation stands have higher leaf biomass that can provide more resources for a higher number of arthropods than single-layered vegetation stands (Dial et al. 2006). Therefore, resource competition among arthropod species may be lower in multi-layered stands because resources, in the form of leaf biomass, are equally distributed (McGlynn et al. 2010; Muller et al. 2018). Additionally, the persistence of a high abundance of individual species in multi-layered forests may arise

from the climate buffering effect of such stands, because the upper canopy shields the lower strata from harsh climatic conditions, such as strong sun or rain (Muller et al. 2018; Scheffers et al. 2014). The present study involved sampling of arthropods within the shrub layer (height of 1–5 m) only (similar to Knuff et al. 2020), which may also profit from the shelter provided by the upper vegetation layers. However, the positive effect of vegetation structure on arthropod abundance was only found in the largest sample, but not in the smaller samples obtained through visual counts and FITs. As we were sampling within the indigenous forest only, this may not be surprising, as the here measured continuum of degradation in vegetation structure is not as severe as when different forest types, e.g., indigenous forest vs. plantations, are compared (Seifert et al. 2022). Furthermore, a recent study in Central Amazonian tropical forest suggested that the abundance of different insect orders varies across different levels of the forest strata (Amorim et al. 2022) and thus degradation of vegetation structure may affect arthropods differently in different forest strata.

In addition, although, vegetation structure had a positive influence on arthropod abundance, the effects of daily maximum temperature and average seasonal maximum temperature were much stronger. Arthropods are ectotherms and therefore their metabolism and activity depend on ambient temperature (Mellanby 1939). Thus, as they are more active during warmer days, higher catching rates can be expected, which may have weakened the effect of vegetation structure on arthropod abundance. In addition, we also found a negative effect of average seasonal maximum temperature on arthropod abundance suggesting an important influence of yearly variation in temperature on arthropods with potential impacts on the breeding populations of insectivorous birds and other vertebrates (Lister and Garcia 2018). In combination with our results on the effects of vegetation structure on arthropod abundance it suggests that the combined effects of forest degradation and climate change may have detrimental effects on arthropods with potential impacts on the breeding populations of insectivorous birds and other vertebrates (Lister and Garcia 2018). Our results also point to higher arthropod abundance and diversity with decreasing fragment sizes. Small forest fragments are dominated by edge habitats and may thus have different vegetation composition and structure in comparison to larger fragments (Campbell et al. 2018; Laurance 2004; Martinez-Ramos et al. 2016). As discussed earlier, forest edges can be considered as sites that are constantly recovering from disturbances related to edge effects (e.g., open canopies resulting from tree falls, rapid increase of light-demanding plants; Laurance 2004; Laurance et al. 1998) and thus have a higher density of fast-growing pioneer shrub and herbaceous vegetation than forest interior (Campbell et al. 2018; Laurance et al. 1998; Martinez-Ramos et al. 2016), which may lead to high turnover of differently specialized arthropods due to increased and/or higher diversity of food resources (Morante-Filho et al. 2016). This is in line with our study as we also found that index of canopy cover was lower and tree height tended to be shorter in smaller fragments than in large ones while vegetation cover within the shrub layer was higher in areas close to the forest edge. However, arthropod species that prefer forest interior may be less abundant in the forest edges as found in Schmitt et al. (2020), but classifying arthropods based on their habitat specialization was not within the scope of our study.

Conclusion

In this paper, we demonstrate that human presence and activities within the indigenous forest and a high proportion of anthropogenic land-use in the vicinity of the indigenous forest correlate with a simplified vegetation structure. Consistent with findings of other studies, we also showed that vegetation structure simplification may be amplified in smaller fragments (Campbell et al. 2018; Laurance et al. 1998; Martinez-Ramos et al. 2016). Additionally, we provide evidence that gazettement of forest fragments as protected reserves may be an effective management strategy because gazetted forests appeared to be in better condition than non-gazetted ones. Taken together our findings suggest that ongoing extraction of forest products for subsistence use by the local people affects forest structure and may be exacerbating forest degradation in the Taita Hills.

Our findings also suggest that forest degradation in the Taita Hills negatively affects the abundance of arthropods in the forest understory, which may have upstream effects on insectivorous birds. Although food resources for birds in form of arthropods may not be deprived in edge dominated small-sized fragments, because numbers peaked in such fragments perhaps due to proliferation of fast-growing successional vegetation (Morante-Filho et al. 2016), this may not benefit insectivorous forest specialists. These are adapted to moist and dark forest interiors and thus may not be physiologically adapted to higher temperatures at the forest edges (Dongmo et al. 2021; Frishkoff et al. 2015). Thus, maintaining a healthy forest structure within the forest interior for highly threatened insectivorous species in the Taita Hills is paramount. Encouraging local communities to plant trees in their farmland may reduce their dependency on forest resources (Wekesa et al. 2021). In addition, we recommend research on indigenous trees that may fulfil this function as exotic trees support less indigenous biodiversity (Seifert et al. 2022). We further recognize that arthropod communities in tropical forest are not well understood (Amorim et al. 2022) and recent studies have uncovered an alarming global decline of arthropods which is propagated by habitat loss, habitat degradation and climate change (Lister and Garcia 2018). More detailed studies on arthropod abundance and distributions in fragmented and degraded tropical forests are therefore urgently needed.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10531-023-02652-5>.

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Authors' contributions G.N.K. analyzed the data and wrote the first draft of the manuscript. M.K., K.M., T.S. and B.A., collected the data. M.G. facilitated data collection. G.N.K., L.C., M.G., J.C.H., C.S., M.T., L.C. and B.A. conceptualized the study. All authors contributed to the revision of the subsequent drafts and approved submission of the final manuscript.

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Data availability The datasets generated and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors declare no competing interests.

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Authors and Affiliations

Gladys Nyakeru Kung'u^{1,4} · Laurence Cousseau^{2,4} · Mwangi Githiru^{3,4} · Jan Christian Habel¹ · Mwangi Kinyanjui⁵ · Kennedy Matheka⁶ · Christine B. Schmitt⁷ · Tobias Seifert¹ · Mike Teucher⁸ · Luc Lens² · Beate Apfelbeck^{1,4}

✉ Gladys Nyakeru Kung'u
gladys.kungu@stud.sbg.ac.at

- ¹ Evolutionary Zoology Group, Department of Environment and Biodiversity, University of Salzburg, Hellbrunnerstr. 34, Salzburg 5020, Austria
- ² Terrestrial Ecology Unit, Ghent University, K. L. Ledeganckstraat 35, Ghent 9000, Belgium
- ³ Wildlife Works, P.O. Box 310-80300, Voi, Kenya
- ⁴ Department of Zoology, National Museums of Kenya, Museum Hill Road, P.O. Box 40658-00100, Nairobi, Kenya
- ⁵ Department of Natural Resources, Karatina University, P.O. Box 1957 – 10101, Karatina, Kenya
- ⁶ Botany Department, East African Herbarium, National Museums of Kenya, Museum Hill Road, P.O. Box 40658 – 00100, Nairobi, Kenya
- ⁷ Chair of Physical Geography with a focus on Human-Environment Research, University of Passau, Passau, Germany
- ⁸ Department of Geoecology, Institute of Geosciences and Geography, Martin Luther University, Halle-Wittenberg, Von-Seckendorff-Platz 4, D-06120 Halle/Saale, Germany