


## ORIGINAL ARTICLE

# 30 years brings changes to the arthropod community of Kibale National Park, Uganda

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## Abstract

World-wide declines in arthropod abundance and diversity are a major concern, particularly given their importance in ecosystem functioning. Yet, data documenting long-term trends are rare from the tropics, particularly the Afrotropics. Here we evaluate changes in the arthropod communities in Kibale National Park, Uganda across almost four decades. Systematic sweep-net sampling was conducted in two forested sections of the park that had been logged and in one old-growth forest area over 12 consecutive months in 1983/1984 and 2020/2021. This data was augmented with intermittent samples taken in 1986 and 1995. Arthropod abundance declined in all areas, but only significantly so in the moderately logged forestry compartment (41%). Permutational multivariate analysis of variance indicated that community compositions of arthropods differed between the censuses. Understanding the drivers of changes in the arthropod communities is difficult as the system is complex and dynamic. We document an increase in temperature, but no change in rainfall, increases in 11 mammal species, including a marked increase in elephant numbers, and changes in forest structure. We also report on changes in the landscape outside of the park, which includes the human population increasing by a factor of four and agricultural intensification that now includes the use of pesticides. We document that many components of the ecosystem we studied changed simultaneously, which signals that for effective conservation planning, more long-term multi-disciplinary efforts are needed.

## KEYWORDS

arthropod decline, climate change, forest dynamics, insect conservation, long-term monitoring, species conservation

## 1 | INTRODUCTION

Long-term reductions in arthropod biomass (Hallmann et al., 2017), abundances (Seibold et al., 2019; Warren et al., 2021), population sizes (Conrad et al., 2006), and species richness and diversity (Salcido et al., 2020; Valtonen et al., 2017) have been reported globally.

Evidence of declines is supported by meta-analyses and reviews (Dirzo et al., 2014; Habel et al., 2019; Potts et al., 2010; Sánchez-Bayo & Wyckhuys, 2019; Van Klink et al., 2020; Wagner, 2020), as well as comparisons of current and past arthropod communities (Akite et al., 2015; Hallmann et al., 2021; Lister & Garcia, 2018); but see (Crossley et al., 2020; Schowalter et al., 2021; Willig & Presley, 2022).

However, most information on long-term arthropod trends comes from Europe (Sánchez-Bayo & Wyckhuys, 2019; Wagner, 2020), while tropical areas are poorly studied (Lister & Garcia, 2018; Salcido et al., 2020; Schowalter et al., 2021). Notably, there is very little information from the Afrotropics (Akite et al., 2015; Wagner, 2020).

The major causes of arthropod declines are habitat loss and degradation, use of pesticides, climate change, and invasive species (Fox, 2013; IPCC, 2022; Wagner, 2020). Currently climate change modeling project that 49% of insect species are at risk of becoming endangered, or worse (IPCC, 2022). One of the most important threats is clearing of tropical forests (Wagner, 2020), where most of our globe's arthropod species live (Stork, 2018). Globally, ~60 million ha of tropical primary forest were lost from 2002 to 2019 (Weisse & Gladman, 2020). To put this in perspective, an area of old-growth tropical forest larger than Madagascar was lost in 18 years. A large proportion of studies reporting arthropod declines in the tropics have been done in protected areas where they may be buffered from some adverse effects, such as pesticide use and invasive species (Akite et al., 2015; Janzen & Hallwachs, 2021; Salcido et al., 2020). Even if not directly threatened by forest clearing, the arthropod populations living in tropical protected areas often suffer from overall habitat fragmentation and isolation (Fahrig, 2017) leading to extinction debts and local extinctions in the long-term (Kuussaari et al., 2009). Presently, large areas of intact tropical forest are rare outside the Amazon and Congo Basins (Chapman & Peres, 2021) and many species are negatively impacted by edge effects (Chapman et al., 2006; Fahrig, 2017).

A considerable body of research has pointed to climate change as a likely cause of arthropod declines in the tropics (Janzen & Hallwachs, 2019; Lister & Garcia, 2018; Salcido et al., 2020) (but see (Schowalter et al., 2021)). Tropical arthropods could be particularly vulnerable to climate warming due to their narrow thermal tolerances (Deutsch et al., 2008) and the high physiological costs that high temperatures inflict on them. Furthermore, changes in precipitation patterns could drive tropical arthropod declines (Salcido et al., 2020).

Agricultural intensification and the use of pesticides is also considered to be directly related to arthropod declines (Raven & Wagner, 2021). Pesticides negatively impact arthropod populations, directly due to drifting insecticides (Geiger et al., 2010), or indirectly by the elimination of important nectar sources and/or larval food plants with herbicides (González-Varo et al., 2013).

In summary, tropical forests support high levels of arthropod diversity, yet studies evaluating long-term changes in diversity and abundance in arthropod groups in tropical areas are very scarce. To address this crucial knowledge gap, we evaluate changes in the arthropod community in Kibale National Park, Uganda across almost four decades in relation to various environmental factors. Systematic sweep-net sampling was conducted over 20 consecutive months in 1983/1985 and 13 consecutive months 2020/2021 and this data was augmented with samples taken in 1986 and 1995. Samples were collected in two forested sections of the park that had been logged to different intensities and in one old-growth forest

area. Environmental factors that we evaluate are changes in rainfall and temperature, mammal abundance, tree community structure, and the agricultural intensification of the surrounding landscape that included the use of pesticides.

## 2 | METHODS

### 2.1 | Study site

Kibale is a 795 km<sup>2</sup> national park located in western Uganda (0° 13' – 0° 41' N and 30° 19' – 30° 32' E) near the foothills of the Rwenzori Mountains (Chapman & Lambert, 2000). The park is dominated by mid-altitude (920–1590m), moist-evergreen forest and near the study sites the area receives a mean annual rainfall of 1646mm (1970–2020), in two rainy seasons (from early March to May and from late August to early December) (Chapman et al., 2021).

Kibale received national park status in 1993. Prior to this, it was a forest reserve and a game corridor, gazetted between 1926 and 1932, with the stated goal of providing sustained hardwood timber production and game (Chapman et al., 2005; Osmaston, 1959; Rode et al., 2006; Struhsaker, 1997). Prior to the 1920s, it was a hunting reserve for nobility (Mackenzie, 2012). The study was conducted in three former forestry compartments in the vicinity of Makerere University Biological Field Station. The two areas to the north of the field station (K15, K14) were logged in the 1960s, while the compartment to the south (K30) has not been disturbed in recorded history. In the K15 (347ha) forestry compartment harvest averaged 21 m<sup>3</sup> ha<sup>-1</sup> or approximately 7.4 stems ha<sup>-1</sup> from September 1968 through April 1969 (Skorupa, 1988; Struhsaker, 1997). Damage caused by the logging operation killed approximately 50% of all trees (Chapman & Chapman, 1997; Skorupa, 1988). Immediately to the south is K14 (405ha) that was logged at low intensity (14m<sup>3</sup>/ha or 5.1 stems/ha) from May through December 1969. Here, approximately 25% of the trees were destroyed by the logging (Skorupa, 1988, Struhsaker, 1997). Regeneration in these areas has been slow (Bonnell et al., 2012; Chapman & Chapman, 1997; Lawes & Chapman, 2006; Osazuwa-Peters et al., 2015). Immediately to the south of K14 is an old-growth area that has not been logged or disturbed in recent times (K30–282ha). However, potsherds and grinding stones have been found in this compartment and those just to the south (Chesterman et al., 2019; Isabirye-Basuta & Lwanga, 2008; Mitani et al., 2000). The decorations on the pottery are typical of the period between 200 and 400 years ago (Isabirye-Basuta & Lwanga, 2008). Thus, it seems likely that the forest has been impacted by human activities prior to when written records were kept.

A description of the tree community and maps of these forestry compartments can be found in the publications of Chapman, Nummelin, and Struhsaker (Balcomb & Chapman, 2003; Chapman et al., 2005, 2021; Chapman & Chapman, 1997; Chapman, Chapman, et al., 2010; Nummelin, 1996; Nummelin & Fürsch, 1992; Nummelin & Zilihona, 2004; Struhsaker, 1997). Nummelin et al.

describe the arthropod community in the study sites during 1983–85 (Nummelin, 1996; Nummelin & Borowiec, 1992; Nummelin & Fürsch, 1992; Nummelin & Hanski, 1989; Nummelin & Zilihona, 2004) and Nummelin (1992) describes the field layer vegetation in 1983–84. Molleman et al. (2022) and Valtonen et al. (2013) describe the fruit-feeding butterfly community.

Human population density surrounding the park is high and increasing rapidly. Between 2000 and 2020 the population within 1 km of the park's boundary almost doubled, going from 123 to 229 people/km<sup>2</sup> (Hartter et al., 2012; Mackenzie, Salerno, Chapman, et al., 2017; WorldPop, 2020). The people are typically smallhold farmers, cultivating less than 5 ha, to grow staple foods, such as bananas, maize, beans, and cassava. Some people also cultivate cash crops, such as tea, eucalyptus, and coffee (Mackenzie, 2012; Mackenzie & Hartter, 2013; Sarkar, Andris, et al., 2019; Sarkar, Chapman, et al., 2019). Tea plantations cover an area of more than 22 km<sup>2</sup> within 2.5 km of the park's edge (Bortolamiol et al., 2013).

Local farmers and the tea plantations both have recently begun to use pesticides. Several pesticides have been found in the surrounding environment. DDT, and its main metabolite p-p'-DDE, and insecticides, such as the organophosphate chlorpyrifos, are found at levels exceeding tolerable daily intake. Other pesticides such as 2,4-D amine, glyphosate, and imidacloprid are used in these surrounding farms and industrial tea plantations and are detected in significant quantities in fresh maize seeds (Wang et al., 2020). Fish collected from rivers in the park are contaminated with chlorpyrifos, p,p'-DDE, and imidacloprid (Krief et al., 2017; Spirhanzlova et al., 2019). Air samples collected in the park detected  $\alpha$ -HCH, HCB,  $\gamma$ -chlordane, heptachlor epoxide, BDE-47, BDE-99, BDE-100, BDE-209, DPs, TNBP, and TCIPP (Wang et al., 2019) and these compounds plus  $\beta$ -HCH, p,p'-DDE, o,p'-DDD, and o,p'-DDT were found in primate feces (Wang et al., 2020).

At the current time there is a large tea plantation just to the west and upstream from the K14 area and it is currently applying glyphosate herbicide (trade name: Round up) for managing their weeds, primarily *Commelina benghalensis* L. and *Bidens pilosa* L. (Kiko tea plantation manager's personal communication). This herbicide is applied at 0.25 L/ha over an area of 275 ha at 55-day intervals, and they use approximately 500 L a year. The tea is not attacked by any major insect pest, so they do not use insecticides.

## 2.2 | Environmental data

For both periods (1983/1985 and 2020/2021), daily rainfall data were collected immediately adjacent to the study area and summarized per month. The data from the 1980s were collected by the Kibale Forest Project (lead by Tom Struhsaker), while members of our team collected the later data. Temperature data (daily minimum,  $T_{\min}$ , and daily maximum,  $T_{\max}$ ) were also collected on the ground. However, thermometers had to be replaced and relocated several times between the two periods and an analysis of the temperature

data from 1970 until 2020 indicated that these changes had impacts on measured temperature that were challenging to control for. Therefore, we used monthly minimum ( $T_{\min}$ ) and monthly maximum temperature ( $T_{\max}$ ) from the CRU TS v. 4.06 dataset (<https://cruta.ta.uea.ac.uk/cru/data/hrg/>; (Harris et al., 2020)) for our comparison.

Changes in large animal populations can directly affect invertebrate populations through predation or by modifying the forest environment (Chapman et al., 2013; Omeja et al., 2014; Smart et al., 1985). We have assessed changes in the populations of 11 mammal species over 23 years and this information can be found in our previous publications (Chapman, Struhsaker, et al., 2010; Hou et al., 2021; Omeja et al., 2016; Sarkar et al., 2021). We present new detailed information on elephants as their foraging and trampling can significantly modify forest habitats (Coverdale et al., 2016; Smart et al., 1985; Struhsaker et al., 1996; Terborgh et al., 2016). Furthermore, elephant numbers in Uganda have been very dynamic as the result of planned culling, killing during periods of political instability, and immigration from neighboring countries (Eltringham & Maplas, 1980; Keigwin et al., 2016; Naughton-Treves, 1999).

Arthropod populations will be affected by the structure of the vegetation which modifies the environmental conditions, such as variation in temperature and humidity, and provides resources, such as host plants. In 1989, we established 26 permanent vegetation plots established in the study area. Each plot was 200 m  $\times$  10 m, providing a total sample area of 5.2 ha. We identified the species of each tree with a dbh >10 cm (measured at 1.2 m from the ground on the uphill side), individually marked each tree with a uniquely numbered aluminum tag and measured its dbh. Unfortunately, we did not assess the shrub layer in 1989. To assess if changes in the arthropod population could have been related to changes in the vegetation in the area, we resampled the plots in 2021. In the resurvey, we relocated all previously tagged trees to assess survival, remeasured them to quantify growth, and identified, tagged, and measured new trees recruiting into the >10 cm dbh size class.

## 2.3 | Sampling methods

Arthropods and snails were collected from each of the three forestry compartments with a sweepnet. The sweepnet was a standard 38-cm diameter arthropod net with a 61-cm handle (Janzen, 1973). During the years 1983–85 the net was made of local materials (bag heavy duty cloth, steel hoop and wooden handle) in later samples standard BioQuip (2021-<https://www.bioquip.com/search/DispProduct.asp?pid=7625HS>) nets were used (bag rugged sailcloth, steel hoop and wooden handle). In the years 1983–85 samples were collected by M. Nummelin, students of the field courses of the Makerere University and field assistants (Nummelin, 1992; Nummelin & Fürsch, 1992), in 1995 by M. Nummelin and students of the field course of the University of Helsinki (Nummelin & Zilihona, 2004), and in 2020–21 by E. Opito, P. Omeja, and field assistants with detailed instructions with video presentations by M. Nummelin (because of the ongoing covid-19 pandemic). This data was augmented

with three intermittent samples taken in 1986 and six samples taken in 1995.

Arthropod and snail samples were collected by sweep netting in all three sites monthly. One sample comprised 800 sweeps. Sweeping was done for continuous bursts of 50 sweeps, then arthropods were sprayed by insecticide before pouring them into the collecting bag. The exercise was repeated until the 800 sweeps were scored.

Half of the sweeps were taken from the sides of small single-person walking trails and the other half were taken from sites located into the forest from these trails. Sweeps were made only in places where the net could hit forest floor vegetation. Thus, open gaps in forest floor vegetation were avoided. Depending on the height of the vegetation, the minimum sweeping height varied from 20 to 80 cm. The net was brushed back and forth through the vegetation so that the dislodged arthropods fall into the net. Sweeping was done in all sites on the same day starting from 9 a.m. No sweeping was done on rainy mornings when the vegetation was wet. Arthropods were sorted into major taxonomic groups (Arachnida, Orthoptera, Hymenoptera, ants, Coleoptera, Diptera, Hemiptera, Lepidoptera, caterpillars) back at the field station and arthropods were divided into two classes: body length <1 cm and body length >1 cm. We also had an "other" category for less common taxa and this consisted mainly of Phasmatodea, Mantodea, and Dermaptera. For more details on the sweeping method see (Janzen, 1973). We only consider the larger body class size as we view this to be a conservative approach where any documented change would unlikely be due to methodological differences. While snail abundance is not typically measured using a sweep net approach, we report differences as the methods were the same across time, the differences were marked, and we hope our findings encourage more detailed research.

## 2.4 | Analysis

To account for seasonal variation in arthropod abundance between the 1983/1984 and 2020/2021 time periods, we used paired *t*-tests where the monthly capture number was paired by month. Analyses were conducted separately for each forestry compartment as it is possible that their history of disturbance would influence changes in arthropod abundance over time.

Patterns in arthropod community compositions (a total of 110 samples; 75 samples from 1983–1985 and 35 from 2020–2021, and three intermittent samples taken in 1986 and six intermittent samples taken in 1995) were visualized using non-metric multidimensional scaling (NMDS) (using package "vegan" (Oksanen, 2022) in R (R-Core-Team, 2021) (R Core Team 2021)). We fitted a permutational multivariate analysis of variance (PERMANOVA; type III sum of squares and 9999 permutations) model, to ask if the arthropod community compositions differ between the two censuses (1983–1985 vs. 2020–2021; fixed factor) or between the three compartments (fixed factor), or if there is a census × compartment interaction. Furthermore, the contribution of each taxon to the

dissimilarity between the two census periods was analyzed with SIMPER-routine. Prior to multivariate analyses, data was square-root transformed (to downweigh the influence of the most dominant taxa) and analyses were based on Bray-Curtis similarities among samples. PERMANOVA and SIMPER analyses were performed using PRIMER-E (version 6.1.15; (Clarke & Gorley, 2006)).

## 3 | RESULTS

### 3.1 | Environmental changes

Mean monthly minimum temperature ( $T_{\min}$ ) was higher in 2020–2021 (15.75°C) than in 1983–1984 (15.22°C,  $t = -3.6673$ ,  $p < .01$ ). Similarly,  $T_{\max}$  was also higher in 2021–2021 (27.18°C) than in 1983–1984 (27.01°C) but this difference was not significant according to the paired *t*-test ( $t = -0.95778$ ,  $p = .3571$ ). General trends in the region suggest that Kibale receives 300mm more rainfall per year than at the start of the century (Chapman et al., 2019) and that both  $T_{\max}$  and  $T_{\min}$  has increased by approximately 0.021°C/year and by 1.05°C over 50 years (Chapman et al., 2021).

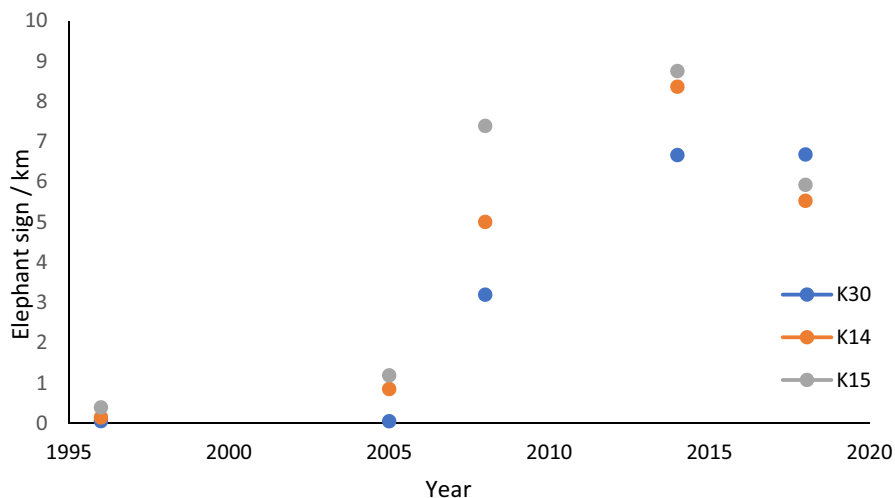
All of the primate species increased in abundance over the 23 years of monitoring. The pattern of increase was similar among the sites, and the increase averaged 4.56% across species and areas. Details are presented in (Sarkar et al., 2021). There was a similar increase in the ungulates (see Hou et al., 2021). Elephant numbers increased gradually over the first decade that we monitored them, then there was a sudden surge in numbers, likely due to immigration, and they have remained high (Keigwin et al., 2016; Omeja et al., 2014; Figure 1).

There was a slight increase in the number of trees >10 cm DBH in the vegetation plots in all forestry compartments. This corresponded to an increase in the cumulative DBH in logged K14 and K15 forestry compartment, but cumulative size of trees in K30 declined (Figure 2).

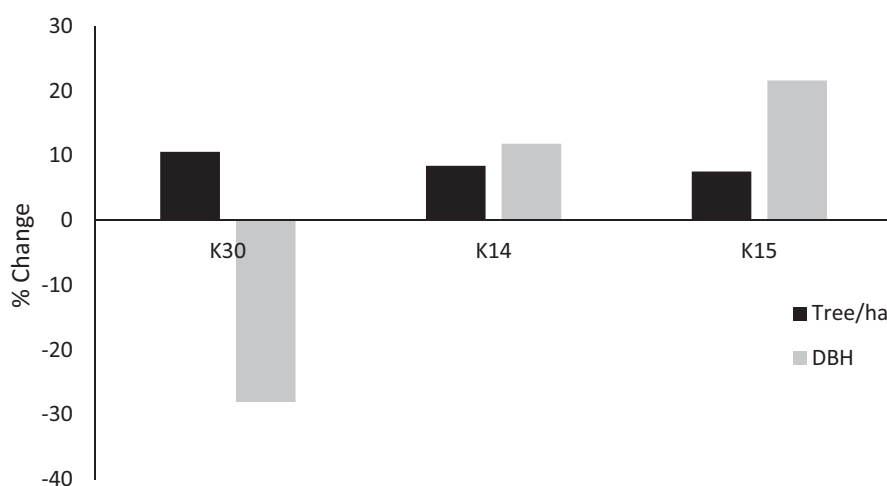
### 3.2 | Changes in the arthropod community

The number of arthropods caught each month in K14 declined by 41.0% between 1983–1984 and 2020–2021 ( $t = -3.87$ , d.f. = 12,  $p = .002$ ; Figure 3). There was a similar decline of 37.8% in K15, but this decline was not significant ( $t = -1.75$ , d.f. = 11,  $p = .108$ ). In the old-growth forest (K30), there was a small, nonsignificant, decline of 5.3% ( $t = 1.30$ , d.f. = 12,  $p = .219$ ). Snail abundance declined significantly in all areas between 1983–1984 and 2020–2021 (K14: 77.5% decline,  $t = -3.18$ , d.f. = 10,  $p = .010$ ; K15: 82.2% decline,  $t = -4.28$ , d.f. = 11,  $p = .001$ ; K30: 97.6% decline  $t = -5.85$ , d.f. = 12,  $p < .001$ : Figure S1 as Supplementary Material). Spatial variation in samples taken at the same time in same forest compartment is large (see Figure 3, samples in April 1985, and July 1995). However, the samples taken in the 1980s and 1990s were typically higher than those take in 2020 and 2021 (Figure 3).

**FIGURE 1** The average number of elephant signs found along 4 km transects sampled each month for 1 year in three forestry compartments in Kibale National Park, Uganda between 1996 and 2018. K15 was heavily logged, K14 was lightly logged, and K30 was not disturbed in recorded history.



**FIGURE 2** The percent change between 1989 and 2021 in the number of trees and the cumulative DBH of those trees found in permanent vegetation plots in three areas of Kibale National Park, Uganda that had experienced different levels of timber extraction in the 1960s. K15 was heavily logged, K14 was lightly logged, and K30 was not disturbed in recorded history.



Based on NMDS ordination, the arthropod community compositions of the two census times (1983–1985 vs. 2020–2021), and the three compartments largely overlap, indicating that the community compositions are not strongly distinct (Figure 4a,b). However, the community compositions differed significantly between the censuses (PERMANOVA; Pseudo- $F_{1,104} = 6.9$ ,  $p < .001$ ), and among the three compartments (Pseudo- $F_{2,104} = 2.4$ ,  $p = .006$ ). The census  $\times$  compartment interaction was non-significant (Pseudo- $F_{2,104} = 0.9$ ,  $p = .57$ ), indicating that the temporal change in the three compartments has been similar. Based on NMDS ordination, the main variation in the community compositions (Figure 4c; Axis 1) reflects the seasonal changes in the arthropod community; the two dry-season communities (January–March and July–September) being more distinct, with more intermediate rainy-season communities.

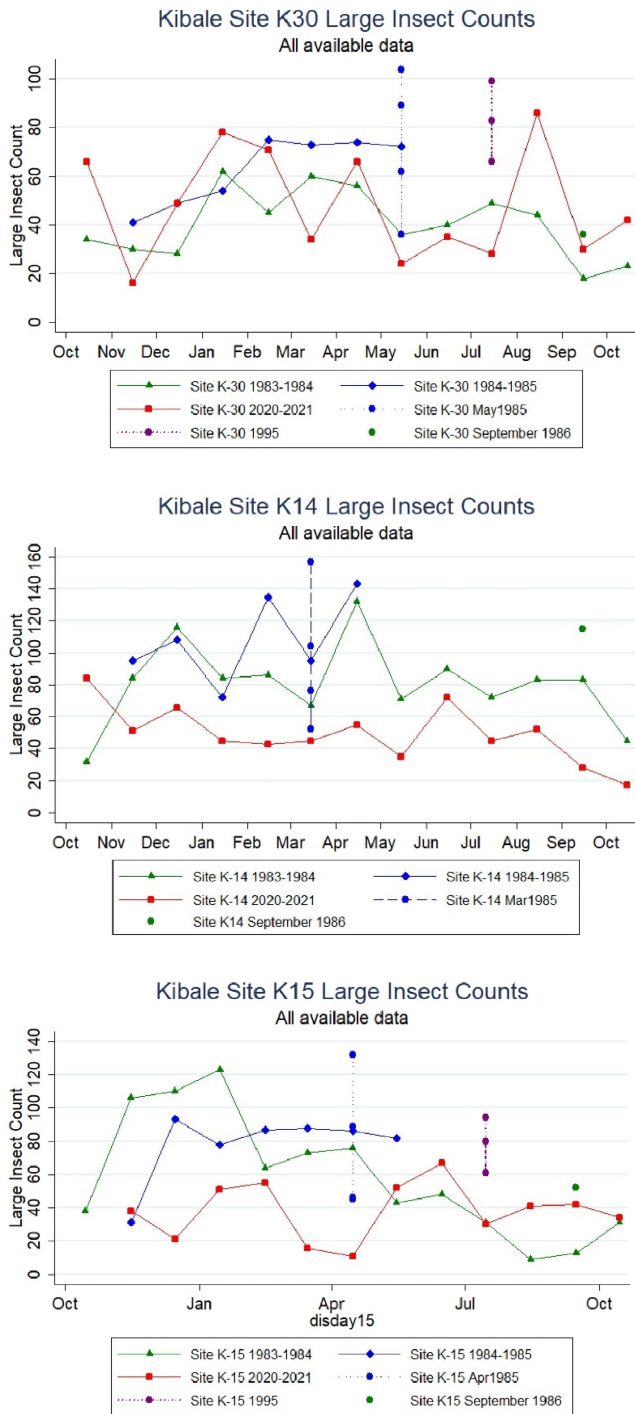
Based on SIMPER analysis, the differences in the community compositions between 1983–1985 and 2020–2021 were explained most strongly with caterpillars (Lepidoptera and Hymenoptera larvae) (14% contribution to dissimilarity), group “others” (13% – mainly of Phasmatodea, Mantodea, and Dermaptera), Orthoptera (13%), Hemiptera (11%), and adult Lepidoptera (10%). The average count of caterpillars (per 800 sweeps) has dropped from 15.5 (1983–1985) to 9.3 (2020–2021), count of group “others” from 8.3 to 2.3, count of

Orthoptera from 19.3 to 12.2, count of Hemiptera from 5.2 to 4.8, and count of adult Lepidoptera from 4.7 to 4.2.

## 4 | DISCUSSION

Our study reveals a complex pattern of change. Arthropod abundance declined in all areas, but only significantly so in the moderately logged forestry compartment. Changes were strongly driven by certain arthropod groups. Snail abundance markedly declined in all areas. There was a general increase in the mammal populations, and the increase was particularly marked for elephants that can strongly impact vegetation structure. There was a general increase in tree density over time, but in the old-growth forest the cumulative DBH of trees declined. This decline was likely the result of the loss of some very large trees and the trees recruiting into the treefall gaps they created have not reached the size we monitor. Finally, the park is now a large forest island embedded in a humanized landscape dominated by agriculture. In this landscape, human population density and agricultural intensification have increased dramatically between our two censuses (Mackenzie, Salerno, Hartter, et al., 2017). Over the last 40 years the landscape has been transformed from a





**FIGURE 3** The number of arthropods >1 cm found in sweep net sampling done in 1983–1984 and 2020–2021 (and in April 1985, and July 1995) in Kibale National Park, Uganda. The sites were immediately adjacent to one another; however, K15 was heavily logged, K14 was lightly logged, and K30 was not disturbed in recorded history.

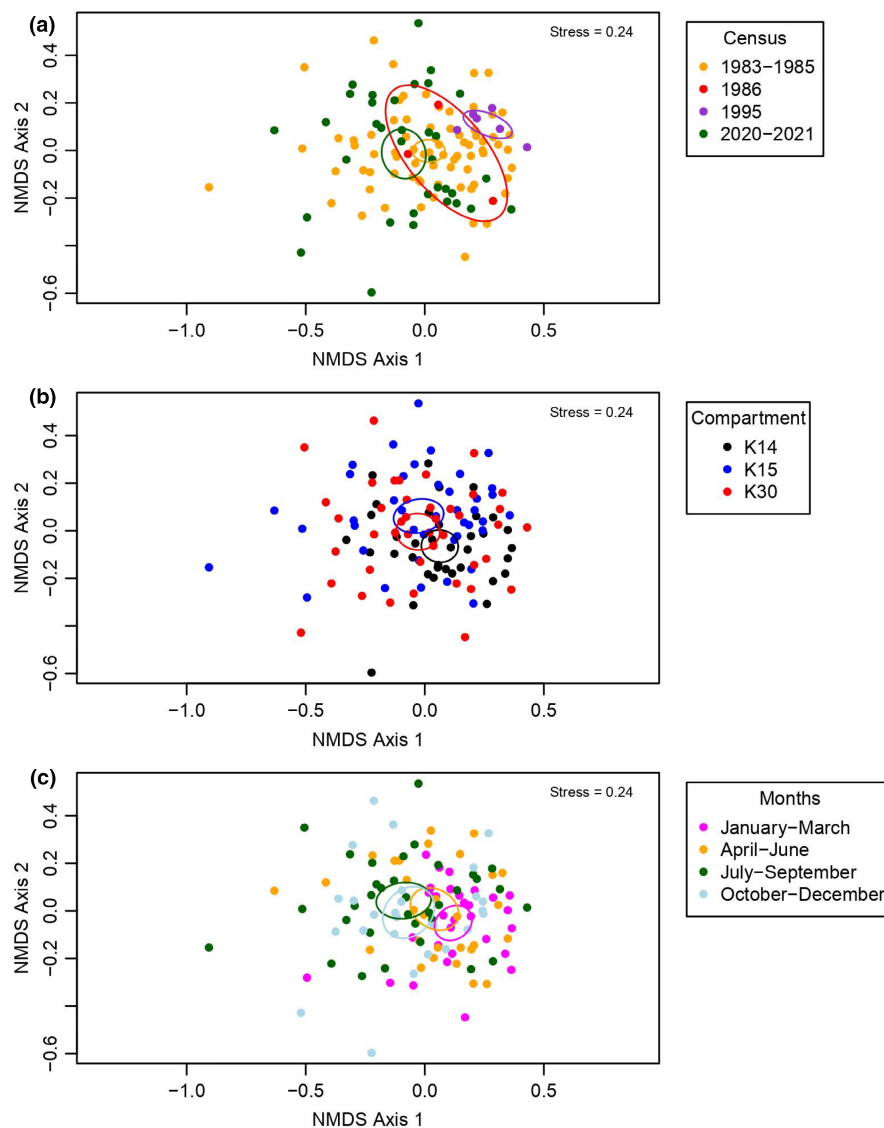
fallow agricultural system where pesticides and fertilizers were not used, to one where there is little land not under current production and where pesticides and herbicides are commonly used (Hartter et al., 2015).

Understanding the drivers of changes in the arthropod community in such a complex and dynamic system is difficult. Different taxa likely respond to these various changes in different ways and at different rates. For arthropods the census  $\times$  compartment interaction in the PERMANOVA was non-significant. This indicates that the temporal change in the three compartments has been similar and suggests that the differences in how the forest changed was not the driving factor determining arthropod community changes. The impact of increasing elephant numbers on arthropod number would likely have occurred through their actions on the plant community, thus it seems unlikely that they are driving the observed changes. Furthermore, elephants are generally most active in the heavily logged area (Keeble, 2022, Chapman unpublished data from 2022), but this area did not show the greatest declines in the arthropod community. Given the consumption rate of arthropods by primates (Rode et al., 2006), it seems very unlikely that they are driving the observed changes. The moderately logged area had the largest decline in large arthropod abundance. This area is immediately adjacent to the tea plantation that has increased its use of pesticides and herbicides, suggesting the effects of synthetic chemicals, warrants more research. The primates in Kibale are known to have been exposed to a variety of synthetic chemicals (Chapman et al., 2022; Wang et al., 2020), as are fish in the park's rivers (Krief et al., 2017).

Changes in arthropod and snail populations and compositions may be linked to increasing temperatures. As for all ectothermic animals, their body temperature is directly influenced by ambient temperature, and temperature has been shown to affect survival and reproduction in insects (Angilletta Jr & Angilletta, 2009). Tropical arthropods are particularly sensitive to increase in ambient temperatures due to their narrow thermal tolerances (Deutsch et al., 2008); even slight increases in temperature can exceed the critical thermal limits (Deutsch et al., 2008; Sunday et al., 2014; Tewksbury et al., 2008), possibly leading to local extinctions (Wiens, 2016). In addition, climate change may have indirect effects on arthropod and snail populations. For example, temperature and rainfall patterns show complex associations with plant phenological patterns, such as the timing of leaf flush and ripe fruit production (Brando et al., 2010; Chapman et al., 2018; Potts et al., 2020; Valtonen et al., 2013), which may, in turn, influence the survival and reproduction of animals that rely on plant food. Both direct and indirect effects warrant further investigations. For example, experimental set ups investigating the effects of varying temperature on survival and reproduction for arthropod and snail groups that declined the most in Kibale may reveal important insights whether this represents a potential pathway. With regard to indirect effects through food availability, systematically considering changes in the diet of the most and least impacted animal groups would help understanding the mechanism behind the observed changes.

Teasing apart the significance of potential drivers of change in the arthropod and snail abundance will require other innovative approaches. One approach that will be useful involves space-for-time substitutions (Blois et al., 2013). Here studies at one point in time of changes along a natural spatial gradient are used to mimic or

**FIGURE 4** The Non-metric multidimensional scaling (NMDS) ordination of arthropod communities in Kibale National Park, Uganda, where (a) the censused years, (b) the three compartments, and (c) the four seasons (January–March and July–September representing the dry seasons; April–June and October–December representing rainy seasons) are shown separately. Each symbol represents one sample (800 sweeps); the closer the symbols are in the ordination space, the more similar were the community compositions. Ellipses shown are the 95% confidence ellipses for location of the class centroids.



substitute for changes that occur over time. In Kibale, the north of the park is at a slightly higher elevation and is colder than areas to the south, and also elevational shifts in well-recorded taxa could be used to make inferences of effects of climate warming (Chen et al., 2009). Furthermore, we suspect there is significant spatial variation in the use of pesticides and herbicides, with use being greater in tea plantations. Studying spatial variation in these chemicals could reveal if they are contributing to the changes we documented.

Since local pesticide use can be managed locally, the use and effect of these chemicals warrant further study. Globally, approximately 2.3 billion kg of pesticides are used each year (Hayes & Hansen, 2017; Sharma et al., 2019). However, there should be elevated concern about pesticide use in tropical countries because as high-income countries restrict the use of environmentally damaging chemicals, these same chemicals are either exported to or manufactured by mid- and low-income countries and used with little restraint (Sanchez-Bayo & Hyne, 2011). Many of the older pesticides banned in high-income countries (i.e., legacy pesticides) have expired patents allowing them to be mass-produced in low-income countries.

These chemicals are then sold at cheaper prices than newer, presumably safer, chemicals (Biscoe et al., 2004). Furthermore, environmental regulations are often scant or not enforced in tropical countries (Landrigan et al., 2018). The use of pesticides is increasing in the tropics. In Africa, the import value of pesticides increased by 261% between 2000 and 2010 (Sharma et al., 2019). Since much of the importation is occurring through non-regulated routes, the use of pesticides is likely much higher. Take Uganda for example. Agriculture contributes approximately 25% of the country's Gross Domestic Product and employs more than 70% of the labor workforce (Wiedemann, 2022). Official statistics indicate an increase in pesticide use from \$7 million in 1995 to \$67 million in 2017 (FAO, 2022). This is an alarming rise, but it still signals a relatively low pesticide application rate. Despite this the European Union has issued repeated warning to Uganda regarding chemical residues in exported agro-imports (Isgren & Andersson, 2021).

There were increases in all the mammal populations that were monitored. This speaks very highly of the efforts of the Uganda Wildlife Authority and their collaborators used over the last four

decades. However, the fact we have documented declines in arthropod populations, means that more attention needs to be given to factors such as climate change and pesticide use and strategies that address these threats need to be put into place.

Our work contributes to understanding how human actions are impacting natural systems and highlights the importance of long-term multi-disciplinary research. If there are only a few samples taken years apart, as is the case with our study, it is possible that what appears to be large changes, represent natural oscillations or that some species were simply missed in one of the surveys (Freeman et al., 2018). To understand drivers of population change requires identifying a signal that is greater than stochastic variation caused by minor ecological or demographic variation, events that are largely stochastic, and sampling error associated with having only a few timepoints.

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## CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Edmond Open Research Data Repository: <https://doi.org/10.17617/3.6J4ZA0> (Opito et al., 2023).

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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