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RESEARCH ARTICLE

Climate-Driven Vegetation Characteristics Shape Phytophagous and Carnivorous Insect Diversity in South African Savannahs

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ABSTRACT

Aim: Despite the evidenced importance of insects in savannah ecosystems, the drivers of their diversity patterns remain poorly understood, particularly in the Afrotropical region. This study addresses part of this gap by investigating the effects of climate, habitat, disturbance and vegetation variables on species richness and community composition of phytophagous and predatory insects in South African savannahs.

Location: Kruger National Park (KNP), South Africa.

Taxon: Phytophagous insects (moths) and carnivorous insects (mantises).

Methods: Moths and mantises were light-trapped in 60 plots distributed across KNP during two seasons. Direct and indirect effects of environmental variables on insect species richness were analysed using structural equation models, and on community composition through distance-based redundancy analyses (db-RDA).

Results: Based on an extensive dataset of 65,593 moth individuals representing 817 species and 3511 mantis individuals representing 38 species, we identified plant communities as the primary driver of species richness and community structure for both insect groups. The effects of vegetation on insect communities were indirectly shaped by climate, particularly mean temperature (negatively correlated with precipitation), through its effects on plant species richness. Additionally, a complex interplay among bedrock type, water availability and disturbance from large herbivores further shaped insect diversity.

Main Conclusions: Our findings highlight the critical role of plant species richness in determining insect diversity patterns in savannah ecosystems. We also confirmed the region's vulnerability to climate change, as decreasing precipitation and increasing temperatures alter vegetation composition and biomass, consequently affecting insect communities. Effective conservation strategies should focus on managing large herbivores to maintain diverse vegetation, which is crucial for supporting insect diversity.

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Priority should be given to balancing water availability and disturbance intensity, particularly in preserving the health of rivers and their surroundings, to mitigate the adverse effects of climate change on these ecosystems.

1 | Introduction

Biodiversity patterns are shaped by numerous environmental factors, including climate, resource availability and biotic interactions (Gaston 2000; Wisz et al. 2013; Peters et al. 2016). In savannah ecosystems, large herbivores, fire disturbances and climatic conditions are among the fundamental biodiversity drivers across spatial and temporal scales (Pickett et al. 2003; Gaget, Parr, and Sirami 2020; Araújo and Oliveira 2021). Previous research on savannah biodiversity has predominantly focused on plants (e.g., Staver, Botha, and Hedin 2017; Hejda et al. 2022) and vertebrates (e.g., Ogada et al. 2008; Davies et al. 2016), often neglecting the drivers of insect diversity, despite their critical roles as pollinators, prey, predators, herbivores and decomposers (e.g., Dennis, Kemp, and Denno 2008; Davies et al. 2012; Castagneyrol et al. 2017; Tonelli et al. 2018).

In savannah ecosystems, plant communities play a key role in determining insect distribution and diversity (e.g., Leal et al. 2016; Parker et al. 2023). According to the resource specialisation hypothesis, high plant diversity provides resources for more herbivorous insect species (e.g., Du et al. 2020). Furthermore, diverse plant communities offer a variety of microclimatic conditions and niches that support both herbivorous and non-herbivorous insect groups (e.g., Price 2002; Randlkofer et al. 2010). Numerous studies in savannah ecosystems have demonstrated a positive relationship between plant diversity and various phytophagous insect taxa, including butterflies in Australia (e.g., Leone et al. 2023), grasshoppers in South Africa (e.g., Gebeyehu and Samways 2002), and omnivorous insects such as ants in South Africa (e.g., Mauda et al. 2018). This relationship also extends to predatory and parasitic arthropods in South African savannahs (e.g., Procheş and Cowling 2006; Botha, Siebert, and Van den Berg 2017). However, in other studies abiotic factors appeared to have stronger effects on insect diversity than plant communities (e.g., Koricheva et al. 2000; Scherber et al. 2006; Axmacher et al. 2009; Prather et al. 2020; Smith and Williams 2023). These findings underscore the need to consider a broader range of factors when explaining insect diversity patterns.

The interplay between insect and plant diversity in savannahs is intricate, being influenced directly and indirectly by climatic conditions, soil chemistry, water and nutrient availability, or disturbances from large herbivores and fire (e.g., Shi et al. 2018; Li et al. 2021). As small-bodied ectotherms, insects are particularly sensitive to environmental temperature which is assumed to drive their species richness patterns through physiological constraints in harsh climate (Currie et al. 2004; Kaspari et al. 2019) or through temperature-dependent resource exploitation (Brown 2014). While some studies have identified environmental temperature as a primary driver of insect diversity across biomes (e.g., Dunn et al. 2009; Chesters et al. 2019), others focusing on savannah ecosystems have found rainfall to be a more reliable predictor, showing strong correlations with insect species richness (Parr et al. 2004; Vasconcelos et al. 2018). For example, Delabye et al. (2022a) described a significant increase in moth diversity along a longitudinal gradient of environmental productivity in South African savannahs, predominantly influenced by precipitation distributed independently of environmental temperature. Zhu et al. (2014) experimentally revealed declines in species richness and abundance across multiple insect groups in response to both increased and decreased precipitation in a meadow steppe in China. Conversely, Andersen, Del Toro, and Parr (2015) reviewed that ant diversity in tropical savannahs correlates globally with both temperature and rainfall.

Disturbances from fire and large vertebrate herbivores also drive biodiversity patterns in savannahs (Bond and Keeley 2005; Joern and Laws 2013). These disturbances not only directly cause insect mortality during fires but also indirectly affect its diversity across trophic levels by altering plant growth, community structure and diversity (e.g., van Klink et al. 2015; Osborne et al. 2018; Mukwevho, Dalu, and Chidawanyika 2023; Mukwevho et al. 2024, 2025). Research on the impact of large herbivores and fire on insect diversity has yielded mixed results, reflecting the diverse responses of insect groups to these disturbances (e.g., Mukwevho, Dalu, and Chidawanyika 2023; Mukwevho et al. 2025). For example, beetles may respond negatively (e.g., Jonsson et al. 2010; Reinhard, Geissler, and Blaum 2019), while grasshoppers and butterflies may exhibit positive responses to habitat opening (Joubert, Pryke, and Samways 2016; Bonnington, Weaver, and Fanning 2008; Pryke, Roets, and Samways 2016; Topp, Tscharntke, and Loos 2022). The magnitude of these responses depends on the intensity, frequency and interannual variability of the disturbances (Jonsson et al. 2010; Coetsee et al. 2019; Korell et al. 2021; Mukwevho, Dalu, and Chidawanyika 2023; Mukwevho et al. 2024).

This study is a part of the MOSAIK project (Monitoring Savanna Biodiversity in the Kruger National Park; Pyšek et al. 2020; Hejda et al. 2022; Čuda et al. 2024), which aims to identify the principal environmental variables driving the spatiotemporal dynamics of savannah ecosystems and their impact on biodiversity across trophic levels. Here, we focus on moths (Lepidoptera) representing phytophagous insects with variable specialisation to host plants and environmental conditions (New 2023), and mantises (Mantodea) representing carnivorous insects with varying specialisation to their prey and habitats (Prete 1999). Both groups are recognised as ecological indicators (New 1997; Battiston et al. 2020) with considerable diversity in Afrotropical ecosystems. Using structural equation models (SEM), we investigate both the direct and indirect effects of climatic and environmental variables on insect species richness (see Figure 1a for the conceptual framework). Consequently, using multivariate analyses we explored their influence on insect community composition.

We hypothesise that (1) climatic drivers affect insect species richness both directly (Figure 1a, path a) and indirectly

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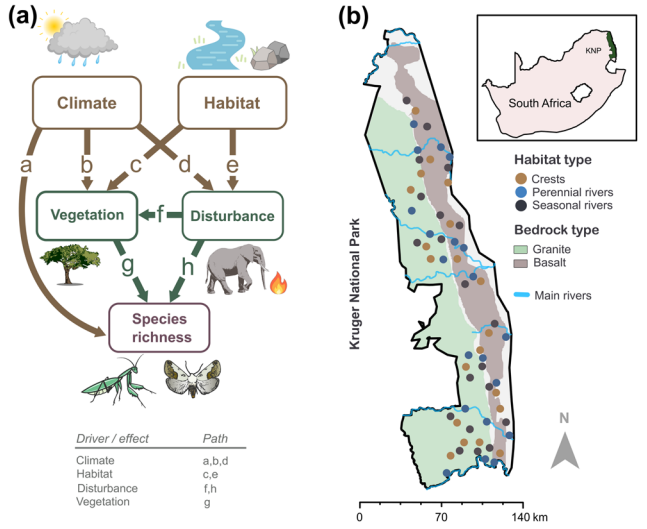

FIGURE 1 | (a) Conceptual framework illustrating the potential direct and/or indirect influence of particular groups of variables on insect species richness. Arrows depict pathways and letters denote different paths corresponding to the hypotheses outlined in Introduction. Climate variables include temperature and rainfall; abiotic habitat characteristics comprise water availability and bedrock type; vegetation is characterised by plant species richness, community composition, and biomass; and disturbance is represented by abundance of large herbivores and fire history. All variables are detailed in Table 1. (b) Map of Kruger National Park, South Africa, showing locations of the 60 study plots.

through vegetation changes (Figure 1a, path b). Specifically, we predict that insect species richness decreases with higher environmental temperatures that exceed the thermal limits of some species and increases with higher precipitation which enhances plant diversity in Kruger National Park (KNP) (Hejda et al. 2022). We also expect that (2) abiotic habitat characteristics (water availability and bedrock type) indirectly affect species richness of both insect groups through their influence on vegetation (Figure 1a, path c) and disturbance drivers (Figure 1a, path e). We expect moderate water availability to support the highest insect species richness due to the reduced presence of large herbivores (Young, Ferreira, and Van Aarde 2009) which promotes higher plant diversity (Hejda et al. 2022). We also predict higher insect diversity on granite bedrock, which is known to support higher plant diversity compared to basalt soils in the studied area (Hejda et al. 2022). Given the lack of a clear mechanism by which water availability or bedrock type could directly influence insect diversity in KNP, we did not include this direct relationship into the SEM analyses. Furthermore, we hypothesise that (3) fire and large herbivore disturbances mainly have an indirect effect on insect species richness through their impacts on vegetation structure and composition (Figure 1a, path f), with a predicted unimodal response peaking at moderate disturbance levels. Finally, we expect (4) strong direct effects of vegetation characteristics on both insect groups' species richness (Figure 1a, path g), with stronger correlations of plant diversity and biomass with moth diversity due to closer trophic relationships of phytophagous insects with host plants. Similarly, we predict that (5) the community composition of phytophagous and carnivorous insects is shaped by abiotic habitat characteristics, climate, disturbances and vegetation variables, with vegetation being the most important predictor, particularly for phytophagous moth communities.

2 | Materials and Methods

2.1 | Study Area and Plots

The study was carried out in KNP (Figure 1b), one of South Africa's largest and oldest national parks, which hosts diverse flora and fauna. Spanning approximately 20,000 km^2, KNP features a gradient of subtropical and tropical climates. It is traversed by five major perennial rivers, Sabie, Olifants, Crocodile, Letaba and Luvuvhu (Figure 1b). Daily temperatures range from 5.6°C in the dry season to 32.6°C in the wet season, and the annual precipitation ranges from 450 mm in the north to 750 mm in the south (Siebert and Eckhardt 2008; Chadwick et al. 2013; Figure S1). The regional vegetation includes various savannah types, with a variety of dominant woody species and varying proportions of woodlands and open grasslands (du Toit, Rogers, and Biggs 2003).

Within the MOSAIK project, 60 plots (50 × 50 m) were strategically established across KNP (Figure 1b). They were spatially organised into triplets, with individual plots representing three levels of water availability: (i) perennial rivers or other permanent water sources, (ii) seasonal rivers which usually dry up during the dry season and (iii) dry crests located at least 5 km from any water source. Particular plots within the triplets were selected to characterise these conditions, with distances of ~7–13 km between them. Each triplet was located on either granite (Skukuza and Phalaborwa landsystems) or basalt bedrock (Satara and Letaba landsystems) (Figure 1b).

2.2 | Insect Sampling

Both insect groups were sampled during the early (November) and late (February–March) wet seasons from 2018 to 2020. Portable light traps, each equipped with a dual-sided strip containing 48 ultraviolet (UV) light-emitting LEDs powered by 12 V batteries, were used to sample insects. Traps operated throughout a complete night, from dusk to dawn, for each plot and season (i.e., each plot was sampled for a night in the early wet season and a night in the late wet season). To minimise the effects of weather and other temporal factors, all plots within a triplet were sampled during the same night. For further details on the sampling protocol, see Delabye et al. 2022b.

From the collected material, we identified all specimens of 12 moth families (Erebidae, Euteliidae, Noctuidae, Nolidae, Notodontidae, Eupterotidae, Lasiocampidae, Saturniidae, Sphingidae, Geometridae, Thyrididae and Limacodidae) and all mantis specimens. The identification of both insect groups was based on external morphological characteristics and, when necessary, dissection of genitalia. Voucher moth specimens are stored at the Nature Education Centre of Jagiellonian University in Kraków, Poland, and at the Biology Centre, Czech Academy of Sciences, České Budějovice, Czechia. Voucher mantis specimens are stored at the Department of Zoology, Faculty of Science, Charles University, Prague, Czechia.

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TABLE 1 | Environmental characteristics of the studied plots in Kruger National Park.

	Variable	Description
Climate	Rainfall (mean)[a]	Average rainfall (mm)
	Rainfall (SD)[a]	Standard deviation of rainfall (mm)
	Temperature (mean)[b]	Average environmental temperature (°C)
	Temperature (SD)[b]	Standard deviation of environmental temperature (°C)
	Temperature (max)[b]	Average maximum temperature (°C)
	Temperature (min)[b]	Average minimum temperature (°C)
Habitat	**Water availability**	Seasonal availability of water: perennial river, seasonal river, crest
	Bedrock type	Basalt, granite
Disturbance	**Number of fires (mean)**[c]	Average number of fires
	Number of fires (SD)[c]	Standard deviation of the number of fires
	Large herbivore abundance[d]	Abundance of large mammal herbivores
Vegetation	**EVI (mean)**[e]	Average Enhanced Vegetation Index (EVI)
	EVI (SD)[e]	Standard deviation of EVI
	Vegetation composition (PC1)[f]	First principal component axis of plant community composition
	Vegetation composition (PC2)[f]	Second principal component axis of plant community composition
	Vegetation composition (PC3)[f]	Third principal component axis of plant community composition
	Vegetation composition (PC4)[f]	Fourth principal component axis of plant community composition
	Plant species richness[f]	Total number of plant species
	Grass species richness[f]	Number of grass species
	Herb species richness[f]	Number of species in the herbaceous layer (%)
	Shrub species richness[f]	Number of species in the shrub layer (%)
	Tree species richness[f]	Number of species in the tree layer
	Plant cover[f]	Total plant cover (%)
	Tree cover[f]	Tree layer cover (%)
	Shrub cover[f]	Shrub layer cover (%)
	Herb cover[f]	Herbaceous layer cover (%)

Note: Variables in bold were included in the analyses after selection based on inter-variable correlations. Data were taken from: [a]Funk et al. (2015), [b]Wan, Hook, and Hulley (2015), [c]Chuvieco et al. (2018), [d]Čuda et al. (2024), [e]Didan (2015) and [f]Hejda et al. (2022). Climate and fire-related disturbance variables refer to values per 4 km^2 grid cell recorded over 20 years (2000–2019). EVI variables refer to values for 250 × 250 m grid cells recorded over the same period. All other variables refer to the 50 × 50 m studied plots and were sampled specifically for the MOSAIK project.

2.3 | Environmental Variables

The 60 sampling plots were characterised by 26 abiotic and biotic environmental variables divided into four groups (Table 1): *climate* (four characteristics of environmental temperature and two characteristics of rainfall), *habitat* (three water availability levels and two bedrock types), *disturbance* (two characteristics of fire history and large herbivore abundance) and *vegetation* (five measures of species richness, four characteristics of vegetation community composition, and six surrogates for plant biomass, such as vegetation cover and Enhanced Vegetation Index [EVI]). Most variables were continuous, except for water availability categorised into three ordinal levels (perennial rivers, seasonal rivers, crests) and bedrock type with two categories (basalt and granite).

Vegetation data from the 60 studied plots were collected during the rainy seasons (January to February in 2019 and 2020) when most plant species are identifiable (see Hejda et al. 2022; Čuda et al. 2024 for more details). All vascular plant species in each plot were recorded, and their abundance was visually estimated using the Braun-Blanquet cover-abundance seven-grade scale; with scores converted into percentage cover values for each species (Hejda et al. 2022). Vegetation composition was represented by the first four axes from a Principal Component Analysis (PCA) of the plant communities.

Large herbivore abundances were estimated using camera traps (Bushnell Essential E3 Camera Trap with low glow IR flash) installed in each plot and serviced approximately every 3 months starting in June 2018. Here we use animal records spanning

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140 days, covering both dry (August–October 2018) and rainy (December 2018–February 2019) seasons. The dataset included 18 herbivore species: buffalo, bushbuck, common duiker, elephant, giraffe, grysbok, hippo, impala, kudu, nyala, black rhino, white rhino, sable antelope, steenbok, tsessebe, waterbuck, wildebeest and zebra (Čuda et al. 2024). Their total abundance per plot was quantified as the sum of all the herbivore species records.

To address potential correlations among variables, we conducted correlation analyses to explore relationships among variables within each group. For highly correlated variables ($r \geq 0.6$, Figure S2), we retained those most meaningful for ecological interpretation. To identify potential collinearity among the preselected variables, we calculated the variance inflation factor (VIF) and selected only variables with VIF > 10 for further analyses (Graham 2003). This procedure resulted in the selection of *mean temperature* as the only variable characterising climate, *plant species richness* and *mean EVI* characterising vegetation, and *mean number of fires* and *large herbivores abundance* characterising disturbance. Habitat remained represented by *water availability* and *bedrock type*.

2.4 | Drivers of Insect Species Richness

To assess the direct and indirect relationships between the observed species richness (i.e., the number of identified species per plot; hereinafter called *species richness*) of each insect group and environmental variables, we employed piecewise structural equations models (piecewise SEMs; Lefcheck 2016; Figure 1a). Unlike classic path analyses, piecewise SEMs allow for independent solutions for each model component, providing flexibility in specifying path relationships (Lefcheck 2016). We log-transformed all variables, except temperature, which was square-root-transformed. All continuous variables were standardised (mean = 0, SD = 1). In the SEMs, each triplet was treated as a random effect, and the distance between triplets (based on GPS coordinates) was modelled as a continuous function.

For both moths and mantises, we constructed an initial SEM ('Saturated model'; see Figure S3) based on the literature and hypothesises outlined in Section 1 (see Figure 1a, and hypotheses in Section 1). The models were further simplified by removing non-significant terms ($p > 0.05$) through backward elimination if their exclusion reduced Akaike's information criterion (AIC). The only excluded variable was *mean number of fires*, not significantly contributing to either insect group. The reduced model fit was assessed by goodness-of-fit statistics, selecting the final model with the lowest AIC values (Grace 2006). Fisher's *C* statistic and Shipley's test of d-separation (Shipley 2000) verified model fit and completeness, respectively.

For each path, we reported standardised path coefficients to estimate the expected change in response variables per SD unit change in explanatory variables, as well as marginal R^2 (variance explained by fixed effects) and conditional R^2 (variance explained by both fixed and random effects). The SEM analyses were conducted using the 'coefs', 'lm' and 'lme' functions from the 'piecewiseSEM', 'nlme' and 'lme4' packages, respectively (Lefcheck 2016; de Boeck et al. 2011; Bates et al. 2015).

2.5 | Drivers of Insect Community Composition

To assess the relationship between community composition of each focal insect group and the four groups of environmental variables, we applied distance-based redundancy analysis (db-RDA) using Bray-Curtis distances. This method was selected based on results from detrended correspondence analysis (DCA; Lepš and Šmilauer 2003). For the db-RDAs, we used the previously selected variables, with vegetation composition variables (represented by the first two axes' scores from PCA; Table 1) replacing plant species richness, as they effectively characterise vegetation changes along environmental gradients and are considered more suitable predictors of insect community composition than plant species richness alone (Schaffers et al. 2008).

Environmental variables significantly influencing community composition of each insect group were identified through forward selection procedure (Lepš and Šmilauer 2003). Selected variables included bedrock type, water availability, mean temperature and vegetation composition PC1 and PC2 for moths, and bedrock type, water availability and vegetation composition PC1 and PC2 for mantises. Prior to conducting db-RDAs (including the forward selection of environmental variables), all variables were transformed and standardised. To reflect the spatial arrangement of the plots into triplets, a split-plot permutation scheme was implemented: triplets were treated as whole plots, with individual plots within these triplets treated as split plots.

Additionally, we performed a nonmetric multidimensional scaling (NMDS) to visualise any key patterns in community composition of particular insect group potentially independent on our hypotheses. The relationships between NMDS axes and environmental variables were tested using the 'envfit' function in the 'vegan' package (Oksanen et al. 2024).

To further examine the contributions of environmental variable, we applied hierarchical partition analysis (HP; Lai et al. 2022). HP identified the independent contribution of each variable to the total variation in community composition, accounting for shared effects among variables. Additionally, we employed variation partitioning analysis (VP) to evaluate relative contributions of the four variable groups (habitat, climate, vegetation and disturbance) to community dissimilarity. VP decomposed the total variance in community dissimilarity into unique contribution of each variable group, shared effects between one or more groups, and unexplained variance (Lai et al. 2022). Together, these analyses provide a comprehensive understanding of how environmental variables and their interactions influence insect community composition.

3 | Results

In the 60 study plots, we captured and identified 65,593 moth individuals representing 817 morphospecies, and 3511 mantis individuals representing 38 morphospecies.

Our SEMs revealed that climate (mean temperature), habitat (bedrock type), disturbance (large herbivore abundance) and

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vegetation (plant species richness) collectively accounted for a significant proportion of the variation in species richness of moths (31%; Figure 2a) and in mantises (19%; Figure 2b). Notably, plant species richness emerged as the only variable with a highly significant and positive direct effect on species richness of both insect groups (Figure 2; Table S1).

Additionally, climate, habitat and disturbance characteristics significantly influenced plant species richness in both final models (Figure 2a,b). Specifically, mean temperature negatively affected plant species richness and large herbivore abundance (Figure 2a,b). Bedrock type also significantly influenced plant species richness, with granite soils supporting species-richer plant communities than basalt soils. Water availability demonstrated a significantly positive relationship with large herbivore abundance and mean EVI (Figure 2a,b). Furthermore, abundance of large herbivores positively influenced plant species richness and mean EVI (Figure 2a,b).

According to the db-RDA models, all variables together significantly affected the species composition of moth ($R^2_{adj} = 16.2\%$) and mantis ($R^2_{adj} = 18.3\%$) communities. After forward selection, the final RDA models retained vegetation composition (PC1 and PC2) and water availability as predictors for both moth and mantis community composition. Additionally, mean temperature was retained for moths and bedrock type for mantises (Figure 3a,b). The final models explained less variation in moth community composition ($R^2_{adj} = 8.3\%$) compared to mantis community composition ($R^2_{adj} = 10.6\%$).

The first axis of the db-RDA (RDA1) accounted for 3.5% of the total variation in moth and 5.6% in mantis community composition explained by the analysed environmental variables (Figure 3a,b). RDA1 primarily differentiated moth and mantis communities along the gradient of water availability. RDA2 contributed to 2.7% of the explained total variation in moths and 3.3% in mantises, reflecting changes in vegetation composition (Figure 3a,b). These db-RDA results were confirmed by NMDS, where the same environmental variables mostly correlated with the two main axes in community composition of both insect groups (Figure S4).

Hierarchical partitioning analyses indicated that vegetation composition (PC1) played a predominant role in the variation of community composition for both moths and mantises. The effect of mean temperature closely followed for moths (Figure 3c,d), while all other variables accounted for less than 1% of the variation in community composition.

Variation partitioning analysis indicated that the combined effects of vegetation and habitat variables accounted for approximately 3% of the variation in moth and 1% in mantis community composition (Figure 3e,f). Additionally, a significant combined effect of climate and vegetation variables was found only for moths, explaining merely 1% of the total variation. When decomposing this variation, vegetation variables alone accounted for 2% of the variance for moths and 3% for mantises. Habitat variables alone explained 1% and 4% of variation in community composition for moths and mantises, respectively (Figure 3e,f).

4 | Discussion

Our study revealed the complex impact of climate, habitat, disturbance and vegetation variables on insect species richness and community composition in the South African savannah ecosystems of KNP. Notably, we confirmed the strong positive impact of plant species richness on the diversity of phytophagous moth and carnivorous mantises, underlining the crucial role of vegetation in supporting diverse insect communities in savannah ecosystems. Furthermore, the effects of climate and habitat characteristics on insect diversity, mediated through plant species richness and large herbivore disturbance suggests complex interplays between environmental variables and dynamics of plant and insect communities, highlighting the nuanced nature of ecological interactions in these ecosystems (Jonsson et al. 2010; Leeuwis, Peel, and de Boer 2018).

The hypothesised strong relationship between plant diversity and species richness of both insect groups aligns with previous research of phytophagous insects (e.g., Kemp, Linder, and Ellis 2017; Leone et al. 2023), as well as insect predators and

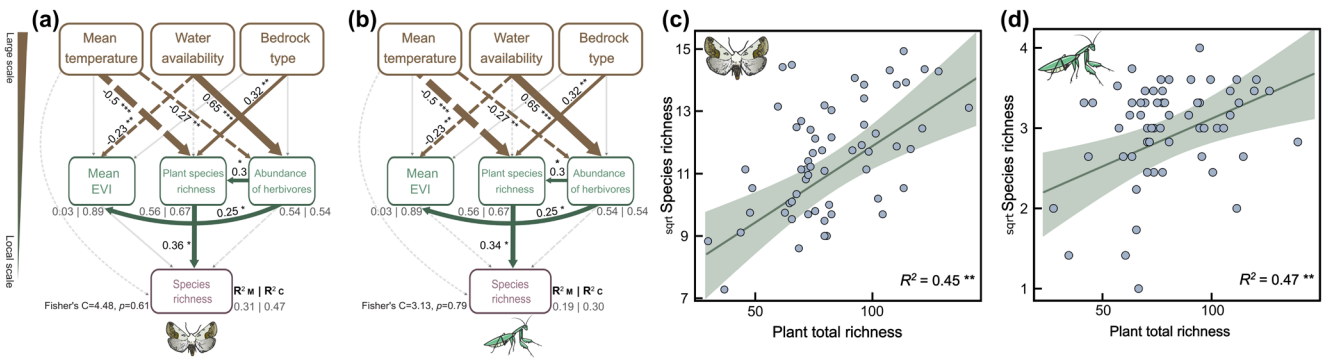

FIGURE 2 | Path diagram illustrating how climate, habitat, disturbance, and vegetation variables affect species richness of (a) moths and (b) mantises in Kruger National Park, South Africa. Based on results from piecewise SEMs, solid lines indicate positive associations, dashed lines indicate negative associations (*$p \leq 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$) and grey lines denote non-significant paths ($p > 0.05$). Arrow widths are proportional to the standardised path coefficients, which are noted alongside each arrow. Values in grey (R^2) represent the proportions of variance explained by fixed (R^2 marginal) and random effects (R^2 conditional). The effect of plant species richness on species richness of (c) moths and (d) mantises. Lines and 95% confidence intervals represent predictions from linear mixed-effect models (**$p < 0.01$).

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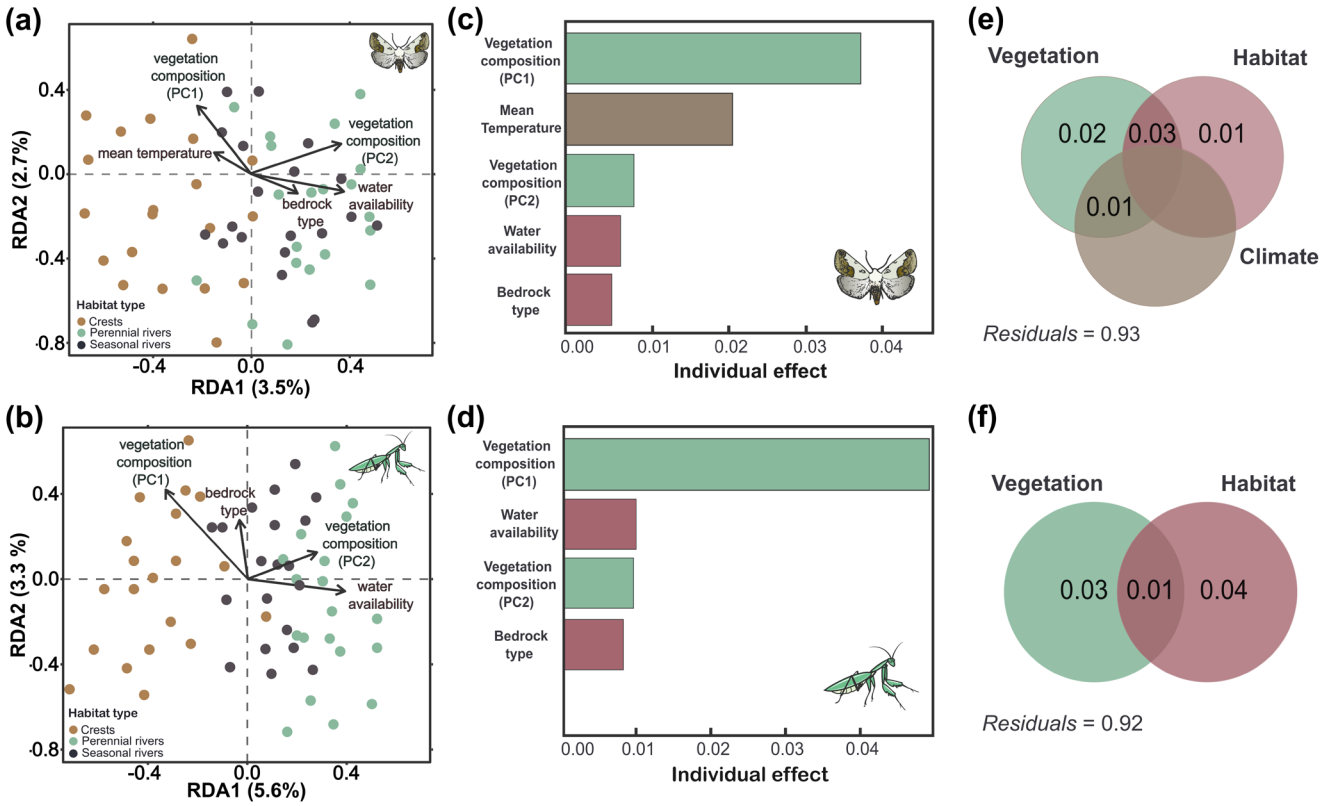

FIGURE 3 | db-RDA ordination diagrams showing the relationship between species composition of (a) moth and (b) mantis communities and the forward-selected environmental variables. Hierarchical and variation partitioning of (c, e) moth and (d, f) mantis communities showing the percentage of variation explained by climate (brown), vegetation (pale green) and habitat (pale red) variables. In the variation partitioning analyses, intersections represent the shared contributions of two groups of variables, and blank spaces indicate 0% of variance explained.

parasitoids (e.g., Procheş and Cowling 2006; Botha, Siebert, and Van den Berg 2017). This highlights that vegetation is essential not only for phytophagous insect communities but also for their natural enemies (Scherber et al. 2010; Balvanera et al. 2006). This may explain the minimal differences between moths and mantises in our results. For phytophagous moth, our findings can be related to the resource specialisation hypothesis, predicting a correlation between the diversity of consumers and their food resources (Keddy 1984). The positive relationship between carnivorous insects and plant diversity likely reflects the increased diversity of herbivorous insect prey, but also the higher complexity of species-rich vegetation providing diverse microhabitats (Letourneau 1987). Unfortunately, our study design did not allow us to separate these two mechanisms for either insect group, partly due to the limited influence of environmental variables on insect community composition.

The lack of a significant relationship between insect richness and proxies for plant biomass was unexpected. Previous studies on moths in South African savannahs (Delabye et al. 2022a) and various herbivorous and other arthropod groups in KNP (Parker et al. 2023) suggested that primary productivity and vegetation complexity, both associated with plant biomass, are key drivers of insect diversity. However, these studies did not analyse plant diversity as a potential driver. Based on our more robust dataset and detailed analyses, we propose that vegetation diversity may be a more important determinant of insect diversity than plant biomass in South African savannahs.

Our results partially supported the hypothesis that climatic factors indirectly affect species richness of both insect groups through their impact on vegetation. While broader ecological theory and some empirical evidence emphasise the role of temperature in shaping insect diversity at a global scale (Mayr et al. 2020; Classen et al. 2015), our results are consistent with the studies revealing the crucial role of plant communities in determining insect diversity at regional and local scales (Kemp and Ellis 2017; Du et al. 2020). This pattern mirrors broader dynamics observed in savannah ecosystems, where large-scale environmental factors influence local vegetation which in turn shapes insect communities (Bock, Jones, and Bock 2007; de Sassi, Lezx, and Tylianakis 2012; Zhu et al. 2014; Kemp, Linder, and Ellis 2017; Shinohara and Yoshida 2021). Although the negative effect of temperature on plant diversity due to heat stress has been reported (Staver, Botha, and Hedin 2017; Hejda et al. 2022), we expect a stronger positive effect of precipitation which is negatively correlated with temperature in KNP (Figure S1). The critical role of precipitation in shaping insect diversity in KNP has already been suggested by D'Souza et al. (2021). Our broader spatial scope within the park revealed that climate variables indirectly affect insect species richness through their influence on vegetation diversity and disturbance by large herbivores.

The hypothesised indirect effects of habitat variables on insect species richness received varied support. Only bedrock type had a significant direct effect on plant species richness, with granite soils supporting higher plant diversity than basalt soils (Hejda

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et al. 2022), which consequently enhanced insect species richness in our study. In contrast, water availability had no direct effect on plant species richness but indirectly influenced insect species richness through its impact on abundance of large herbivores. Higher water availability supported greater herbivore abundance along permanent rivers, which, contrary to our expectations, positively affected plant diversity. This finding aligns with studies suggesting that mammal herbivore disturbances may facilitate species coexistence by creating diverse habitats and food resources for insects in savannah ecosystems (e.g., Bonnington, Weaver, and Fanning 2008; Wilkerson, Roche, and Young 2013; Pryke, Roets, and Samways 2016). However, the positive effect of large herbivore disturbances on insect species richness is inconsistent with the expected unimodal response based on theoretical models and numerous studies (e.g., Mouillot et al. 2013; Bonnington, Weaver, and Fanning 2008). It can be inferred that the intensity of herbivore disturbances in our study did not reach levels high enough to reduce biodiversity.

4.1 | Conclusions and Implications for Conservation

Our findings emphasised the key role of vegetation in shaping insect diversity in Afrotropical savannahs and highlighted the complex interactions among vegetation, climate, abiotic conditions and disturbances from large herbivores, all of which have direct and indirect effects on insect diversity. Understanding these dynamics is crucial for developing effective conservation strategies, particularly in the face of climate change (Nooten, Andrew, and Hughes 2014). Our analyses confirmed that climate impacts insect communities primarily through the negative correlations of temperature (and thus positive correlation of precipitation in KNP) with plant diversity. This underscores the vulnerability of savannah ecosystems to climate change, with significant implications for multiple trophic levels including plant and insect communities.

Kruger National Park, along with the broader Southern Africa region, has been identified as highly vulnerable to climate change impacts (Engelbrecht et al. 2024; Rouault et al. 2024). Predictions indicate a decrease in precipitation during the rainy season, compounded by the drying effects of elevated temperatures, leading to a substantial reduction in soil moisture (Thavhana et al. 2024). These changes are expected to alter vegetation structure and composition, with negative consequences for insect diversity. The decline in grass biomass reported during the 2016 drought in KNP already indicated the potential impacts of changing climate (Wigley-Coetsee and Staver 2020).

Our results also emphasised the necessity of a complex approach to conservation of African savannah biodiversity. Future studies should elucidate the mechanisms underlying the observed relationships by exploring finer-scale interactions and incorporating additional factors such as plant-insect interactions and predator–prey dynamics (Hertzog et al. 2017). Integrating long-term monitoring and including variables such as water stress would significantly enhance our understanding of how temporal dynamics shape insect communities in response to changing environmental conditions.

Additionally, our study revealed the importance of rivers in balancing water availability and disturbance intensity, positioning them among the fundamental conservation priorities. To protect insect diversity, it is essential to maintain diverse vegetation through strategic management of large herbivores. Our study supports the effectiveness of such practices, which have been successfully implemented in KNP over recent decades (e.g., Robson and Van Aarde 2018), in sustaining insect diversity. Integrating both seasonal and perennial rivers into these conservation strategies appears to be a particularly efficient approach.

Author Contributions

Petr Pyšek, David Storch, Klára Pyšková and Robert Tropek conceived the ideas and planned the research; Llewellyn C. Foxcroft, Martin Hejda, Sandra MacFadyen, Klára Pyšková, David Storch, Petr Pyšek and Robert Tropek designed the study and established the study plots within the MOSAIK project; Sylvain Delabye, Robert Tropek and Ondřej Sedláček sampled the insects; Jan Čuda, Llewellyn C. Foxcroft, Martin Hejda, Sandra MacFadyen, Klára Pyšková and Petr Pyšek sampled a part of the environmental variables; Fernando P. Gaona, Sylvain Delabye, Pavel Potocký, Valeriy Govorov, Rafał Garlacz and Tomasz Pyrcz identified the insects; Fernando P. Gaona and Robert Tropek performed the analyses and wrote the first draft; all authors contributed to writing and approved the final manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data are provided via the Zenodo platform: https://zenodo.org/records/12204570.

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