



Indigenous forest edges increase habitat complexity and refuge opportunities for grassland butterflies

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Abstract

Heterogeneity at local and landscape scales can promote insect diversity and moderate insect declines that stem from global change. Determining how species respond to different landscape components provides insight into the role of heterogeneity in landscapes undergoing change. We examine how indigenous forest-grassland edges are used by butterflies. We assessed butterfly diversity and behaviour at forest edges and adjoining grassland, and tested whether these patterns are influenced by differing weather conditions between seasons. Forest edges supported a species rich butterfly assemblage. Forest specialists were more diverse at forest edges than in grassland, whereas grassland specialists and habitat generalists were as diverse at forest edges as in grassland. All butterfly groups showed more inter- and intra-specific interactions and more patrolling behaviour at forest edges, but more feeding and transient behaviour in grassland. Occurrence and behavioural patterns were not mediated by season, suggesting that the influence of forests does not change with varying environmental conditions. Nonetheless, certain species preferentially utilized forest edges in the hot and windy season, indicating that shelter provided by forest edges influences butterfly habitat use. We found no evidence that complementary nectar sources influence butterfly distribution patterns.

Implications for insect conservation: The diverse butterfly assemblages and range of behaviours supported by indigenous forest edges indicate that forest patches are an important habitat component for butterflies. Conserving forest patches in these coastal grasslands may help buffer butterfly populations against global change.

Keywords Butterfly conservation · Butterfly behaviour · Edges · Habitat heterogeneity · Insect conservation, Lepidoptera

Introduction

Solutions are needed to mitigate global insect declines due to a range of anthropogenic stressors such as habitat loss, climate change and land-use intensification (Cardoso et al. 2020; Harvey et al. 2022). The maintenance of spatial heterogeneity at local and landscape scales is a primary strategy

towards moderating insect losses (Samways et al. 2020; Seibold et al. 2019). Relationships between heterogeneity and the diversity of ecological communities can be complex due to trade-offs between suitable habitat area and heterogeneity (Allouche et al. 2012; Heidrich et al. 2020). However, in many cases, heterogeneity increases insect diversity in various ways.

At the community level, heterogeneity provides diverse ecological niches which allow species with different habitat requirements to coexist (Fahrig et al. 2011). For example, different vegetation types, heterogeneous vegetation structure, environmental gradients, and small natural features can increase species richness (Hunter et al. 2017; Löffler and Fartmann 2017; Pryke et al. 2013). Individual species also benefit from heterogeneity, as many species need a wide range of resources to fulfil their ecological and behavioural needs. This includes consumable resources such as larval host plants and adult food, as well as structural

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elements such as bare ground or tall vegetation that are needed for roosting, overwintering, egg-laying, and mate location (Dennis et al. 2003; Schultz et al. 2012). These varied resources often do not co-occur in the same biotope, and a mix of biotopes within a species' dispersal range can be a prerequisite for population persistence (Kalarus et al. 2013; Slamova et al. 2013).

In addition, individual vegetation types undergo gradual changes in the phenology of their food resources throughout the season, and seldom provide a continuous food supply over time. However, different landscape elements can provide phenological complementarity in food resources that allows species to persist throughout the season by tracking seasonal patterns in resource availability (Bertrand et al. 2019; Mallinger et al. 2016; Mandelik et al. 2012). Furthermore, structurally diverse landscapes provide shelter during adverse weather conditions and refuge from human disturbances (Dennis and Sparks 2005, 2006; Marini et al. 2009). By using refuges, species can remain active for longer periods and persist in areas that would otherwise be unsuitable under fluctuating environmental conditions (Dennis and Sparks 2005, 2006; Fartmann 2006). In this way, these refuges boost the resilience of arthropod populations to global change (Fartmann et al. 2022; Selwood and Zimmer 2020).

Indigenous forest patches and forest edges can increase the structural and compositional complexity of open ecosystems such as grasslands (Akeboshi et al. 2015). In many regions, grassland insect assemblages benefit from the presence of indigenous forest (Bergman et al. 2018; Marini et al. 2009; Öckinger et al. 2012), and in some cases, forests close to grassland can buffer the negative effects of habitat loss and fragmentation on grassland insects (Öckinger et al. 2012). Supplementary food resources, shelter, and a diversity of microclimates at forest edges, are often proposed as reasons for these positive effects (Habel et al. 2022; Liivamägi et al. 2014; Toivonen et al. 2017).

In South Africa, indigenous forest patches embedded in grassland ecosystems have high conservation value, but are limited in extent, with the forest biome covering < 1% of land area in South Africa (Mucina and Rutherford 2006). Forest patches support specialist forest arthropods, and assemblages that complement those in grassland (Eckert et al. 2022; Gaigher et al. 2019; Yekwayo et al. 2017). Forests also influence insect assemblages in nearby grassland (Pryke and Samways 2012). This latter effect is especially evident for butterflies, which are responsive to amount and configuration of woody vegetation at the landscape scale (van Schalkwyk et al. 2021). In these systems, certain butterflies in grassland benefit from forest cover in the landscape, even in highly transformed landscapes, suggesting that they utilize the forests and/or their edges (Gaigher et al. 2021). However, the different ways in which these forests are used

by grassland species have not been assessed in detail. As the influence of forests on grassland insects has important implications for insect species distribution and persistence, a more detailed understanding of the mechanisms behind these influences will enable us to predict the role that forests may play in changing landscapes.

Here, we evaluate the extent to which indigenous forest edges are utilized by grassland butterflies and investigate two potential benefits provided by forest edges: shelter from adverse weather conditions and complementary adult nectar sources, both factors which can strongly influence butterfly distribution and behaviour (Dennis and Sparks 2005, 2006; Evans et al. 2020; Fischer and Fiedler 2001). First, we assess patterns of butterfly diversity at forest edges and adjacent grassland. We expect species with different habitat preferences to respond in different ways to forest edges and open grassland, and therefore we assess patterns for forest specialists, grassland specialists, and habitat generalist butterflies separately. High butterfly diversity at forest edges, especially of grassland specialists, would indicate the importance of forest edges for supporting species other than the expected forest-associated species. In addition to promoting biodiversity, certain landscape elements can be preferentially used for certain behaviours and can thus be important for population persistence (Crous et al. 2014; Evans et al. 2020; Pryke et al. 2012). We therefore also assess whether butterfly behaviour differs between forest edges and adjacent grassland. Furthermore, we compare single-species abundance patterns of the dominant butterfly species at forest edges and in grassland.

We also test for the effect of season as a proxy for coarse-scale climatic conditions, as the average conditions between the two sampling seasons of this study differ greatly, with summer having significantly higher wind speeds, air temperature, insolation, and significantly lower relative humidity than is the case in autumn. A mediating effect of season on the occurrence and behaviour patterns would indicate that prevailing weather conditions influence the relative importance of the forest edge as a component of butterfly habitat. This would help us to determine whether forest edges provide shelter from adverse conditions, which we expected in our high-wind and high-temperature study area. It would also help explain any species-level shifts in habitat use between seasons. Finally, we assess whether flowering plants that butterflies visit differ between forest edges and grassland, and between seasons, to determine whether the two biotopes support complementary adult food sources which may influence butterfly habitat use.

Methods

Study design

The study area is located on the east coast of South Africa in the Maputaland-Pondoland-Albany biodiversity hotspot (Myers et al. 2000). The landscape is a flat, coastal plain which is dominated by two vegetation types that exist as an intricate mosaic: Maputaland Coastal Belt and Maputaland Wooded Grassland, which, in the study area, consists largely of dry and hygrophilous grassland with scattered shrubs and small trees. Grassland sites had an average of $8.52\% \pm 1.53$ S.E. shrub cover and an average of $3.98\% \pm$

0.89 S.E. tree cover. Small patches of Northern Coastal Forest and Swamp Forest are embedded in the grassland matrix. These are medium-height, subtropical, coastal forests with high plant species richness (Mucina et al. 2006). The forest-grassland edges are soft, consisting of transition vegetation, with the ecotones ranging from 2 to 20 m in width. Forest edge sites had an average of $20.78\% \pm 3.31$ S.E. shrub cover and an average of $36.56\% \pm 3.60$ S.E. tree cover. Sixteen sites were selected where forest patches >2.5 ha were next to open grassland (Fig. 1). Both indigenous forest types (Northern Coastal Forest: 11 sites, Swamp Forest: 5 sites) and both grassland types (Maputaland Coastal Belt: 9 sites, Maputaland Wooded Grassland: 7 sites) were

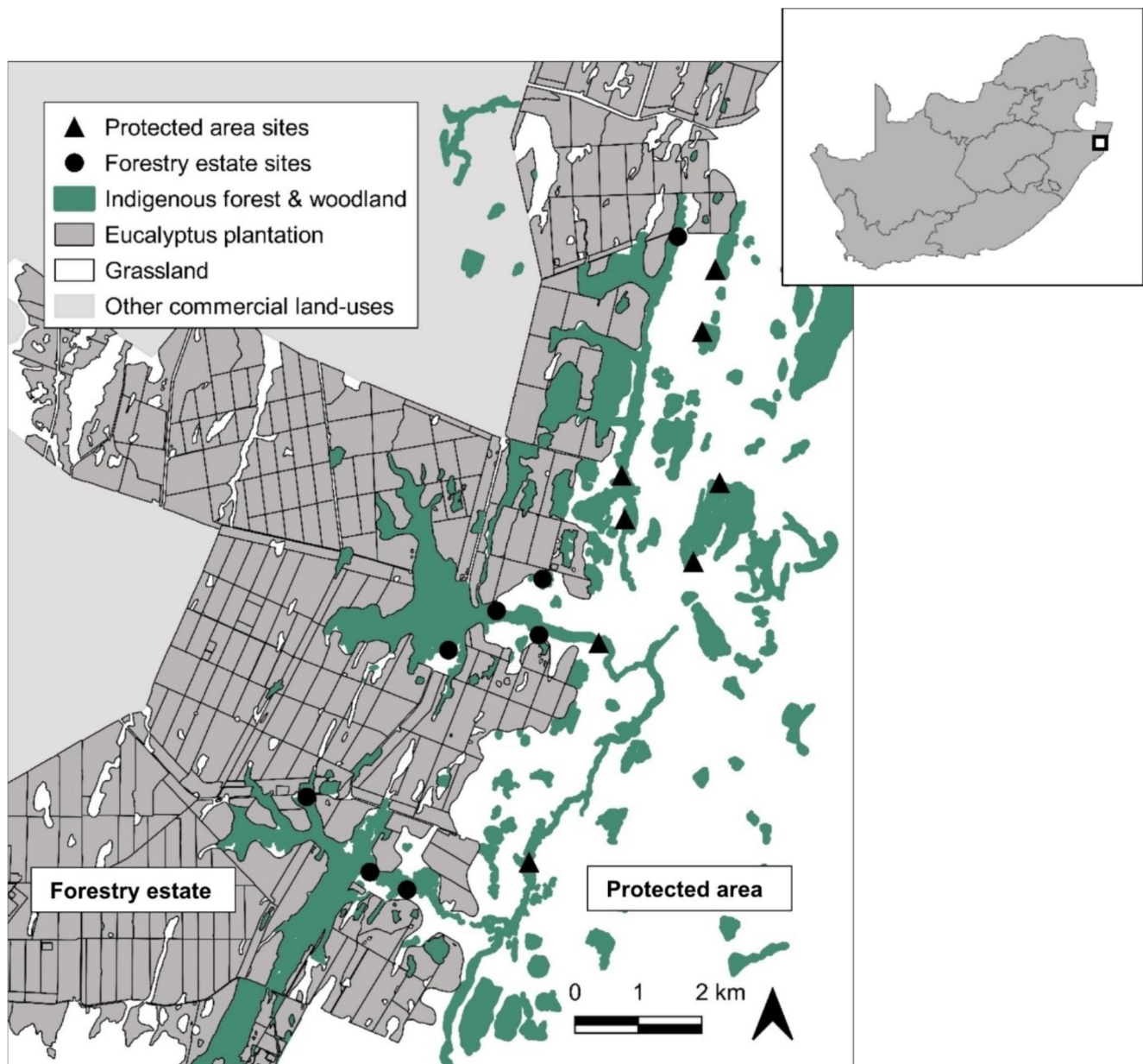


Fig. 1 Map of the study area in KwaZulu-Natal, South Africa, indicating the location of study sites in the forestry estate and adjacent protected area

included (Scott-Shaw and Escott, 2011). Eight of the sites were in large-scale conservation corridors in a forestry plantation estate owned by SiyaQhubeka Forestry and managed by Mondi Group. The production areas of the plantations are planted monocultures of *Eucalyptus* with limited understory vegetation. Another eight sites were in the adjacent protected area, iSimangaliso Wetland Park, east of the plantations. Distances between sites ranged from 600 m to 11 km. The grassland in the protected area and the conservation corridors undergo similar fire regimes, with prescribed burns every 2–5 years to mimic natural fire disturbances (SANBI 2014). Grazing between the areas is also similar, as the border between them is unfenced, which allows wild megaherbivores to move freely and graze the vegetation in both areas. Coarse vegetation structure and composition during the study period was similar between grasslands of the two areas (Gaigher et al. 2021).

Sampling methods

Butterflies were sampled twice at each site, once during 19–25 January 2017 (summer) and once during 27 April–5 May 2017 (autumn). Both seasons are periods of high activity for subtropical butterflies in the region (Woodhall 2005). To characterise the weather conditions in the two study periods, hourly weather data on solar radiation and rainfall were obtained from a weather station close to the study area (28°21'08.56"S, 32°14'46.42"E) and hourly data on wind speed, air temperature, and relative humidity were obtained from the ERA5 global weather dataset, and were derived from a point close to the study area (28°15'00.01"S, 32°14'59.97"E) (Hersbach et al. 2020). Linear models were performed in lme4 (Bates et al. 2014) to test whether these measures differed significantly between the two study periods. Wind speed, air temperature and solar radiation were significantly higher in summer, whereas relative humidity was higher in autumn, and rainfall did not differ between seasons (Supplementary material, Table S1).

We sampled butterflies between 08h00 and 15h00 and avoided overcast, rainy, and very windy conditions (wind speeds of > 10 m/s), although it was not possible to avoid windy conditions altogether. At each site, butterflies were recorded along two transects. One transect was along the forest edge in the transition zone which consisted of a mix of grassland and forest vegetation, and one transect was in the adjacent grassland between 50 and 150 m from the forest edge. Sampling in the forest interiors was not possible due to safety restrictions in these areas with free-roaming wild megaherbivores. Each transect consisted of two observers simultaneously walking along a slow, meandering route, recording all butterflies in a 5 m radius along the transect. Observers walked in opposite directions and

stayed in contact to avoid recording the same individual twice. In total, each transect lasted for 30 min (Kadlec et al. 2012), adding up to one hour of observations per transect per season, and was approximately 300 m long in total. We surveyed the ground vegetation layer, and if shrubs and trees were present at a site, we also surveyed the shrubs, and lower tree canopies. The behaviour of each butterfly when it was first sighted was recorded and classified as transient (high, fast flight), patrolling (low, slow, searching flight), settling behaviour (resting and basking), feeding, and inter- and intraspecific interactions (territorial and reproductive behaviour) (Dover 1989). For all feeding events, we identified the flowering plants visited using Pooley (1993; 1998). Butterflies that could not be identified in flight were captured for identification according to Pennington et al. (1978) and Woodhall (2005). Species were classified as forest specialists, grassland specialists, or habitat generalists, based on historical data on their occurrence in different vegetation types (Supplementary material, Table S2) (Mecenero et al. 2013).

Statistical analysis

All records of the Boisduval tree nymph, *Sevenia boisduvali boisduvali*, were removed from the dataset, as this species shows periodic swarming behaviour in the study region (Mecenero et al. 2013) and there was great variation in its abundance among sites. An outlier site in the plantation estate was excluded from analysis due to elevated butterfly numbers caused by a mass-flowering event in summer (Zuur et al. 2010). All analyses were done in R version 4.2.0 (R Core Team 2022). To assess sampling adequacy, individual-based rarefaction and extrapolation sampling curves were made using the iNEXT package (Hsieh et al. 2016).

We performed generalized linear mixed models using the glmmTMB package (Brooks et al. 2017) to test for the effect of location in the landscape (forest edge or grassland), season (summer or autumn), and their interaction on species richness and abundance of the overall assemblage, and that of forest specialists, grassland specialists, and habitat generalists. Poisson distribution was used for species richness models, and negative binomial distribution for abundance models (Bolker et al. 2009). In all models, location, season, and their interaction were included as fixed factors. We also included area (protected area or plantation estate) as a fixed factor to assess possible effects of the larger landscape setting and transect as a random factor to account for repeated measurements at the same location (Bolker et al. 2009). Model selection and averaging were used to identify the most influential set of variables for each response variable (Burnham and Anderson 2001). Models consisting of all possible combinations of variables, including the null

model, were ranked based on AICc in the MuMIn package (Barton 2022). All models within 2 AICc of the top model were averaged and estimates from conditional model averaging are reported. Effects were considered significant if the 95% confidence intervals of the estimate did not include zero (Burnham and Anderson 2001). Significant interactions were further assessed by testing for the effect of location or season on the responses separated by season or location, respectively.

To assess differences in behaviours between locations and seasons, we converted the number of occurrences per behavioural category to a proportion of the total number of behavioural occurrences per transect and used this as response variable in models. This was done because the absolute number of behavioural occurrences is dependent on the number of butterfly individuals recorded. The same modelling procedure was used as above, except that we used linear mixed models because the proportions were continuous, non-binomial data and best fitted a Gaussian distribution (Bolker et al. 2009; Warton and Hui 2011). This procedure was done for the overall butterfly assemblage, and for forest specialists, grassland specialists, and generalists separately.

The same modelling procedure as above was used to assess abundance patterns of dominant species (here defined as species that were observed more than ten times per season) between locations and seasons. We used negative binomial distribution for these abundance models (Bolker et al. 2009). For all models, we checked for overdispersion, and assessed the model fit of alternative models by visualizing the model residuals using the DHARMA package (Hartig 2020). We confirmed there was no spatial autocorrelation in the model residuals by assessing correlograms using the ncf package (Bjornstad and Cai 2020).

Changes in butterfly assemblage composition due to differences in species phenology between seasons may have influenced the abovementioned occurrence and behavioural patterns between forest edges and grassland. To evaluate this possibility, we assessed differences in the butterfly assemblages occurring in summer and autumn using the manyglm function in mvabund (Wang et al. 2012). This model-based procedure fits generalized linear models separately to the abundance of each species and was used due to its greater power properties compared to more commonly used distance-based approaches (Wang et al. 2012; Warton et al. 2012). The multivariate model included season as fixed effect and was fitted using a negative binomial distribution, assuming quadratic mean-variance. Test statistics were calculated based on the 'PIT-trap' resampling method with 999 permutations (Wang et al. 2012).

We used the same multivariate procedure to test whether the flowering plant assemblages visited by butterflies

differed between forest edges and grassland, and between seasons. The model included location, season, their interaction, and area as fixed factors. The response matrix consisted of the number of butterfly visitations per visited flowering plant species per site. We did not include all flowering plant species present at the sites, but only those that were visited, because we could confirm that they were utilized by butterflies.

Results

We sampled a total of 2 572 butterflies in 65 species (Supplementary material, Table S2). From this, 846 butterflies in 48 species were sampled in summer and 1726 butterflies in 52 species were sampled in autumn. In total, 20 species were forest specialists, 14 were grassland specialists, and 31 were habitat generalists. The rarefaction curve for forest edge sampling approaches an asymptote, whereas the curve for grassland sites still increases, indicating that additional species would be recorded with further sampling (Supplementary material, Fig. S1).

For the overall assemblage, butterfly species richness and abundance were significantly higher at the forest edges than in grassland and were significantly higher in autumn than in summer (Table 1; Fig. 2A-B). Species richness of forest specialists was higher at the forest edges than in grassland (Table 1; Fig. 2C). The abundance of forest specialists showed an interaction between location and season, with lower abundance in grassland than at forest edges in summer (estimate: -1.66, S.E.: 0.35, 95% C.I.: -2.39, -0.94), but not in autumn (null model performed best) (Table 1; Fig. 2D). Grassland specialists and habitat generalists were equally species rich and abundant at forest edges and in grassland, with both groups more species rich and abundant in autumn than in summer (Table 1; Fig. 2E-H). Area did not have a significant effect on any of the butterfly responses (Table 1).

For the overall butterfly assemblage, the number of settling behavioural events was similar between forest edges and grassland but was significantly higher in summer than in autumn (Table 2; Fig. 3). There were more feeding behavioural events in the open grassland than at forest edges (Table 2; Fig. 3). There were more intra- and interspecific interactions at the forest edges than in grassland, and more in summer than in autumn (Table 2; Fig. 3). Patrolling was more frequent at the forest edges than in grassland and was more frequent in autumn than in summer (Table 2; Fig. 3). There were more transient behavioural events in the grassland than at forest edges, and more in summer than in autumn (Table 2; Fig. 3). There were no significant interactions between location and season, and no effect of area on any of the behavioural categories. Trends in behaviour of

Table 1 Model-averaged estimates, standard errors, and confidence intervals from generalized linear mixed models explaining species richness and abundance of the overall butterfly assemblage, forest specialists, grassland specialists and habitat generalists. Predictors with significant effects are in bold. Models with an asterisk next to the response had only a single top model and therefore no model averaging was performed. RI=relative importance of a predictor, calculated as the sum of Akaike weights over all models in which the variable was included. The reference levels in the calculation of the coefficients are as follows: Location = forest edge, Season = Summer, Area = forestry estate

Responses	Predictors	Estimate	SE	Lower CI	Upper CI	RI
<i>Species richness</i>						
Overall assemblage*	Location	-0.26	0.08	-0.41	-0.11	NA
	Season	0.53	0.08	0.38	0.69	NA
Forest specialists	Location	-0.90	0.27	-1.43	-0.36	1.00
	Season	0.35	0.18	-0.01	0.71	1.00
	Location x Season	0.51	0.32	-0.13	1.16	0.53
Grassland specialists	Season	0.54	0.15	0.23	0.85	1.00
	Location	-0.12	0.15	-0.42	0.18	0.31
Habitat generalists*	Season	0.59	0.12	0.36	0.83	NA
<i>Abundance</i>						
Overall assemblage	Location	-0.50	0.17	-0.83	-0.16	1.00
	Season	0.72	0.13	0.46	0.98	1.00
Forest specialists	Location x Season	0.27	0.20	-0.13	0.67	0.31
	Area	0.16	0.14	-0.12	0.44	0.24
	Location	-1.63	0.34	-2.31	-0.94	1.00
	Season	0.76	0.18	0.40	1.12	1.00
	Location x Season	1.25	0.30	0.65	1.85	1.00
	Area	0.31	0.27	-0.24	0.85	0.34
Grassland specialists	Location	-0.33	0.18	-0.69	0.03	1.00
	Season	0.68	0.18	0.32	1.05	0.69
	Area	0.18	0.18	-0.19	0.54	0.22
Habitat generalists	Season	0.54	0.11	0.31	0.76	1.00
	Location	-0.16	0.11	-0.38	0.06	0.47

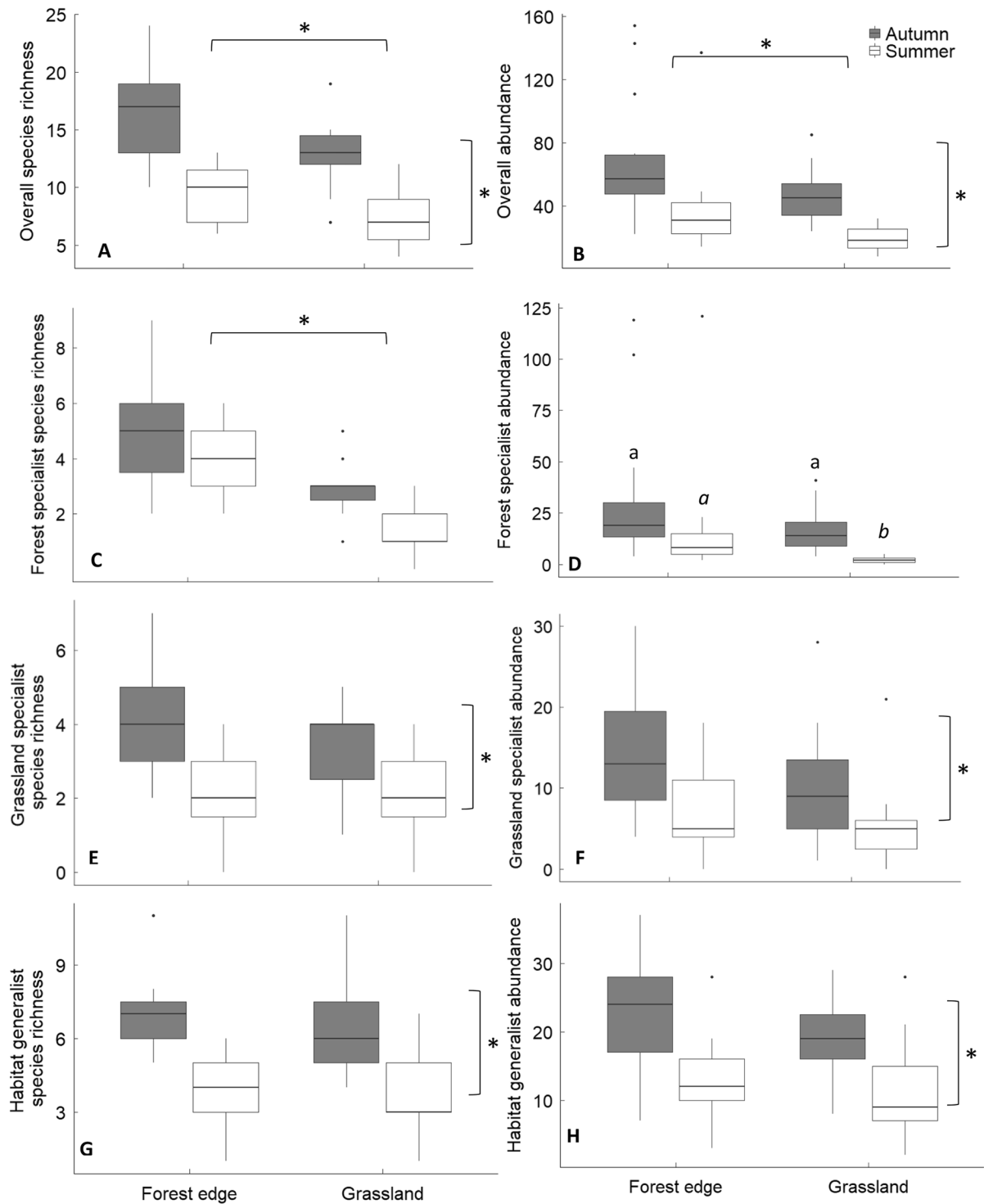


Fig. 2 Butterfly species richness and abundance at forest edges and in grassland in summer and autumn for **A–B**) the overall assemblage, **C–D**) forest specialists, **E–F**) grassland specialists and **G–H**) habitat generalists. Horizontal brackets indicate significant main effects of location, vertical brackets indicate significant main effects of season. For the significant interaction in D, means with letters in common are

not significantly different. Letters in roman relate to the comparison between locations in autumn, and letters in italics relate to the comparison between locations in summer. The boxplots represent the median (central horizontal line), inter-quantile range (boxes), minimum and maximum values (whiskers) and outliers (points)

Table 2 Model-averaged estimates, standard errors, and confidence intervals from generalized linear mixed models explaining proportions of the different behaviours. Predictors with significant effects are in bold. RI = relative importance of a predictor, calculated as the sum of Akaike weights over all models in which the variable was included. The reference levels in the calculation of the coefficients are as follows: Location = forest edge, Season = Summer, Area = forestry estate

Responses	Predictors	Estimate	SE	Lower CI	Upper CI	RI
Settling	Location	-0.04	0.02	-0.08	0.00	0.81
	Season	-0.06	0.02	-0.10	-0.02	1.00
	Location x Season	0.04	0.03	-0.04	0.10	0.38
	Area	-0.02	0.02	-0.04	0.02	0.25
Feeding	Location	0.05	0.02	0.01	0.09	1.00
	Area	-0.02	0.02	-0.06	0.03	0.28
Interactions	Location	-0.05	0.02	-0.09	-0.01	1.00
	Season	-0.05	0.02	-0.08	-0.02	1.00
	Location x Season	0.03	0.03	-0.03	0.08	0.24
	Area	0.02	0.02	-0.02	0.05	0.26
Patrolling	Location	-0.12	0.04	-0.19	-0.05	1.00
	Season	0.19	0.04	0.12	0.27	1.00
	Location x Season	0.05	0.06	-0.07	0.17	0.30
Transient	Location	0.15	0.04	0.08	0.23	1.00
	Season	-0.08	0.04	-0.06	-0.01	1.00
	Location x Season	-0.07	0.06	-0.19	0.04	0.40

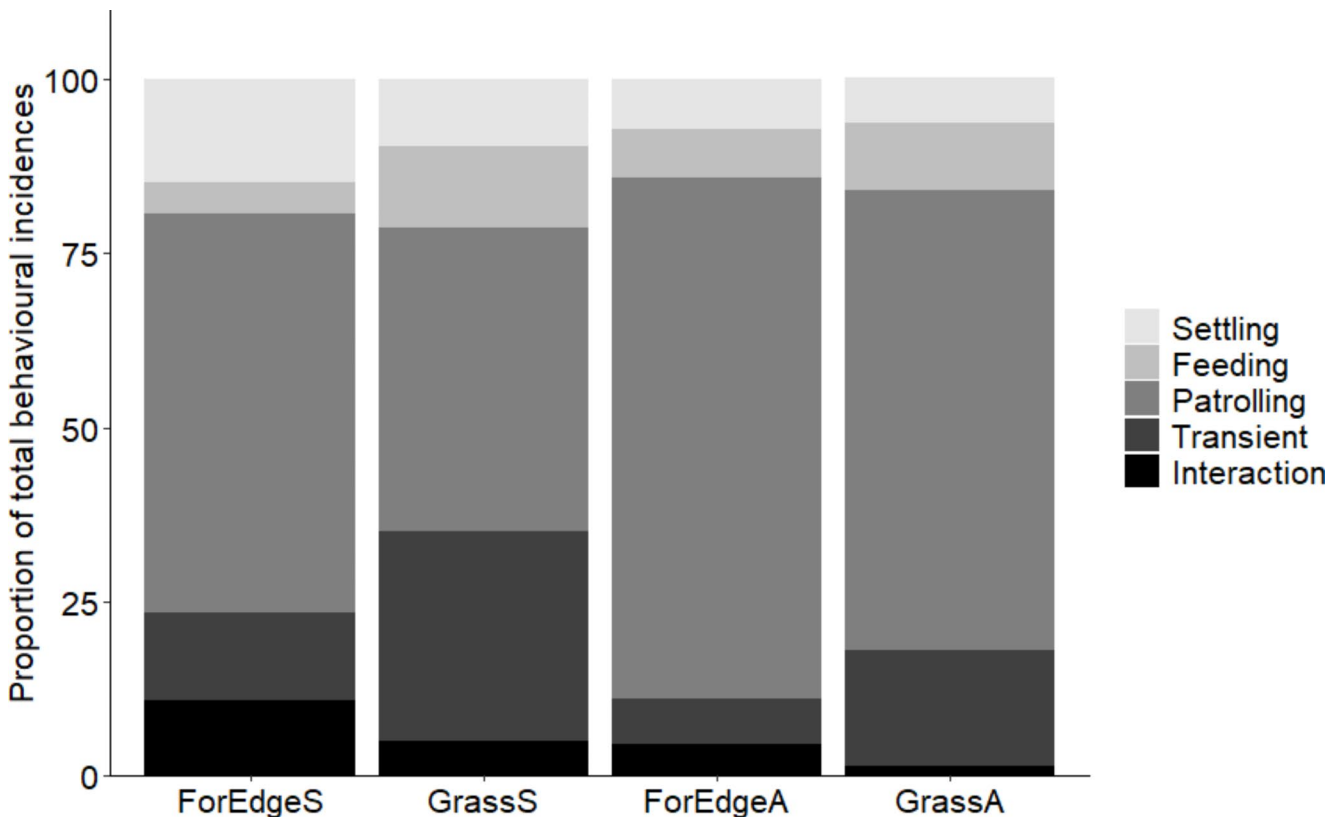


Fig. 3 Different butterfly behaviours, expressed as proportion of total behavioural incidences, at forest edges and in adjacent grassland in summer and autumn. (ForEdgeS = forest edge summer, GrassS = grassland summer, ForEdgeA = forest edge autumn, GrassA = grassland autumn)

the three butterfly groupings in the different locations and seasons were similar to the overall assemblage, except that the grassland specialists showed fewer overall transient behaviours, but more settling and feeding behaviours than

the other butterfly groups, and forest specialists showed fewer overall settling and feeding behavioural events than the other butterfly groups (Supplementary material, Figure S2).

Of the dominant forest specialist species, the novice, *Amauris ochlea ochlea*, and the mocker swallowtail, *Papilio dardanus cenea*, were significantly more abundant at forest edges than in grassland across both seasons (Table 3; Supplementary material, Table S3). The layman, *Amauris albimaculata albimaculata*, was significantly more abundant at forest edges than in grassland in summer (estimate: -3.32, S.E.: 1.61, 95% C.I.: -6.48, -0.16), but did not differ between locations in autumn (estimate: -0.43, S.E.: 0.45, 95% C.I.: -1.16, 0.30) (Table 3; Supplementary material, Table S3). The small orange Acraea, *Hyalites eponina*, was not influenced by location (Table 3; Supplementary material, Table S3). Of the dominant grassland specialists, the spotted joker, *Byblia ilithyia*, was significantly more abundant at forest edges than in grassland in both seasons (Table 3; Supplementary material, Table S3). Neither the common grass yellow, *Eurema hecabe solifera*, nor the broad-bordered grass yellow, *Eurema brigitta brigitta*, were influenced by location (Table 3; Supplementary material, Table S3). The abundance of the blue pansy, *Junonia oenone oenone*, was not influenced by any of the predictors (Table 3; Supplementary material, Table S3). Of the dominant habitat generalists, the citrus swallowtail, *Papilio demodocus demodocus*, was significantly more abundant at forest edges than in grassland in summer (estimate: -1.40, S.E.: 0.40, 95% C.I.: -2.27, -0.54), but its abundance did not differ between locations in autumn (estimate: -0.36, S.E.: 0.23, 95% C.I.: -0.85, 0.12) (Table 3; Supplementary material, Table S3). The window Acraea, *Acraea oncaea*, was influenced only by area, being significantly more abundant in grassland sites on the plantation estate (Table 3; Supplementary material, Table S3). The abundance of the four remaining habitat generalists, Barker's smoky blue, *Euchrysops barkeri*, African monarch, *Danaus chrysippus aegyptius*, African migrant, *Catopsilia florella*, and African common white, *Belenois creona severina*, were not influenced by any of the predictors (Table 3; Supplementary material, Table S3).

Although many of the same butterfly species occurred in both seasons (Table S2), there was a significant difference in butterfly assemblage composition between summer and autumn (Deviance = 375.1, $P = 0.001$).

In total, 201 flower visitations to 48 flowering plant species were recorded. In summer, there were 56 visitations to 21 flowering plant species, and in autumn there were 145 visitations to 36 flowering plant species. The flowering plants visited were a mix of herbaceous and woody plants (Supplementary material, Table S3). The plant assemblage visited did not differ between forest edges and grassland (Wald $\chi^2 = 2.52$, $P = 0.47$), between seasons (Wald $\chi^2 = 2.73$, $P = 0.68$), or between the protected area and plantation estate (Wald $\chi^2 = 3.30$, $P = 0.49$), and there was no interaction between location and season (Wald $\chi^2 = 0.72$, $P = 0.41$).

Discussion

We found that indigenous forest edges are important habitat components for butterflies, supporting rich butterfly assemblages consisting of a mix of forest specialists, habitat generalists, and grassland specialists. Certain behaviours indicative of habitat use, such as territory defence and courtship behaviour, were more prevalent at forest edges than in grassland. Furthermore, certain species preferentially used forest edges, especially during hotter and windier summer conditions. Forest edges therefore appear to increase habitat complexity and provide refuge for butterflies in the study region.

Importance of forest edges for maintaining high butterfly diversity and supporting certain behaviours

Edges between forests and open habitats often support diverse arthropod assemblages (Schmitt et al. 2020; Yekwayo et al. 2016), and this was also observed here. The high diversity at forest edges was driven largely by high numbers of forest specialists. Yet, grassland specialists and habitat generalists were equally species rich and abundant at the forest edges compared to grassland. Although certain grassland butterflies favour expansive unwooded grasslands (Gaigher et al. 2021; Schmitt and Seitz 2000), our results show that a significant component of the overall local butterfly assemblage utilizes forest edges.

Edges between forests and open areas often benefit arthropods, as they provide easy access to resources from both adjacent biotopes (Ries et al. 2004) and have gradients of solar radiation, temperature, and moisture that provide varied microhabitats supporting species with different microclimatic needs (Liivamägi et al. 2014; Schultz et al. 2012). In addition, these ecotones can provide rich floral resources (Bergman et al. 2018), dense larval host plants (Habel et al. 2022), and protection from adverse weather such as strong winds (Toivonen et al. 2017) and extreme temperatures (van Halder et al. 2011). In this high-wind and hot environment, we expected shelter from harsh weather to strongly influence butterfly distribution and behaviour. Such a sheltering effect would have been evident if butterfly species richness and abundance patterns in the different landscape locations were mediated by the effect of season, or if settling behaviours were more frequent at forest edges than in grassland. Such patterns have been demonstrated for butterflies and grasshoppers that shift in their microsite selection according to shifting weather conditions (Dennis and Sparks 2006; Dover et al. 1997; Matenaar et al. 2014).

We did not observe these effects, but instead saw similar butterfly patterns between summer and autumn for all

Table 3 Model-averaged estimates, standard errors, and confidence intervals from generalized linear mixed models explaining the abundance of individual species. Predictors with significant effects are in bold. Models with an asterisk next to the response had only a single top model and therefore no model averaging was performed. RI = relative importance of a predictor, calculated as the sum of Akaike weights over all models in which the variable was included. The reference levels in the calculation of the coefficients are as follows: Location = forest edge, Season = summer, Area = forestry estate

Species	Predictors	Estimate	SE	Lower CI	Upper CI	RI
Forest specialists						
<i>Hyalites eponina</i>	Season	2.29	0.46	1.36	3.21	1.00
	Area	-0.99	0.53	-2.07	0.07	0.64
<i>Amauris ochlea ochlea</i>	Location	-1.17	0.44	-2.06	-0.28	1.00
	Area	0.72	0.43	-0.14	1.58	0.52
<i>Papilio dardanus cenea</i> *	Season	-0.34	0.34	-1.03	0.35	0.33
	Location	-2.11	0.55	-3.18	-1.04	NA
<i>Amauris albimaculata albimaculata</i>	Location	-3.08	1.11	-5.30	-0.86	1.00
	Season	2.12	0.33	1.46	2.77	1.00
	Location x Season	3.08	1.07	0.92	5.23	1.00
	Area	0.38	0.41	-0.44	1.21	0.33
Grassland specialists						
<i>Byblia ithyia</i>	Location	-1.07	0.44	-1.96	-0.19	1.00
	Season	-1.17	0.46	-2.09	-0.25	1.00
<i>Eurema hecabe solifera</i> *	Area	0.59	0.40	-0.22	1.39	0.36
	Location x Season	0.77	0.82	-0.86	2.41	0.20
	Location	-0.55	0.34	-1.22	0.12	NA
	Season	0.82	0.26	0.31	1.33	NA
<i>Eurema brigitta brigitta</i>	Location x Season	0.08	0.42	-0.73	0.90	NA
	Season	0.78	0.28	0.22	1.34	1.00
<i>Junonia oenone oenone</i>	Location	0.46	0.34	-0.22	1.14	0.42
	Season	0.83	0.51	-0.20	1.85	0.52
	Area	0.55	0.52	-0.49	1.58	0.35
Habitat generalists						
<i>Acraea oncaea</i>	Area	-1.39	0.55	-2.49	-0.29	1.00
	Location	0.55	0.52	-0.48	1.58	0.35
<i>Papilio demodocus demodocus</i>	Location	-1.39	0.36	-2.10	-0.67	1.00
	Season	0.29	0.28	-0.27	0.84	1.00
	Location x Season	1.03	0.45	0.12	1.94	1.00
<i>Euchrypsis barkeri</i>	Area	-0.26	0.21	-0.69	0.17	0.37
	Season	0.48	0.57	-0.67	1.63	0.24
	Area	0.48	0.58	-0.69	1.63	0.23
<i>Danaus chrysipus aegyptius</i>	Season	0.26	0.31	-0.35	0.87	0.85
	Area	0.36	0.34	-0.32	1.04	0.30
	Location	-0.27	0.41	-1.08	0.58	0.14
<i>Catopsilia florella</i>	Location x Season	0.78	0.42	-0.06	1.63	0.14
	Season	-0.90	0.46	-1.83	0.02	1.00
	Location	0.56	0.47	-0.38	1.50	0.39

Table 3 (continued)

Species	Predictors	Estimate	SE	Lower CI	Upper CI	RI
<i>Belenois creona severina</i>	Location x Season	-1.20	0.67	-2.55	0.15	0.22
	Area	-0.35	0.34	-1.03	0.34	0.21
	Area	-0.98	0.56	-2.11	0.15	0.57

three butterfly groups. A possible reason for this may be that our use of the average seasonal conditions was too coarse to detect effects of weather conditions which can vary over shorter time scales. Furthermore, butterfly assemblage composition differed between seasons, and varying climatological preferences of different species occurring in the different seasons may have partly masked the occurrence and behavioural patterns at the assemblage level. Nonetheless, the single species patterns provided an indication that forest edges provide refuge for certain species. For example, *A. albimaculata albimaculata* and *P. demodocus demodocus*, preferred forest edges over grassland during summer, whereas they utilized forest edges and grassland equally during autumn. These are both mobile strong-flying butterflies which may benefit from the ability to actively seek out sheltered areas during harsher periods to avoid the effects of the wind, such as convective heat loss and mechanical disturbance (Barton 2014; Matenaar et al. 2014), or to prevent overheating from high (> 30 °C) temperatures (van Halder et al. 2011). Open areas are then used more frequently during calmer conditions and moderate temperatures, which has also been shown for butterflies in other landscapes comprised of habitats that vary in structure (Dennis and Sparks 2006). These results suggest that forest edges provide important refuge opportunities, at least for certain butterfly species.

We also investigated whether forest edges provide abundant or complementary nectar sources to grassland, which benefits grassland butterflies in other regions (Bergman et al. 2018). However, we recorded more feeding behaviours in grasslands than at forest edges for grassland specialists and habitat generalists in both seasons. Few nectaring events were observed for forest specialists overall. A possible reason for the higher feeding activity in grassland may be higher floral abundance in grassland, which we did not measure directly in this study. Furthermore, we found no evidence of complementarity in the nectar sources between grassland and forest edges, as similar flower species were visited in both locations. This is contrary to other studies showing complementarity in pollinator food sources among different biotopes (Bertrand et al. 2019; Mallinger et al. 2016). It is therefore unlikely that adult nectar sources at forest edges are a reason for the edges being so highly utilized, at least in the lower vegetation layers. We were unable to survey flower visitations in the upper tree canopies, which may provide additional food sources.

In addition to flower visitations, the prevalence of other behaviours also varied between forest edges and grasslands. We observed proportionally more inter- and intra-species interactions at the forest edges than in grassland, which included territorial behaviours (aerial contests such as aggressive spiral flights and chases indicative of territory defence), courtship behaviours (slow, spiral flights between

conspicuous), and mating. These patterns were consistent for all butterfly groups in both seasons. The high number of interactions at the forest edges may be because wooded habitats in predominantly open landscapes are clearly visible landmarks, which are often needed for visually cued butterfly behaviours like mate location and territory defence (Merckx and van Dyck 2005). Also, the heterogeneous conditions at forest edges increases an individual's likelihood of locating a suitable microclimate. As microclimate is a crucial component of habitat quality for butterflies (Stuhlreher and Fartmann 2018), edges likely represent valuable territories for many species. By promoting these behaviours related to reproduction, forest edges may play an important role in preventing population decline and influencing the spatial distribution of subsequent butterfly generations (Dennis and Sparks 2006; Habel et al. 2022).

We also observed more patrolling (slow flight with high returning frequency) at the forest edges than in grassland, for all butterfly groups in both seasons. Although the motivation for patrolling varies between butterfly species, it generally relates to foraging, mate-location, and searching for shelter (Van Dyck and Baguette 2005) in habitats that are perceived as favourable (Evans et al. 2020; Schultz et al. 2012). Considering that proportions of total behaviours were analysed, the high frequency of nectar feeding in the grassland may partly explain why certain other behaviours were more frequent at forest edges. Nonetheless, the behavioural results show that the diversity of butterflies at the forest edges is not just due to passive mixing or accumulation at the edges (Ries et al. 2004), but that different butterfly groups are intentionally using forest edges as an important habitat element.

An additional factor which may have influenced butterfly occurrence at forest edges, is larval host plant distribution, which can strongly influence adult habitat selection (Habel et al. 2022; Krauss et al. 2005). This was not included in this assemblage-level study due to the huge diversity of host plants used by the various species (Woodhall 2005). Future work focused on single-species habitat use would be valuable to determine the role that host plant distribution plays in the observed butterfly occurrence patterns.

Importantly, although forest specialists were most abundant at forest edges, they also frequently utilized the grassland, mostly for transient behaviour (fast, directed flight associated with displacement) and patrolling, especially during the more moderate conditions in autumn. High-quality grassland remnants are important as habitat and as movement conduits for grassland butterflies in transformed landscapes (Pryke and Samways 2001), and our results suggest that they are also important for forest-associated butterflies. Conserving the integrity of the grassland surrounding forest patches is therefore crucial for maintaining

forest butterfly diversity, which aligns with previous work on other taxonomic groups (Kotze and Samways 1999; Yekwayo et al. 2016).

Conservation implications

Indigenous forest edges are ecologically significant features for butterflies in these landscapes. They not only support a high diversity of forest-associated species, but also benefit butterflies in the broader grassland matrix. By providing shelter and varied microclimatic conditions, these forest edges increase opportunities for butterflies to satisfy their ecological and behavioural needs, which may become increasingly important under changing environmental conditions. Indeed, the maintenance of microhabitat diversity is identified as a primary management strategy towards buffering insect populations against global change (Harvey et al. 2022; Samways et al. 2020). Future research on the importance of forest patches and other landscape elements to long-term insect population persistence would help guide conservation planning in the study region. Furthermore, an understanding of the level of landscape heterogeneity that maximizes biodiversity would help fine-tune conservation action. Overall, our results indicate that the continued conservation of indigenous forest patches, along with the maintenance of a high-quality grassland matrix will be important for safeguarding overall butterfly diversity in these systems and in similar areas threatened by land-use change.

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Declarations

Competing interests James Pryke is co-editor in chief, René Gaigher is an associate editor, and Michael Samways is a patron of the Journal of Insect Conservation. None of the authors here were involved in the reviewing process. The authors have no further competing interests,

financial or non-financial, to disclose.

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