

RESEARCH ARTICLE

Divergent fire management leads to multiple beneficial outcomes for butterfly conservation in a production mosaic

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Funding information

Mondi Group

Handling Editor: Don Driscoll

Abstract

1. Fire is an intrinsic component of many natural ecosystems. In human-modified landscapes that occur in fire-driven ecosystems, it can be difficult to make fire management decisions, as there must be a trade-off between ideal conservation management and the practicalities of management in an altered landscape.
2. We assess how biodiversity is influenced by differences in fire regime in a landscape fragmented by timber production. Here, optimal fire management for maintaining grassland integrity is not always possible, due to logistical constraints and fire risk to plantations. We investigate thicket establishment arising from reduced fire frequency, and how this affects butterfly diversity, assemblage structure, indicator species and species associations to larval host plants with different growth forms. Butterflies were sampled along a gradient of woodiness in large-scale conservation corridors that separate timber compartments.
3. The two extreme stages along the successional gradient, recently burned grassland and natural forests, supported relatively diverse and complementary butterfly assemblages. Grassland corridors without fire for 2 years were as high in butterfly diversity and similar in composition to recently burned grasslands. However, corridors without fire for >5 years were encroached by thicket and supported lower butterfly diversity. Thicket, with its intermediate vegetation character, was poor habitat for species adapted to either open grassland or to forests. Also, thicket-encroached areas carry high fire risk to plantations.
4. *Synthesis and applications.* In this fragmented, fire-driven ecosystem, there is more than one burning strategy for achieving positive biodiversity outcomes. We recommend a divergent management approach that covers both extremes of the fire frequency continuum, with the choice depending on the stage of succession and management logistics for each site: (a) frequent burning to prevent woody encroachment in less-encroached, logistically easier sites or (b) letting succession run its course through thicket to forest by excluding fire in heavily encroached, logistically challenging sites. Both options are practicable and maintain biotopes that have high value for butterfly conservation and low fire risk to plantations. This divergent management approach is a flexible strategy that benefits both conservation and commercial interests across fire-prone plantation mosaics.

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KEYWORDS

butterfly, fire management, fire-prone ecosystem, fragmented landscape, grassland succession, indigenous forest, timber plantation, woody encroachment

1 | INTRODUCTION

Mimicking natural disturbance is one of the cornerstones of biodiversity conservation in human-modified landscapes, as it helps to maintain ecosystem dynamics (Lindenmayer et al., 2008). In naturally fire-driven ecosystems such as grassland, fire maintains the integrity of grassland vegetation by stimulating growth, limiting spread of alien and indigenous weeds and preventing succession to a woody plant community (Cadman, DeVilliers, Lechmere-Oertel, & McCulloch, 2013; O'Connor, Puttick, & Hoffman, 2014). However, it can be challenging to maintain these natural processes in fragmented landscapes that are concurrently used for commercial purposes (Cunningham et al., 2013; Lindenmayer, Hobbs, & Salt, 2003). In areas with multiple land-use priorities, there may be conflicting burning practices for different purposes (e.g. biodiversity conservation or managing plant biomass for asset protection; O'Connor, Uys, & Mills, 2004). As the need for conservation in transformed landscapes increases, it is important to understand how changes in these dynamics influence biodiversity (Driscoll et al., 2010).

We focus here on highly dynamic, fire-driven grassland ecosystems in KwaZulu-Natal (KZN) South Africa, in the Maputaland-Pondoland-Albany biodiversity hotspot, which is also favoured for plantation forestry. In many of these plantations, the unplanted areas occupy 10%–33% of the plantation and are composed of grasslands and indigenous forest patches, as well as rivers and wetlands, that together make up interconnected conservation corridors in the form of large-scale ecological networks (ENs), that contribute significantly to regional conservation (Pryke & Samways, 2012; Samways & Pryke, 2016).

Grassland corridors in the ENs are burned every 1–3 years to protect the timber compartments from wildfires and for biodiversity conservation. However, sometimes certain areas are left unburned where burning poses a risk to timber compartments or where it is logistically unfeasible to burn. These areas usually undergo succession, initially increasing in alien weed and shrub cover, such as *Bidens pilosa* and *Rubus cuneifolius*, and indigenous weedy species, such as *Pteridium aquilinum*. Eventually, encroachment by indigenous trees and shrubs, such as *Leucosidea sericea* and alien trees like *Acacia mearnsii*, can convert the grassland to thicket (Cadman et al., 2013; Titshall, O'Connor, & Morris, 2000).

Shrub thickening in grassland vegetation is often mirrored by changes in their associated faunal assemblages (Blaum, Seymour, Rossmanith, Schwager, & Jeltsch, 2009; Seymour & Dean, 2010; Stanton et al., 2018). Certain taxa in fire-prone systems depend on the habitat maintenance provided by fire (Driessen & Kirkpatrick, 2017). Shrub and tree encroachment can be a major threat to

indigenous species that require early successional stages (Ockinger, Eriksson, & Smith, 2006). Globally, this has resulted in the decline of many specialist early stage grassland species, and also in shifts in community composition due to changes in land use (Seymour & Dean, 2010; Stefanescu, Peñuelas, & Filella, 2009).

However, some faunal groups benefit from the presence of late seral stages in the landscape (Blaum et al., 2009; Little, Hockey, & Jansen, 2013). Late seral stages can be important for disturbance-sensitive species (Skorka, Settele, & Woyciechowski, 2007) or species that require complex vegetation structure (Fiedler, Wrabka, & Dullinger, 2017). Additionally, some species simultaneously use resources that occur in separate patches in different successional stages and rely on the presence of mosaics of seral stages (Dover & Settele, 2009). The effect of fire frequency on grassland fauna is therefore likely to be site specific and depends on the specific fire dynamics of the ecosystem (Parr & Andersen, 2006).

In the KZN ENs, differences in vegetation structure due to different burning regimes strongly influence arthropods and birds (Bazelet & Samways, 2011; Joubert, Pryke, & Samways, 2016; Lipsey & Hockey, 2010). However, previous studies have assessed responses to different burn intervals of up to 3 years, and the effect of advanced woody encroachment after a prolonged time since fire has yet to be investigated. Thicket represents a habitat type that is not historically represented in these landscapes, which consist of an open grassland matrix and forest patches embedded in this matrix (Eeley, Lawes, Piper, & Forest, 1999; Lawes, Macfarlane, & Eeley, 2004). Even though these intermediate seral stages are not common in unfragmented natural systems, suboptimal habitat patches can often play important roles in transformed landscape mosaics (Dennis, 2004; Dover & Settele, 2009; Ricketts, Daily, Ehrlich, & Fay, 2001). Considering that these unburned areas are common in the ENs, it is important to know their conservation value. We also have to consider how they interact with the production areas, as encroached areas pose a greater fire risk to adjacent timber compartments than either open grasslands or fire-resistant natural forests (Le Maitre, Kruger, & Forsyth, 2014).

To assess the potential habitat value of late seral stages of grasslands, we focused on arthropod biodiversity along a gradient of succession in a large-scale EN, using butterflies as focal taxon. Butterflies were specifically selected as they are good indicators of ecological change (New, Pyle, Thomas, Thomas, & Hammond, 1995) and are particularly sensitive to changes in woody plant cover (Dover & Settele, 2009). They are well studied globally, and detailed information is available on local species (Mecenero et al., 2013). They are also suitable surrogates for other arthropod taxa locally (Bazelet & Samways, 2012) and in other regions (Thomas, 2005).

Our first objective is to compare species richness and assemblage structure between successional stages to determine whether the intermediate seral stages can support similar levels of diversity and compositionally similar assemblages to the seral stages that are historically represented in the landscape. Secondly, we test for the effect of variables relating to vegetation structure and composition, which are expected to differ between seral stages, on butterfly species richness and assemblage structure. Thirdly, we identify species that are strongly associated with each seral stage to determine whether there are species that rely heavily on the intermediate seral stages. Finally, we assess how species using larval host plants with different growth forms are associated with the different seral stages to investigate a possible mechanism driving differences between assemblages. These data then enable us to develop management approaches in such fire-prone systems, especially focusing on how best to deal with these successional stages as part of conservation and fire risk management.

2 | MATERIALS AND METHODS

2.1 | Study area and design

The study was conducted in the KZN Midlands, South Africa, in the commercial timber estate Good Hope (29.6709S, 29.9639E; Figure 1). The estate covers 6 009 ha, of which two-thirds comprise exotic pine plantations and one-third is set aside for conservation. We sampled in the following seral stages:

1. 'Reference': large (>200 m wide) grasslands that had been burned less than 1 year prior to sampling. These sites served as natural reference sites, as large, well-managed corridors on Good Hope estate have been shown to be similar in habitat quality and species composition to nearby protected areas (Joubert &

Samways, 2014) and to unfragmented, privately owned grassland outside the estate (Pryke & Samways, 2003; Figure S1).

2. 'Burned': small (<150 m wide) grassland corridors that had been burned less than 1 year prior to sampling. These sites were similar in size to the remaining site categories. The reference sites would not have been directly comparable to the other sites, as biotope size can influence butterfly assemblage structure (Steffan-Dewenter & Tschardt, 2000; Figure S1).
3. 'Unburned': small grassland corridors that had been burned 1–2 years prior to sampling. These sites had taller vegetation and more alien and weedy species than the recently burned sites, including *R. cuneifolius*, *B. pilosa*, *P. aquilinum*, *Onopordum acanthium* and *Verbena bonariensis* (Figure S1).
4. 'Thicket': grassland sites that had not been burned for 5+ years and had been invaded by woody species, mostly *L. sericea*. Thicket sites had tall grasses, especially species characteristic of a late successional stage, such as *Cymbopogon* spp. and 21%–66% canopy cover. Certain sites had some indigenous forest trees (Figure S1).
5. 'Forest': patches of indigenous AfriMontane Mistbelt mixed *Podocarpus* forest, with tall indigenous trees and relatively closed canopy (56%–69% cover). These patches do not burn naturally and represent the expected climax successional stage when fire is excluded in the long term (Figure S1).

Seral stages were replicated as follows: eight reference sites, nine burned sites, seven unburned sites, eight thicket sites and four forest sites. The number of replicates depended on availability of sites in the study area. Seral stages were not equally distributed among the three sub-estates (See Figure 1, Sub-estate 1, 2 and 3), but were selected to be as equally distributed as possible. Sites of the same seral stage were always >450 m apart (Figure 1).

2.2 | Butterfly and environmental sampling

Sampling was conducted in 2016 from February to April. The majority of species fly year-round, with two emergence peaks after the rains in September–October and February–March, with the second peak, which corresponds with our sampling period, often being stronger for many of the species (Woodhall, 2005). Although we may have missed species with flight periods outside of the sampling period, our timing allowed for maximal detection of a large enough subset of the local species pool to make meaningful comparisons between seral stages. Butterfly sampling was done between 08.30 and 15.30 hr on warm, windless days with <30% cloud cover. Each site was sampled twice on a rotational basis to minimize bias with respect to preferred flying times. Each sample consisted of two observers walking along a random route throughout the site for 30 min, recording each butterfly within a 5-m radius along the route. This added up to 2 hr of observations per site. Timed transects were used and are suitable when the terrain and vegetation structure does not allow for fixed linear transects (Kadlec, Tropek, & Konvicka, 2012). We walked at a slow pace and paused frequently to scan the vegetation, which enabled us to detect less conspicuous species, especially

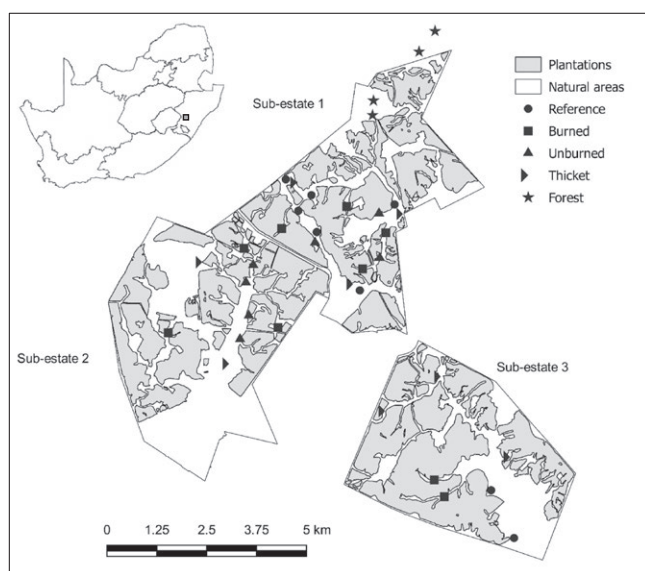


FIGURE 1 The study area showing the distribution of seral stages among the three sub-estates in Good Hope Estate in KwaZulu-Natal, South Africa

those using the canopies of wooded sites. This allowed us to make direct comparisons between open and wooded biotopes, although this does not completely remove the possibility of underestimation of butterfly numbers in lower visibility wooded sites. This bias was also accounted for statistically by using rarefied species richness in the analyses. Observers were always >50 m apart to prevent recording of the same individuals twice. Butterflies that could not be identified in flight were captured and preserved for later identification using Woodhall (2005). Specimens of each species are kept at the Stellenbosch University Entomological Museum. Information on the larval host plant growth forms for each species was obtained from Woodhall (2005) and Pennington, Dickson, and Kroon (1997) (Table S1).

Environmental variables were recorded within five 2 m² quadrats in the middle of each site, with each quadrat separated by 10 m. Variables included estimates of plant structure (canopy height, understorey plant height), plant composition (percentage grass cover, percentage woody and herbaceous plant cover, percentage alien plant cover) and adult food resources (floral abundance; Table S2). Records of time since last fire per site were provided by forestry managers.

2.3 | Statistical analyses

To assess sampling adequacy, species accumulation curves were constructed for observed species richness. The accumulation curve for observed richness did not reach an asymptote. Therefore, we performed individual-based rarefaction with 17 permutations using the rarefy function in the vegan package (Oksanen, Kindt, Legendre, & O'Hara, 2006) in R version 3.2.2 (R Core Team, 2014) and plotted rarefied species accumulation curves per seral stage, which did approach an asymptote (Figure S2). We used rarefied species richness as the response variable in univariate analyses. The rarefaction also accounted for the unequal sampling efficiency among seral stages (Gotelli & Colwell, 2009).

As rarefied richness data were normally distributed according to Shapiro–Wilk tests, a linear mixed model (LMM) was used to determine the effect of seral stage on overall species richness (Bolker et al., 2009) using the 'lme4' package in R (Bates, Maechler, Bolker, & Walker, 2014). Sub-estate was included as a random variable in the model to account for the unequal spatial distribution of seral stages. Post hoc Tukey tests were done to test for significant pairwise differences between seral stages using the multcomp package in R (Hothorn, Bretz, & Westfall, 2008).

In addition, we performed model selection and averaging to determine which environmental variables influenced variation in overall species richness (Burnham & Anderson, 2002). Where variables were strongly correlated based on Spearman's rank order correlations ($R < -0.65$, $R > 0.65$, $p < 0.05$), only one was included in the models. Five variables were included in the final model set: percentage overall canopy cover (which was positively correlated with percentage woody vegetation cover and canopy height), percentage alien plant cover, percentage grass cover (which was negatively

correlated with percentage herbaceous vegetation cover), floral abundance and understorey plant height. We constructed LMMs consisting of all possible combinations of explanatory variables, including an intercept-only model, which added up to 32 candidate models. Sub-estate was included as a random variable in all models. To allow for direct comparisons between their effect sizes, all variables were standardized to a mean of 0 and SD of 0.5 prior to analysis. Second-order Akaike's information criterion (AIC_c) was used as a selection criterion to rank candidate models using the dredge function in the 'MuMIn' package in R (Barton, 2018). Eleven models had a $\Delta AIC_c \leq 2$ and were included in the subset of best models (Burnham & Anderson, 2002). The values of the parameters were estimated by full model averaging of the best model subset using the model.avg function in the 'MuMIn' package in R (Barton, 2018), and unconditional estimates and 95% confidence intervals are reported. A variable can be considered as having a significant effect if the confidence interval does not include zero.

To test for the effect of seral stage on butterfly assemblage structure, permutational multivariate analysis of variance (PERMANOVA) was performed using the Permanova+ add-on in Primer 6 (Clarke & Gorley, 2006), with sub-estate included as random variable (Anderson, 2001). The resemblance matrix used in the PERMANOVA was based on Bray–Curtis similarity indices derived from square-root transformed abundance data (Clarke & Warwick, 2001). Distance-based linear modelling using the distLM routine in the Permanova+ add-on in Primer was performed to identify environmental variables that influenced butterfly assemblage structure (Legendre & Anderson, 1999). The same five variables that were used in the LMM model selection were included in dbRDAs. The backwards selection procedure was used to identify the combination of variables that best explain variation in the assemblages, using the AIC_c selection criterion. Environmental data were normalized prior to analysis, and Euclidean distance was used to calculate resemblance matrices (Anderson, 2001). Pseudo- F statistics and p values were estimated using 9,999 permutations.

IndVal analysis was used to identify species that are characteristic of each seral stage (Dufrene & Legendre, 1997). This method combines data on the specificity (relative abundance) and fidelity (frequency of occurrence) of each species to different habitats, with species with IndVal percentages $\geq 70\%$ being highly indicative of a habitat (McGeoch, Van Rensburg, & Botes, 2014). The 'labdsv' package in R was used for the analysis (Roberts, 2015).

To gain a more mechanistic understanding of the drivers of butterfly assemblages along the succession gradient, we assessed how butterflies with different larval host plant preferences were associated with the seral stages. We classified each species according to the growth form of their host plants (woody, herbaceous or grass; Table S1) and plotted the ordination of species and sites in the different seral stages, highlighting the species identified in the IndVal analyses, as they play an important role in distinguishing among assemblages. We used a detrended correspondence analysis (DCA) based on $\log(x + 1)$ transformed abundance data in CANOCO 5 (Ter Braak & Smilauer, 2012).

3 | RESULTS

Two 159 butterfly individuals were recorded in 48 species, 35 genera and five families, namely, Hesperidae, Lycaenidae, Nymphalidae, Papilionidae and Pieridae (Table S2). Our observed species richness values correspond to those from similar butterfly surveys in Afromontane grassland (43 spp. Crous, Samways, & Pryke, 2014, 31 spp. Pryke & Samways, 2003). A few morphologically similar species were difficult to distinguish in flight, and thus, their abundances were combined for analyses. This was done for *Belenois creona severina*, *B. aurota aurota* and *B. gidica abyssinica*, for *Cacyreus marshalli* and *Cacyreus tespis tespis* as well as for *Leptotes babaulti* and *L. pirithous pirithous*, adding up to 44 species included in analyses. Combined species all had larval host plants with the same growth form (Table S1).

Butterfly species richness differed significantly between seral stages ($\chi^2 = 16.67$, $p < 0.001$). Thickets had significantly lower species richness than the three open seral stages (Reference, Burned and Unburned), and lower richness than forests, although this latter difference was non-significant (Figure 2). The top 11 models identified by model selection ($\Delta AIC_c \leq 2$) all included percentage overall canopy cover (Table 1), which also represents percentage woody vegetation cover and canopy height, which were positively correlated with canopy cover, and were therefore not included in the models. Model averaging results indicate that canopy cover was the only variable that had a significant effect on butterfly species richness and showed a negative relationship with species richness (estimate: -2.51 , 95% CI -3.97 , -1.06 ; Table 1).

Butterfly assemblage structure differed significantly between seral stages (Pseudo- $F = 7.37$, $p < 0.0001$). PERMANOVA pairwise comparisons show that all open sites different significantly from wooded sites (Table 2). This is supported by the DCA ordination, which shows a clear separation of open and wooded sites (Figure 3). The first ordination axis thus appears to represent a

gradient of canopy cover. Assemblages of reference grassland and unburned grassland also differed significantly from each other (Table 2). Distance-based linear modelling results indicate that the best-fitting model contained only percentage overall canopy cover, which explained 39% of the variation in assemblage structure (Pseudo- $F = 22.18$, $p < 0.0001$; Table 3). Alien vegetation cover (Pseudo- $F = 1.72$, $p = 0.06$) and floral abundance (Pseudo- $F = 1.80$, $p = 0.05$) had marginally significant effects on assemblage structure, although they each explained only 3% of the variation and their inclusion in the model did not improve the model fit (Table 3).

Three butterfly taxa were highly characteristic of a seral stage (IndVal % $\geq 70\%$; Table 4). They were *Papilio dardanus cenea*, *Nepheronia argia* and *Mylothris agathina agathina* that occurred frequently and exclusively in indigenous forests. They are all species with woody larval host plants, and *P. dardanus cenea* and *N. argia* are forest specialists, whereas *M. agathina agathina* is a habitat generalist (Mecenero et al., 2013). The other species identified in the analysis had IndVal percentages between 39% and 60%, which indicates a moderate degree of habitat preference (McGeoch et al., 2014). This included six additional species that were moderately indicative of indigenous forests, namely, *Cacyreus lingens*, *Catopsilia florella*, *Bicyclus satifza satifza*, *Metisella metis*, *Paralethe dendrophilus* and *Papilio nireus lyaeus*. They are all forest specialists, except for *C. florella*, which is a habitat generalist (Mecenero et al., 2013). *Papilio nireus* and *C. florella* have woody larval host plants, *C. lingens* has herbaceous larval host plants and *B. satifza satifza*, *M. metis* and *P. dendrophilus* have grass as larval host plants. The latter three and *P. nireus* also occurred in moderate to high frequencies in thickets. Five species were moderately indicative of reference grassland, which were *Danaus chrysippus orientis*, *Eretis umbra umbra*, *Eurema brigitta brigitta*, *Junonia hierta cebrene* and *Precis octavia*. They all have herbaceous larval host plants, except for *D. chrysippus orientis*, which has woody larval host plants. *Eurema umbra umbra*, *E. brigitta brigitta* and *J. hierta*

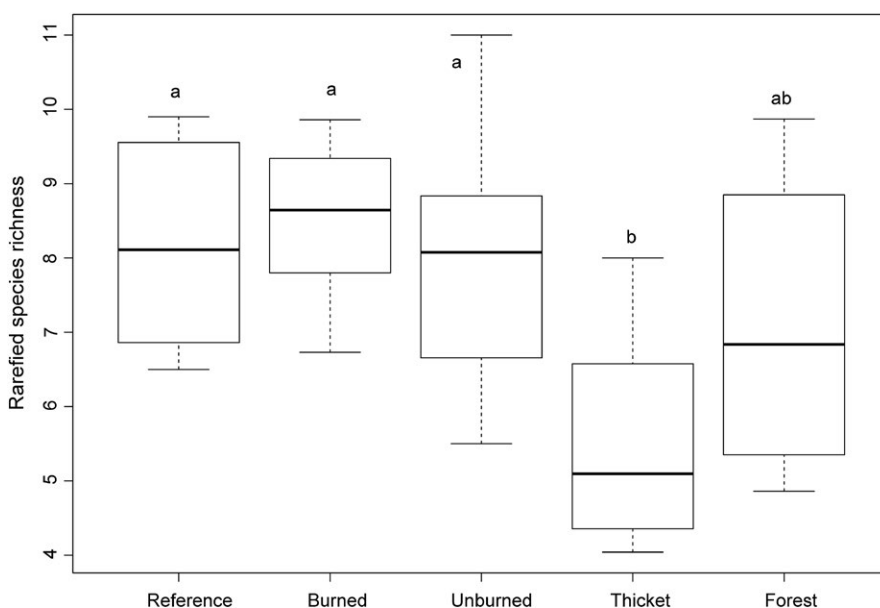


FIGURE 2 Rarefied species richness in the different seral stages. Medians with letters in common are not significantly different at $p < 0.05$

TABLE 1 Model-averaged estimates of environmental variables predicting rarefied butterfly species richness

Variable	Estimate	SE	95% CI	Relative importance	Number of containing models
Overall canopy cover	-2.51	0.72	-3.97, -1.06	1.00	11
Understorey vegetation height	0.52	0.66	-0.79, 1.83	0.61	7
Alien vegetation cover	-0.31	0.58	-1.47, 0.84	0.55	6
Grass cover	-0.68	0.82	-2.32, 0.95	0.36	4
Floral abundance	-0.19	0.45	-1.09, 0.72	0.28	4

Relative importance: Sum of Akaike weights over all models in the top subset in which the variable was included.
Significant effects are highlighted in bold.

TABLE 2 Permanova pairwise comparisons (t-values shown) of butterfly assemblage structure between seral stages

	Reference	Burned	Unburned	Thicket
Burned	0.94			
Unburned	1.38*	0.77		
Thicket	3.26**	3.37***	2.91*	
Forest	3.58**	2.77*	2.85**	1.12

* $p < 0.05$, ** $p < 0.001$, *** $p < 0.0001$.

cebre are grassland specialists (Mecenero et al., 2013) and were also recorded in the other open grassland seral stages. *Danaus chrysippus orientis* and *P. octavia* are habitat generalists that were recorded in all seral stages except indigenous forest. *Cacyreus marshalli/tespis* and *Cassionympha cassius* were moderately indicative of unburned grassland and thickets respectively. They both have woody larval host plants, possibly reflecting the greater woody plant cover in these seral stages. *Cassionympha marshalli/tespis* are habitat generalists, whereas *C. cassius* is a forest specialist (Mecenero et al., 2013).

The DCA ordination indicates how the species in the different seral stages differ in terms of their larval host plant growth form (Figure 3). The majority of species with herbaceous host plants was associated with the open grassland seral stages. Although species with woody host plants occurred everywhere, species with woody and grass host plants were more prevalent in the wooded sites, and those with grassy host plants were more closely associated with thickets than with forests. The first two axes of the DCA ordination explained 31.9% of the variability in the butterfly assemblages.

4 | DISCUSSION

4.1 | Habitat value of the different seral stages

The different seral stages of grassland differed in their habitat value for butterflies. The two extreme stages along the successional gradient, recently burned grassland and indigenous forest, supported relatively diverse and complementary butterfly assemblages with species that are adapted to either of these two stages. Butterfly

FIGURE 3 Biplot from detrended correspondence analysis showing sites in the different seral stages and butterfly species classified according to their larval host plant growth form, with the names of species identified in IndVal analysis included. The three species in bold are those with IndVal scores $\geq 75\%$, indicating a strong association with forests

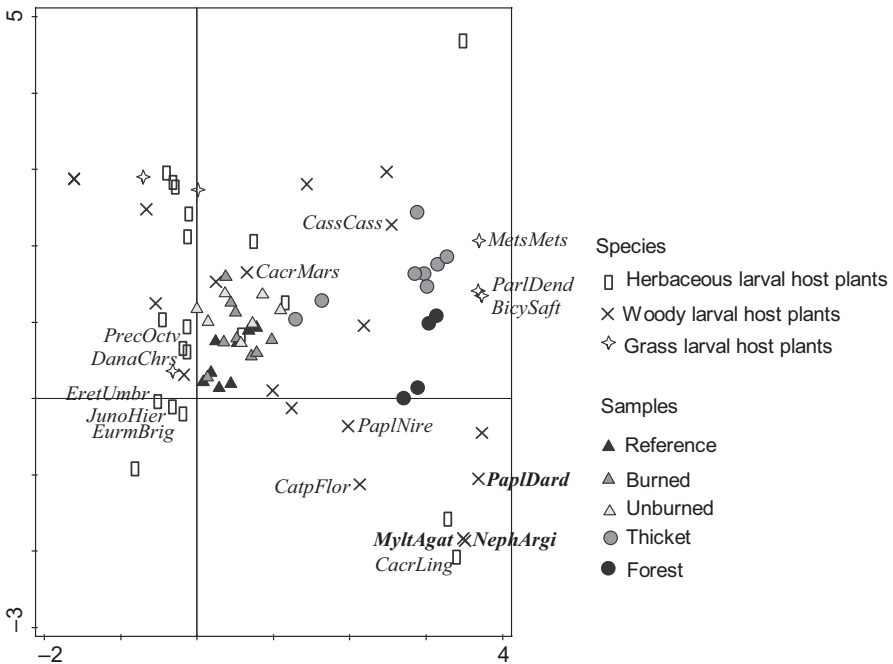


TABLE 3 Sequential test results from distance-based linear modelling of the influence of environmental variables on butterfly assemblage structure, using a backwards selection procedure

Variable	AIC _c	Pseudo-F	p-value	Proportion variation explained	Cumulative proportion variation explained
Full model	266.76				0.49
Grass cover	264.80	0.79	0.66	0.01	0.48
Alien vegetation cover	264.03	1.72	0.06	0.03	0.45
Floral abundance	263.47	1.80	0.05	0.03	0.42
Understorey vegetation height	262.82	1.63	0.08	0.03	0.39
Best solution: Overall canopy cover	262.82	22.18	0.0001	0.39	0.39

The effects of individual variables are shown as they are sequentially removed from the model. Significant and near significant effects are highlighted in bold.

TABLE 4 Results from IndVal analysis, which identified species associated with the different seral stages. Indicator value percentages, p-values and frequency in each seral stage are shown per species

	IndVal results		Reference	Burned	Unburned	Thicket	Forest
	IndVal %	p-Value	Frequency	Frequency	Frequency	Frequency	Frequency
Reference							
<i>Danaus chrysippus orientis</i>	54	0.002	100	100	72	12	0
<i>Eretis umbra umbra</i>	52	0.005	75	33	14	0	0
<i>Eurema brigitta brigitta</i>	47	0.022	75	67	57	0	0
<i>Junonia hierta cebrene</i>	47	0.009	100	78	71	0	0
<i>Precis octavia</i>	42	0.016	100	89	57	12	0
Unburned							
<i>Cacyreus marshalli</i> and <i>C. tespis tespis</i>	56	0.012	38	67	86	0	25
Thicket							
<i>Cassionympha cassius</i>	52	0.003	38	89	71	100	100
Forest							
<i>Papilio dardanus cenea</i>	100	0.001	0	0	0	0	100
<i>Nepheronia argia</i>	75	0.001	0	0	0	0	75
<i>Mylothris agathina agathina</i>	75	0.001	0	0	0	0	75
<i>Bicyclus safitza safitza</i>	60	0.002	0	0	0	75	100
<i>Metisella metis</i>	58	0.004	0	0	0	87	100
<i>Paraethe dendrophilus</i>	53	0.009	0	11	0	75	75
<i>Cacyreus lingeus</i>	50	0.012	0	0	0	0	50
<i>Catopsilia florella</i>	43	0.018	37	11	14	0	75
<i>Papilio nireus lyaeus</i>	39	0.041	50	56	43	37	75

assemblages in unburned grassland still resembled those of the recently burned grassland. However, after 5+ years of management cessation, once the grassland had turned to thicket, there was a shift to butterfly assemblages that are more characteristic of indigenous forest, but with fewer species than in forest, and with a lack of highly characteristic forest-associated species. Therefore, areas that had

undergone encroachment make a lower contribution than the other seral stages to butterfly diversity in the overall landscape mosaic.

Butterflies in these ENs are highly sensitive to habitat structure (Pryke & Samways, 2012), and here, overall canopy cover was consistently the strongest influencing factor on butterfly species richness and assemblage composition. Butterfly richness declined with

an increase in canopy cover. This negative effect of shrub thickening can be seen in many regions, with encroachment by pioneer trees and shrubs having led to declines in grassland butterfly diversity, including that of many species of conservation concern (Ockinger et al., 2006). Additionally, shifts in butterfly assemblage structure in response to encroachment by woody vegetation can occur (Stefanescu et al., 2009), which has also been observed for other invertebrates (Blaum et al., 2009), birds (Seymour & Dean, 2010), mammals and herpetofauna (Stanton et al., 2018). We observed a similar trend here, with a general shift in the assemblage from one being dominated by grassland specialists that use herbaceous host plants in the open grassland sites to one dominated by forest specialists, with both woody and grass host plants in the wooded sites. Overall, this indicates that the butterfly fauna tracks the changes in vegetation structure along the succession gradient.

Here, we expected that thickets would be used by some forest specialist butterflies, especially in sites with dense canopies and some large trees, as older thickets and forests are structurally similar. This would indicate that, even though thickets represent sub-optimal habitat for grassland species, they still have value for forest butterflies as supplementary or stepping-stone habitats (Dennis, 2004). Indeed, thicket assemblages included species with a moderate preference for forests, such as *B. safitza safitza*, *M. metis* and *P. dendrophilus*, and therefore could play a role in extending the forested habitat in the landscape for such species. However, overall species richness was lower in thickets than in forests, partly due to a lack of highly characteristic forest species, such as *P. dardanus cenea*, *N. argia* and *M. agathina agathina*. This is not that surprising, because even though forests and thickets are often superficially similar in structure, the indigenous forests are much older and less disturbed (Eeley et al., 1999), and so have higher and denser canopies, as well as having a richer diversity of floral and vegetative resources. The forest indicator species, which use all woody plants as hosts for their larvae, also may have benefited from the greater tree and shrub diversity in the indigenous forests.

The lower richness in thickets may be because it represents an intermediate habitat structure, and not a fine-grained mosaic of open and forested habitats. It therefore probably has few of the features that butterflies would use in true grassland or forest biotopes. Our geographical region is characterized by forest patches in a grassland matrix, with sharp ecotones that are naturally maintained by fire (Eeley et al., 1999; Lawes et al., 2004). There are highly distinct ground-dwelling arthropod assemblages between forests and grasslands (Kotze & Samways, 2001; Yekwayo, Pryke, Roets, & Samways, 2017), suggesting that many of the local species are adapted to this patch-matrix structure. We found here that there were distinct grassland and forest butterfly assemblages in the grasslands and forests, respectively, but neither of these groups were well supported by thickets.

Unburned grassland supported relatively rich butterfly assemblages which resembled those of the more recently burned grasslands. This is despite vegetation structure in unburned sites being different from that in the recently burned sites, with taller vegetation and more alien plants, including low-growing woody species.

Indeed, the more heterogeneous vegetation structure may have favoured certain butterflies, as occurs in abandoned grassland in other regions (Ockinger et al., 2006). Also, flowering alien plants, such as *V. bonariensis*, which was common in our unburned sites, are important nectar sources that can influence butterfly distribution in these ENs (Pryke & Samways, 2003). Grassland butterflies may therefore not be greatly influenced by a longer burn interval, as long as woody encroachment is not yet widespread.

4.2 | Management implications

Ecological networks made up of conservation corridors are important remnant offsets for sustainable forestry (Samways & Pryke, 2016), and conservation management aims to maintain as much of the natural biodiversity as possible. This is a major challenge considering that, historically, this is a highly dynamic system in an area subject to frequent natural fires (Corrigan, Kneen, Geldenhuys, & Van Wyk, 2010; Eeley et al., 1999), with these dynamics being greatly influenced by the surrounding commercial land use (Lawes et al., 2004). This means that deciding on what management approach to take, and which management goals to aim for, does not have a distinct target. For the butterflies in these ENs, we recommend a divergent management approach that aims to maintain each site at either of the two extremes of the fire frequency continuum. The choice of which extreme will depend on how far succession has proceeded, and the logistics and risks associated with managing each site.

In these ENs, restoration of areas that have already undergone advanced succession to thicket is challenging. Due to the high fuel loads, it is risky to burn thickets, and mechanical management requires heavy machinery. Therefore, in areas where encroachment is not yet widespread and where it is feasible to burn, fire to prevent succession would be the most effective management option. To prevent encroachment, it is recommended that this type of grassland is burned every 2–4 years (Cadman et al., 2013), and this seems to be suitable for EN grassland butterflies, as they are not negatively influenced by a longer burn interval of up to about 4 years. Studies on other arthropods and birds in these systems also indicate that this is an appropriate burn interval (Bazelet & Samways, 2011; Joubert et al., 2016; Lipsey & Hockey, 2010).

For heavily encroached areas that have not been burned for 5+ years, or areas where burning is unfeasible, it would be best to let them undergo further succession by excluding fire from these sites. This succession is a natural process, leading eventually to forest growth in the absence of fire in the long term (Geldenhuys, 1994). The thickets themselves have only moderate habitat value and may take many years to resemble primary forest. However, older thicket that resembles secondary forest can support some forest-dependent species (Ehlers-Smith, Ehlers-Smith, & Downs, 2017) and will eventually have greater habitat value for the forest butterflies as well as for other taxa not included here (Kotze & Samways, 2001; Yekwayo et al., 2017).

Balancing production and conservation in this system means that there may not necessarily be a single, linear management approach.

The solution lies in making localized, divergent management decisions by foresters for each part of the plantation mosaic: to burn every 2–4 years versus leaving the vegetation to undergo long-term succession, which are equally valid conservation goals. This would not be adverse to the overall butterfly assemblage in the long term, provided that both open grassland and indigenous forest remain on the landscape. Steering away from thicket development would not only promote biodiversity but would also reduce the spatial extent of the successional stage with its associated high fire risk to plantations. This divergent management approach, therefore, benefits both conservation and production, while providing flexibility to the landscape management decision-making process.

ACKNOWLEDGEMENTS

The study was funded by Mondi Group. The authors thank C. Deacon, K.J. Theron and L. van der Merwe for field and laboratory assistance. P. Belebese, B. Corcoran, S. Mbense, A. Moorhead, L. Shaw and J. Shuttleworth from Mondi South Africa provided logistical assistance and information on fire history for the study area. Ezemvelo KwaZulu-Natal Wildlife approved butterfly collecting under permit number OP121/2016. We thank J. Barlow, D. Driscoll (editors) and three anonymous referees for their constructive comments.

AUTHORS' CONTRIBUTIONS

R.G., J.S.P. and M.J.S. conceived the ideas, contributed critically to the draft and approved submission of the manuscript, R.G. and J.S.P. designed the methodology and analysed the data. R.G. collected the data and led the writing of the manuscript.

DATA ACCESSIBILITY

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.1jc66q0> (Gaigher, Pryke, & Samways, 2019).

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How to cite this article: Gaigher R, Pryke JS, Samways MJ. Divergent fire management leads to multiple beneficial outcomes for butterfly conservation in a production mosaic. *J Appl Ecol*. 2019;56:1322–1332. <https://doi.org/10.1111/1365-2664.13357>