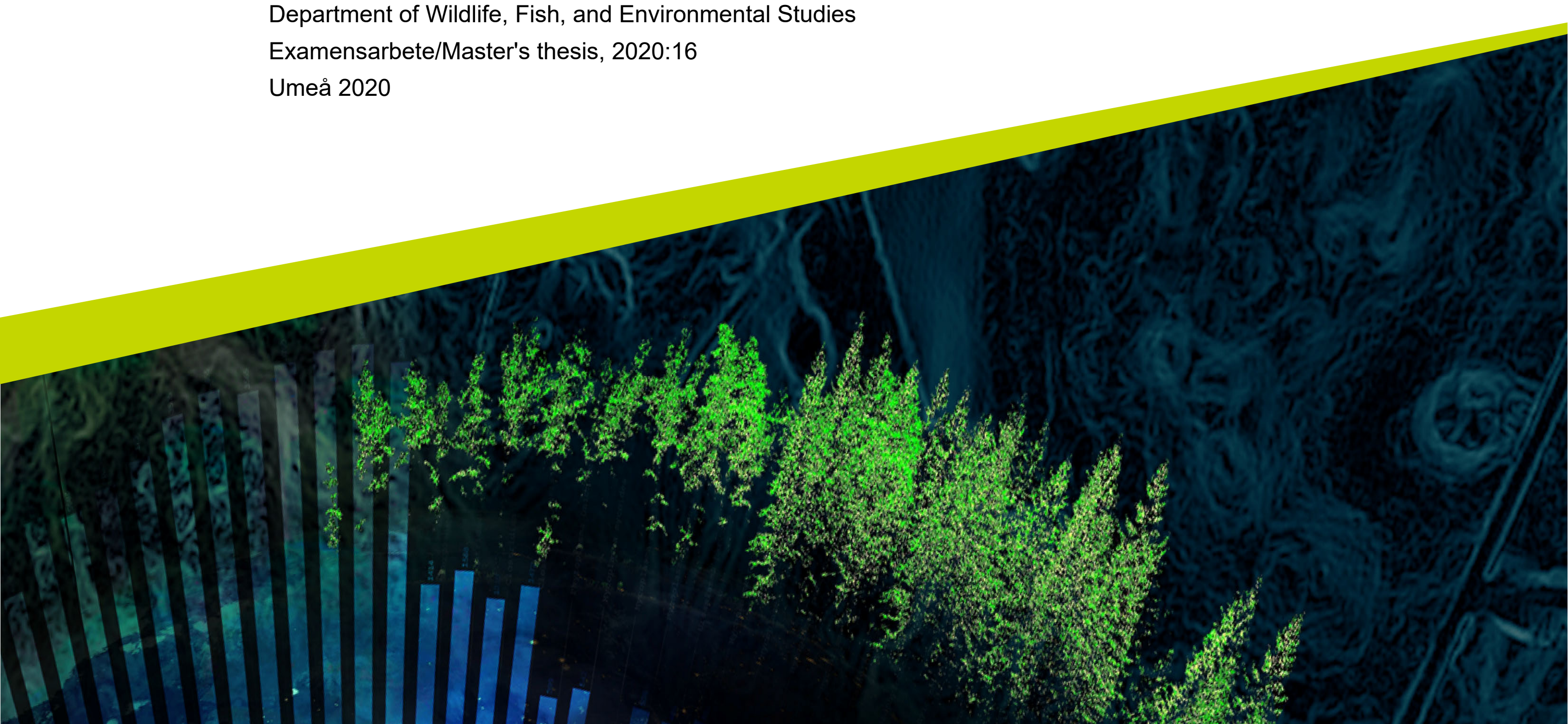
The effect of the interplay between fire frequency and grassland structure on tick abundances in the Hluhluwe-iMfolozi Park, South Africa

Thilo Heinecke

Master's thesis • 30 hp
Swedish University of Agricultural Sciences, SLU
Department of Wildlife, Fish, and Environmental Studies
Examensarbete/Master's thesis, 2020:16
Umeå 2020



The effect of the interplay between fire frequency and grassland structure on tick abundances in the Hluhluwe-iMfolozi Park, South Africa

Thilo Heinecke

Supervisor:	**Joris Cromsigt, Swedish University of Agricultural Sciences, Department of Wildlife, Fish, and Environmental Studies**
Assistant supervisor:	Elizabeth le Roux, Nelson Mandela University, Department of Zoology
Examiner:	Tim Hofmeester, Swedish University of Agricultural Sciences, Department of Wildlife, Fish, and Environmental Studies

Credits:	30 hp
Level:	Second cycle, A2E
Course title:	Master thesis in Biology
Course code:	EX0937
Course coordinating dept:	Department of Wildlife, Fish, and Environmental Studies
Place of publication:	Umeå
Year of publication:	2020
Title of series:	Examensarbete/Master's thesis
Part number:	2020:16
Keywords:	ticks, acari, pyrodiversity, grassland structure, fire ecology, fire frequency, grazing lawn

Swedish University of Agricultural Sciences
Faculty of Forest Sciences
Department of Wildlife, Fish, and Environmental Studies

Publishing and archiving

Approved students' theses at SLU are published electronically. As a student, you have the copyright to your own work and need to approve the electronic publishing. If you check the box for **YES**, the full text (pdf file) and metadata will be visible and searchable online. If you check the box for **NO**, only the metadata and the abstract will be visiable and searchable online. Nevertheless, when the document is uploaded it will still be archived as a digital file.

If you are more than one author you all need to agree on a decision. You can find more information about publishing and archiving here: https://www.slu.se/en/subweb/library/publish-and-analyse/register-and-publish/agreement-for-publishing/

☒ YES, I/we hereby give permission to publish the present thesis in accordance with the SLU agreement regarding the transfer of the right to publish a work.

☐ NO, I/we do not give permission to publish the present work. The work will still be archived and its metadata and abstract will be visible and searchable.

Abstract

Fire in ecology is a very variable factor and its effects are best described as a complex feedback system with other biotic and abiotic factors. These feedback systems need to be understood to enable generalized conclusions about the influence of fire regimes. The concept of pyrodiversity describes the variability in the characteristics of fire, such as fire intensity or frequency. This study investigated how the feedback mechanism between grassland structure in the form of grazing lawn abundance and distribution, and fire frequency affect the abundance of ticks (Class: Arachnida, Subclass: Acari), which are highly connected to both factors. I sampled tick abundances in 30 plots in the Hluhluwe-iMfolozi Park (South Africa) via tick drags. While neither of the parameters had an effect in itself, the interaction between grazing lawn coverage and long-term fire frequency significantly affected tick abundances leading to lower abundances with increasing lawn coverage in areas of low, but not at high, fire frequencies. The heterogeneity of their distribution was dependant on the heterogeneity of grass biomass, herbivore density and an interaction between the average grass biomass and the short-term fire frequency in the last 17 years. Tick distribution was more heterogeneous in areas of high grass biomass or zero short-term fire frequency, but more variable in areas with low fire frequencies above zero. This indicates that the effect of pyrodiversity on certain species could vary with other environmental factors important for the species. It also suggests that the disappearance of grazing lawns could lead to an increase in tick abundance if fire management plans are not adapted accordingly, potentially leading to higher herbivore tick infestations.

Keywords: ticks, acari, pyrodiversity, grassland structure, fire ecology, fire frequency, grazing lawns

Table of contents

List of Figures........ 6

1. **Introduction**........ 7

2. **Material and Methods**........ 10

        2.1 Site selection and sampling procedure 10

    2.2 Explanatory variables and statistical analysis 12

        2.2.1 Fire-frequency 12

        2.2.2 Grassland structure 13

        2.2.3 Additional Covariates 14

    2.3 Dependant variables and statistical analysis........ 14

3. **Results** 16

    3.1 Total tick abundance (TTA)........ 16

    3.2 Heterogeneity of tick distribution (CVT) 17

4. **Discussion**........ 20

Acknowledgements........ 23

References........ 23

Appendix........ 26

List of Figures

Figure 1. Hypothesized relationship between grassland-structure (proportional amount of grazing lawn in an area), fire frequency (red line, right y-axis) and the expected tick abundance (black line, left y-axis). Dashed lines indicate the variability of fire-frequency in bunch grass dominated areas and its associated effect on tick abundance. 9

Figure 2. Plots sampled (1-30) in the Hluhluwe-iMfolozi Park, South Africa in relation to A - long-term fire frequency from 1955 - 2019; B - days since last burn; C - percentage of lawn coverage and D - in a unconstrained PCA with all independent variables (Total inertia 9, PC1 48%, PC2 17%). Maps A+B in 500m resolution, major rivers (blue) and section boundaries (dark red) added in map C. Small inset map in map B shows position of the park in southern Africa. 11

Figure 3. Picture of Thilo Heinecke conducting a tick drag on grazing lawn.. 12

Figure 4. The conditional effect and confidence intervals of lawn percentage on long-term fire frequency (A) and vice versa (B) for their significant interaction as identified in a double Poisson model (DPO, t (5,28) = 2.988, p = .007**) with a histogram added (top). C and D show the tick abundance (TTA) against the gradient of FF5519 (C) and La_p (D) with the other variable categorized at the thresholds indicated by the vertical lines in A and B. Points are observed TTA, horizontal lines are the predicted TTA as returned by the DPO model and the vertical, dotted lines show the confidence interval of the fit at the points of observation. 17

Figure 5. Observed (points) and predicted (line) relation between average grass biomass (Mean DPM) and lawn coverage on the sampled plots. Relation is significant in an inverse Gaussian (IG) model (upper right)... 18

Figure 6. The conditional effect of average DPM (Mean DPM) on short-term fire frequency 2002-2019 (A) and vice versa (B) for their significant interaction as identified in a Weibull model (WEI, t (7,29) = 3.278, p = .003**) with a histogram added (top). C and D show the tick distribution heterogeneity (CVT) against the gradient of FF0219 (C) and Mean DPM (D) with the other variable categorized at the thresholds indicated by the vertical lines in A and B. Points are observed CVT, horizontal lines are the predicted CVT as returned by the WEI model and the vertical, dotted lines show the confidence interval of the fit at the points of observation. 19

1. Introduction

The view on fire in ecology and conservation has changed considerably over the last few decades. Before the 1970s, it was often treated as a disruptive event that “upsets the balance of nature” based on equilibrium theory (Parr and Andersen 2006). This lead, in its most extreme form of application, to the enforced complete exclusion of fire, while it is now seen as a necessary factor driving ecosystem dynamics in both ecology and conservation (Parr and Andersen 2006). This is especially true for biomes like savannahs, in which frequent burning leads to a diversity of flora and fauna that have adapted to these disturbance events, making fire a key ecosystem driver (Parr and Andersen 2006; Abades, Gaxiola, and Marquet 2014). However, fire is a highly variable factor. Individual fires differ in their properties such as fire extent and intensity, which will alter their direct impact on the environment but lead, over time, to distinct fire regimes (Archibald et al. 2013). These fire regimes are characterized by a typical combination of attributes such as size, intensity, frequency, seasonality and their spatial and temporal dimensions which are summarized by the concept of pyrodiversity (Martin and Sapsis 1992; Hempson et al. 2018). When this concept was first established by Martin and Sapsis (1992), they additionally hypothesized that “pyrodiversity begets biodiversity” by promoting habitat heterogeneity and consequently offering a higher amount of ecological niches (Martin and Sapsis 1992; Parr and Andersen 2006; Hempson et al. 2018). While this concept was highly influential in shaping fire management strategies (eg. in the form of patch mosaic burning which introduces heterogeneity in fire management), the empirical evidence for this paradigm is rather inconclusive with different outcomes depending on species, scale and biome (Kelly, Brotons, and McCarthy 2017). Potential reasons for this are that different studies used different proxies for pyrodiversity and/or that the effects of pyrodiversity interact with other environmental variables, such as local climate. For example in a study over the whole African savannah biome, the positive relationship between pyrodiversity and the species richness of birds and mammals was much stronger in wet savannahs (>650 mm/yr.) than in dry savannahs (Beale et al. 2018). Additionally, individual factors within the concept of pyrodiversity, like fire frequency, could interact with other environmental variables important for a particular species, introducing further variability (Bowman et al. 2016). If for example abundances and composition within a certain species guild are dependent on pyrodiversity in some of their habitats, but not in others, studies about this connection could come to conflicting conclusions depending on which habitat was investigated. Recent research therefore rather highlights that pyrodiversity interacts with other drivers such as landscape structure, climate and herbivory in a complex feedback system (Bowman et al. 2016; Archibald and Hempson 2016; Hempson et al. 2018).

One of these feedback mechanisms in savannahs is the interaction between grassland structure (as created and maintained by herbivory) and fire-patterns. As herbivores and fire compete for the same resource (vegetation), they consequently influence each other on several levels (Bowman et al. 2016; Archibald and Hempson 2016; Johnson et al. 2018). Grazing, for example, may reduce fire frequency by reducing grass fuel load (Archibald and Hempson 2016). An extreme example of this are grazing lawns, which are distinct grass communities dominated by short, prostrate-growing stoloniferous grasses. These occur as patches of different size surrounded by tall, upward-growing bunch-grass. Grazing lawns are considered to be too short in stature to carry fire (Archibald et al. 2005; Waldram, Bond, and Stock 2008). They are highly nutritious grazing areas as the grasses are kept in a constant young-growth state (Archibald et al. 2005; Bonnet et al. 2010; Cromsigt and te Beest 2014). While they are maintained by multiple herbivores, their abundance and size is substantially higher in areas with white rhino (*Ceratotherium sinum sinum*) and hippopotamus (*Hippopotamus amphibious*), suggesting a strong link between large grass-feeding herbivores and lawn occurrence (Lock 1972; Cromsigt and te Beest 2014). Since grazing lawns need high grazing pressure to be maintained, it can be assumed that the disappearance of these large herbivores would lead to a substantial drop in their occurrence and size. Furthermore, these grazing lawns stand in a complex relationship with fire. On the one hand, they stop fires from spreading, and therefore modulate pyrodiversity, by acting as natural fire barriers which lowers local fire frequencies and increase the spatial heterogeneity of fire spread (Archibald and Hempson 2016; Donaldson et al. 2018; Archibald 2008). It was suggested that above a threshold of 30% proportional amount of grazing lawn, an area burns infrequently if at all (Archibald et al. 2005). On the other hand, herbivores are attracted to the fresh re-growth on recently burned areas which can disperse them widely and prevent the highly intense and localized grazing necessary for lawn maintenance, turning them into more flammable bunch grass again (Archibald et al. 2005; Donaldson et al. 2018). Furthermore, as fire frequency is dependent on a lot of factors, areas more dominated by bunch grasses can have low fire frequencies as well (eg. by low ignition events), while it will be uniformly low in areas dominated by grazing lawn. While multiple recent studies have established more universal measurements of pyrodiversity, the factors driving it and its impact on biodiversity on a large, biome-wide scale, more investigation is needed on the elasticity of individual genera to these feedback systems (Parr and Andersen 2006; Hempson et al. 2018).

A taxon highly impacted by both of these factors, grassland-structure and fire, are ticks (Class: Arachnida, Subclass: Acari). Ticks are obligate, blood-feeding ectoparasites with an almost world-wide distribution (but a particular abundance in the afrotropical region) that feed on basically all mammals, birds and reptiles (Madder, Horak, and Stoltsz 2014). Ticks may influences their hosts negatively, either directly (e.g. exsanguination, anemia) and/or indirectly as a common vector for pathogens (Madder, Horak, and Stoltsz 2014). Therefore, an improved understanding of the drivers of tick abundances and distribution will contribute towards understanding parasite risk. On domesticated cattle in sub-saharan Africa, there are four groups of tick-borne diseases, anaplasmoses, babesiosis (African and Asiatic redwater), bovine ehrlichioses (Heartwater) and theilerosis (Yawa et al. 2018). Ticks can be found on short grasses, but they are often described as being in higher numbers in taller grasses (Fyumagwa et al. 2007; Yawa et al. 2018). Fire lowers their abundance in an area considerably due to direct mortality and/or because of the reduction/ elimination of their refugia in the field layer (Goodenough et al. 2017). In fact, beside acaricides, fire is the most common strategy to control tick populations on commercially used land (Gleim et al. 2014). The direct timing when their populations recover to pre-burn levels was shown to be at least three years in African savannah in Tanzania (Fyumagwa et al. 2007), but could be shorter in other biomes (Adams et al. 2013). Another study in the South African Highveld on tick abundance showed that tick abundance peaked 2-3 years after a fire (Goodenough et al. 2017).

This leads to an intriguing problem in terms of predicting general tick abundances on a landscape level. The higher the proportional amount of grazing lawns, the lower the fire frequency (fig.1, red lines). In bunch grass dominated landscapes, the fire frequency varies more than in lawn dominated landscapes (Fig.1, dashed red line). Areas with higher fire frequencies are expected to have relatively low tick abundances as their refugia and populations constantly need to recover (Fig.1, red area). At the same time, areas with high proportional amounts of grazing lawns experience barely, if any, burnings. However, the expected relative abundance of ticks in these areas is lower as well due to the short-grass dominated habitats that are unfavourable for ticks due to the lack of a humid micro-climate (Fig.1, green area). The investigation of this dynamic would shed further light on the interplay between landscape structure and pyrodiversity and its direct consequence to tick populations. Additionally it would further reveal the impact of natural or managed fire regimes on the parasitic load of a landscape, with the possibility to potentially adapt fire management towards targeted control. To investigate these relationships, this study will answer the following hypotheses:

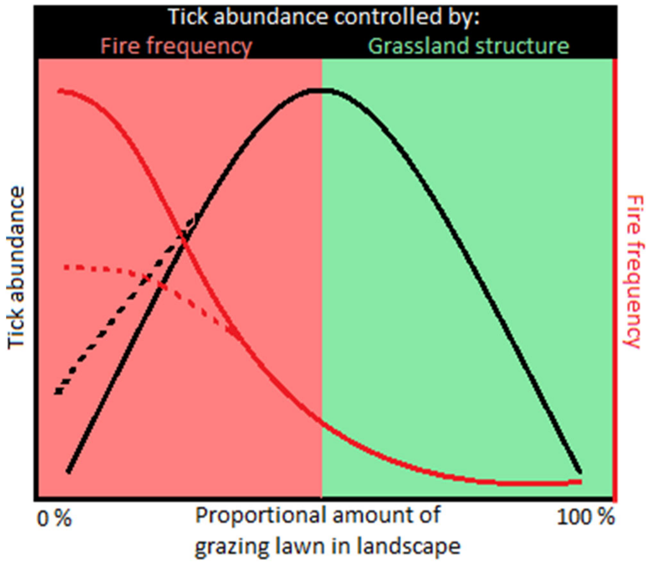


Figure 1. Hypothesized relationship between grassland-structure (proportional amount of grazing lawn in an area), fire frequency (red line, right y-axis) and the expected tick abundance (black line, left y-axis). Dashed lines indicate the variability of fire-frequency in bunch grass dominated areas and its associated effect on tick abundance.

1) The higher the proportional amount of grazing lawn in an area, the lower the tick abundance.
2) The higher the fire frequency of an area, the lower the tick abundance.
3) The lowest tick abundances will be in areas that burn very frequently or have a high proportional amount of grazing lawn.

2. Material and Methods

2.1 Site selection and sampling procedure

I conducted the study in the Hluhluwe-iMfolozi Park (KwaZulu Natal, South Africa; hereafter HiP), a provincial protected area that is known for its high density of white rhino. In total, 30 plots were selected and sampled in HiP (appendix, Tab.A1). Their selection was based firstly on accessibility and a near continuous grass layer with a woody component sparse enough to allow tick drags over the whole area. Secondly, I selected plots that varied strongly in the dominance of lawn versus bunch grass and that spanned the full range of fire frequencies between 1955 and 2019 and time since last burn (Fig.2 A, B, C). On each plot seven parallel transects spaced 50m apart were sampled. Each transect was 300m long and tick-drags of 10m were conducted every 60m along them. This resulted in 35 approximately equally spaced tick drags on each plot covering 350 m in total. The exceptions were Plot 1 which consists of five 500m and two 300m transects with tick drags of 20m every 100m and 50m respectively (coverage 680m) and Plot 2 with five 20m, seven 10m and 23 5m drags along 300m transects (coverage 285m). This inconsistency was due to an early adjustment to sampling protocol due to unforeseen logistical constraints. They were subsequently excluded from the analysis of certain response variables as specified in each analysis below. This resulted in 1047 usable tick drags records from all plots. The device used for the tick drags was a 1.10 x 1.10 m thick canvas cotton cloth, which was attached at the front side of a back-angled T-frame constructed from wood and a broom-stick (Fig.3). This design ensured the controlled contact of the cloth with the surface for the whole drag and minimized the potential human influence on the sampling by enabling the cloth to be pushed in front of the researcher (Fig.3). A study in the south-eastern US showed that tick drag methods are comparable to other methods to sample ticks on grassland (Mays, Houston, and Trout Fryxell 2016). The cloth had two equally spaced cuts of 70cm in the back which divided the lower part of it into three strips with wire spreader bars inserted into their ends to avoid twisting during a drag. A centred 1x1m field was marked on the underside of the cloth and only ticks within this area were counted. Each drag was conducted by slowly walking 10m while pushing the drag device with the cloth in full contact with the surface at all time (Fig.3). After each drag, the number of tick immatures and adults within the marked area on the cloth were counted. While the immatures were removed after the drag, the adults were collected in 70% ethanol for later identification.

Additionally, another study conducted at the same time measured the grassland structure along the same transects. Disc pasture measurements (DPM), which measure grass biomass by dropping a round metal plate from a fixed height and recording how far it compressed the grass from the guiding rod, were conducted every 5 m and the dominant grassland type (lawn or bunch grass) was recorded (resulting in 60 measurements per transect, 420 per plot, 12600 in total). Furthermore the approximate number of trees and shrubs in a 10m radius was assessed every 50m in five categories (0-15; 15-30; 30-45; 45-60; 60+).

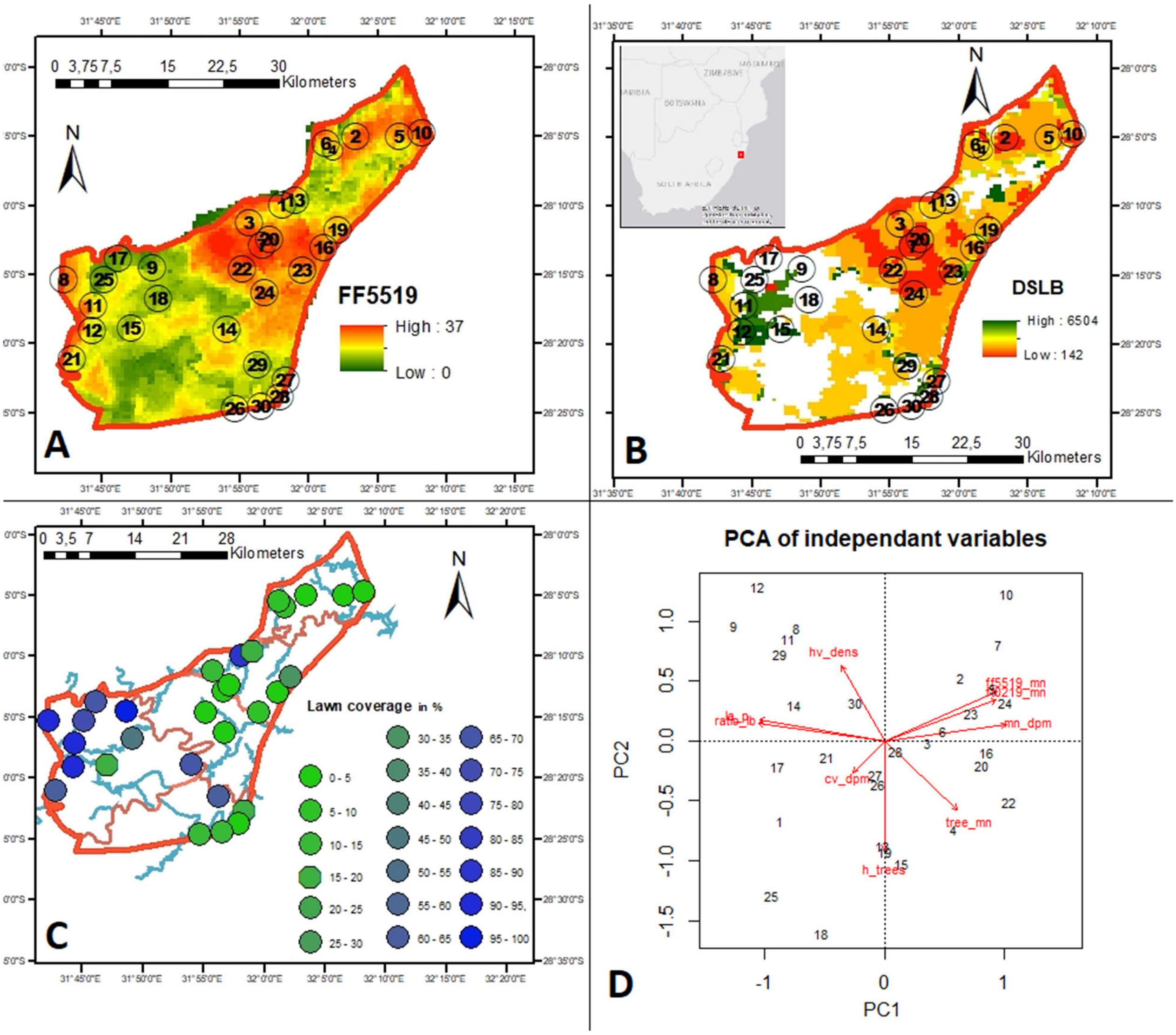


Figure 2. Plots sampled (1-30) in the Hluhluwe-iMfolozi Park, South Africa in relation to A - long-term fire frequency from 1955 - 2019; B - days since last burn; C - percentage of lawn coverage and D - in a unconstrained PCA with all independent variables (Total inertia 9, PC1 48%, PC2 17%). Maps A+B in 500m resolution, major rivers (blue) and section boundaries (dark red) added in map C. Small inset map in map B shows position of the park in southern Africa.

Figure 3. Picture of Thilo Heinecke conducting a tick drag on grazing lawn.

2.2 Explanatory variables and statistical analysis

All geographic information and maps were calculated and visualized in ArcGIS (version 10.6) while all statistical analysis was conducted in R and RStudio (RStudio Team 2018; R Core Team 2019).

2.2.1 Fire-frequency

The fire frequency for HiP was calculated using a 500 x 500 m raster map from three different sources (Fig.2 A).

1) For the years 1955 – 2002 historic fire maps as recorded annually and provided by HiP management were used. These showed the total area of the park that burned each year and were combined by summing the number of times at least 50% of each raster cell was covered by a recorded burn (47 polygons, one per year).
2) For 2002 – 2015, shapefiles which combine the records from HiP (mentioned above) with burned area satellite maps from the MODIS MCD64A product were used (Herkenrath 2019). These maps were additionally ground-truthed during the animal census every second year along 34 line transects spread across the park. As such, these maps were likely the most accurate of the three sources, albeit only available for a shorter time period.
3) The years 2016 – 2019 were mapped purely from the MODIS MCD64A burned area satellite product (Giglio et al. 2018). These monthly satellite images in 500m resolution record if a pixel burnt through changes in surface reflectance. The number of times each pixel was recorded as burnt between January ’16 and March ’19 were summed.

The three sources described above were combined to obtain a fire frequency value for the entire period 1955 – 2019. Furthermore, as the MODIS MCD64A additionally records the date a pixel burnt, the last time each raster cell was recorded as burning since November 2000 was extracted from the images and converted into days before the 01.04.2019. This information was used to create three maps for the fire characteristics of HiP:

FF5519: The fire frequency from 1955 – 2019 from all three sources in a 500 m resolution ranging in total from 0 to 37 fires (Fig.2 A).

FF0219: The more recent fire frequency from 2002 – 2019 based only on the last two fire frequency sources in a 500 m resolution ranging in total from 0 to 13 fires.

DSLB: The days since each 500 m raster cell burned before the 01.04.2019, ranging in total from 142 to 6608 days (Fig.2 B).

The sampled plots did not exactly align with the raster cells of the maps. However, there was mostly no geographical/physical reason within the field plots to expect a differing fire regime (eg. roads or rivers that split the plot). Exceptions are the plots 4, 6 and 7 in which roads had to be crossed to successfully sample full and comparable transects. The sometimes large differences in fire variable estimates between adjacent raster cells are expected by the nature of their compilation. Therefore the fire frequency for each individual drag in a plot was extracted and their mean value used to characterize the plot in general. For the days since last burn, the minimum recorded value was used as there are several reasons why the satellite product would not be able to identify a fire (eg. satellite passing interval, reflectance change too small to be registered). Therefore it is a reasonable assumption that if a fire was identified, it would impact the whole plot and the major uncertainty is if there was a later fire that was not picked up by the satellite. As some of the plots were in areas that could not be assigned a DSLB as they did not burn in the timeframe for which satellite data are available, the variable was analysed as a category for plots that burned within the last year (0-1), within the last 19 years (1-19) or not within the last 19 years (19+).

2.2.2 Grassland structure

The grassland structure of each plot was characterized by compiling the grassland measurements from the accompanying study into the following variables.

La_p: The number of DPM measurements on lawn grass species at the plot in percent with a range between 0 – 95.06% (Fig.2 C).

Ratio_lb: The ratio between the measurements on lawn and bunch grass in percentage (La_p - bunch %)/ (100/(La_p + bunch %))), thereby putting the lawn cover percentage in relation to bunch grass and eliminating other surfaces (bare soil, forbs, etc.), which ranged from -100 (pure bunch grass) to 92.26 (almost pure lawn grass).

Mn_dpm: The mean DPM measurement value across all measurements on the plot which ranged from 2.6 to 25.2 to quantify grass biomass.

Cv_dpm: The coefficient of variation of the DPM measurements on the plot ((Standard Deviation/Mean) x 100) to characterize the variability of grass biomass within the plot, ranging from 26.78 to 75.83.

2.2.3 Additional Covariates

Additional variables that were available and expected to have an influence on tick abundances were the following:

Tree_mn: The mean number of trees per plot, calculated by taking the mean number of the recorded categories (7.5, 22.5, 37.5, 52.5 and 66.5) and multiplying this value by the number of times this category was recorded. This approximately quantifies the overall openness of the plot and ranges from 12.26 to 61.48 trees.

H_trees: The evenness of the tree count, calculated via a Shannon index of the categorical counts on a plot. It characterizes the variation in the openness of a plot and ranges from 0.62 to 1.6 with low values indicating homogenous and high values indicating heterogeneous distribution of trees.

Hv_dens: The herbivore density (from the size of a red duiker to a white rhino, not containing elephants and black rhino) as compiled by combining the annual census counts of the last 14 years from transect based, distance sampled density estimates and supplied by HiP park management. After resampling the map to the same 500m resolution, the density at the point of each individual drag was extracted and their mean used to characterize the plot in the same way as the fire frequencies. It ranged from 25.72 to 93.48.

Collinearity between independent explanatory variables were assessed by calculating their Variance inflation factor (VIF; (package: usdm (Naimi et al. 2014)). Above the commonly used threshold of five were the two fire-frequency variables (FF5519 and FF0219) and the two lawn variables (La_p and Ratio_lb) (Akinwande, Dikko, and Samson 2015). Furthermore, a pairwise correlation VIF test revealed the mean DPM to be highly correlated with the lawn variables (La_p: -0.81, Ratio_lb: -0.82). An additional PCA showed that both lawn variables and both fire-frequency variables have similar explanatory power (Fig.2 C, Package: vegan (Oksanen et al. 2008)). All these variables were therefore modelled separately of each other. A relative high level of correlation was additionally present between the fire-variables and La_p/Ratio_lb (-0.58 to -0.63) and Mn_dpm (0.71 to 0.73). As these dynamics are however of major interest to this study, they were tested in separate pairs including their interaction.

2.3 Dependant variables and statistical analysis

The general abundance of ticks was investigated via two response variables. Firstly by the total number of ticks counted on an individual plot and secondly by the coefficient of variation of the tick counts amongst the individual drags on a plot. To exclude potential differences in tick activity over the time of day, which could influence their potential to be collected in a tick drag and thereby introducing a sampling bias, the tick counts in each drag were modelled against the sampling time. The counts in the individual tick drags were highly zero inflated and best described by a Zero-Inflated Sichel distribution (ZISICHEL, GAIC 7505.43). They were modelled against the predictor time with the plot as a random effect.

The general analysis and model selection followed the same scheme for both response variables. As they showed quite unusual and complicated distributions, the models were fitted in the more flexible gamlss framework (Generalized additive models for location, scale and shape, Package:

gamlss (Rigby and Stasinopoulos 2005)). This framework expands the range of potential distributions and allows a high level of control by enabling the modulation of individual distribution parameters. Initially the best fitting distribution was identified via the lowest Akaike information criterion (AIC), followed by the fitting of six saturated models (all non-inflated co-variates and a combination of three grassland variables and two fire-frequency variables). This was done in all distributions within a range of two units in generalized AIC (bias corrected for small sample size, GAICc) of the best fitting one. The GAICc was used on a plot level due to the small sample size of 28-29 and was consequently minimized via step-wise deletion of terms until a minimal adequate model was identified. These models were then again analysed if another distribution would lead to a further reduction in GAICc. To avoid over-parameterization, only the interaction between fire and grassland variable was included at first. When a minimal adequate model was found, the additional interactions were included stepwise and checked for improvements in GAICc. All resulting models were further checked if the addition of smoothing terms or a modulation of the gamlss specific distribution parameters for scale (σ) or shape (ν), which allow the variance to vary along the linear scale and can correct for highly skewed or kurtotic density estimates, would improve the model. In all steps, the general fit of the models were validated and the models disregarded when they showed problematic signs.

The tick counts per plot ranged from 22 to 3819 ticks (Total tick abundance, TTA). For modelling purposes, the plots one and two were excluded as they differed from the other plots in their sampling effort through the drag distance. An initial assessment showed the data to be severely over-dispersed (Residual Deviance 16738 on 27 df, Ratio variance/mean = 654). Within the gamlss framework, the model was first fitted with the geometric (GEOM, GAICc 431.57, 1 df) and the negative binomial (NBI, GAICc 433.97, 2 df) distribution, which are both robust against over-dispersion. While the NBI model was not within the desired range of 2 units in GAICc from the geometric model, it was still included to achieve more statistical reliability. Both models contained the same combination of independent variables in their reduced minimal adequate state (GAICc: GEOM 431.49; NBI 432.65) and could not be further improved. However, in this combination of explanatory variables a double Poisson (DPO) distribution showed an improvement of GAICc to 430.55.

To evaluate the pattern of tick distribution within plots, the coefficient of variation between the individual drags on a plot level ((Standard Deviation/Mean) x 100) was additionally tested as a response to the available independent variables and ranged between 120.47 and 398.27 (CVT). Plot 2 was excluded due to the different drag distances, while plot 1 was included as the individual drags were consistent in length (20m), which makes its heterogeneity comparable. A histogram of the CVT showed a pronounced right skew (D'Agostino test = 0.96) and slight leptokurtosis (Anscombe-Glynn test = 3.15). The distributions Inverted Gamma (IGAMMA, GAICc 323.05, 2 df), inverse Gaussian (IG, GAICc 323.96, 2 df), log-normal (LOGNO2, GAICc 324.09, 2 df) and Box-Cox-Cole-Green (BCCGo, GAICc 324.85, 3 df) were all within a range of two units in GAICc. As the BCCGo distribution required 1 more degree of freedom, the six saturated models were only reduced in the first three distributions (IGAMMA, IG and LOGNO2). Their minimal adequate models again contained the same independent terms (GAICc: IGAMMA 315.71; IG 314.12; LOGNO2 315.73). The gamlss framework showed a Weibull (WEI) model to decrease the GAICc further (GAICc: WEI 313.72) which could not be further improved.

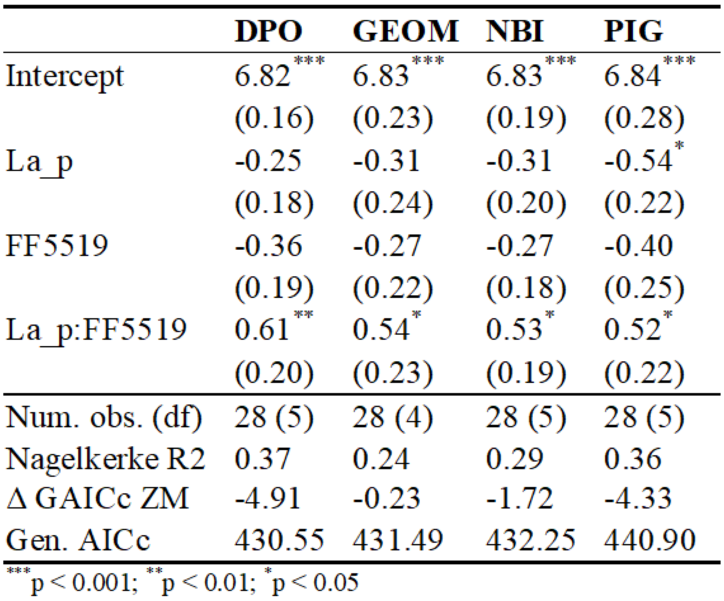
3. Results

The time of sampling had no significant effect on the number of ticks collected (ZISICHEL; t (33.6, 1047) = 0.496, *p*= .62).

3.1 Total tick abundance (TTA)

For the total tick abundance (TTA) the minimal adequate models in all distributions included the same independent variables, lawn percentage (La_p), fire frequency 1955-2019 (FF5519) and their interaction (Tab.1, La_p:FF5519). The lowest GAICc was achieved in the DPO model at 430.55, with the GEOM (431.49) and NBI (432.25) models within the comparable explanatory range. As the GEOM model requires one degree of freedom less, parsimony would make it preferable. However, for both the GEOM and the NBI model the difference in GAICc between these models and their respective zero-models, with only a random intercept fitted, was less than two units (Tab.1, ΔGAICc ZM: GEOM -0.23, NBI -1.72). Additionally, the DPO and PIG models explained considerably more of the variation within the tick counts (Tab. 1, Nagelkerke R2). All models showed the interaction between lawn percentage and long-term fire frequency (La_p:FF5519) to be significant (Tab.1; DPO: t (5, 28) = 2.988, *p* = .007; GEOM: t (4, 28) = 2.339, *p* = .03; NBI: t (5, 28) = 2.777, *p* = .01; PIG: t (5, 28) = 2.33*, p* = .03). While the models returned similar intercepts, the individual term coefficients varied by some margin with only the GEOM and the NBI models returning comparable values. The DPO model shows the direction of the interaction effect to change from negative to zero or positive at a threshold of approximately 30% lawn coverage and a log-term fire frequency of approximately 18 (Fig.4 A+B). Tick abundances decreased when fire frequency increased in plots with low lawn coverage while being relatively stable in areas with high lawn coverage (Fig.4 C). At low fire frequencies below 18/64 yrs., tick abundance declined with increasing lawn coverage, but not at higher fire frequencies (Fig.4 D).

Table 1. Coefficients for the intercept and the variables lawn percentage (La_p), fire frequency 1955-2019 (FF5519) and their interaction with standard error in brackets and significance level as returned by the double Poisson (DPO), geometric (GEOM), negative binomial (NBI) and Poisson inversed Gaussian (PIG) models for the total tick abundance (TTA). Lower part shows goodness of fit statistics including ΔGAICc ZM which indicates the difference in GAICc of the model to a zero model with only a random intercept fitted.



	DPO	**GEOM**	**NBI**	**PIG**
Intercept	6.82***	6.83***	6.83***	6.84***
	(0.16)	(0.23)	(0.19)	(0.28)
La_p	-0.25	-0.31	-0.31	-0.54*
	(0.18)	(0.24)	(0.20)	(0.22)
FF5519	-0.36	-0.27	-0.27	-0.40
	(0.19)	(0.22)	(0.18)	(0.25)
La_p:FF5519	0.61**	0.54*	0.53*	0.52*
	(0.20)	(0.23)	(0.19)	(0.22)
Num. obs. (df)	28 (5)	28 (4)	28 (5)	28 (5)
Nagelkerke R2	0.37	0.24	0.29	0.36
Δ GAICc ZM	-4.91	-0.23	-1.72	-4.33
Gen. AICc	430.55	431.49	432.25	440.90

$^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$

While the variances in the residuals of both variables are notable, tick abundances were considerably higher in areas of low lawn coverage and low historic fire frequency. The slopes even indicate a slight increase of TTA in high lawn, high fire frequency areas, however, this is mostly due to plot 8 that showed the unusual combination of very high lawn (92%), high fire frequency (24.3/64 yrs.) and high TTA (1624 ticks). As the plot showed a much lower short-term fire frequency (3.7/17 yrs.), the areas probably underwent considerable structural changes within the last decades and transitioned to a grazing lawn.

3.2 Heterogeneity of tick distribution (CVT)

Regarding the homogeneity of the number of ticks in the individual drags, the minimal adequate model in all distributions again contained the same terms, the heterogeneity of the DPM measurements (Cv_dpm), the herbivore density (Hv_dens) and the interaction between average grass biomass (Mn_dpm) and the short-term fire frequency in the last 17 years (Tab.2, FF0219). The lowest GAICc was achieved by the WEI model, with the IG, IGAMMA and LOGNO models within the same explanatory range (Tab.2, Gen. AICc). While all models returned similar coefficients and levels of significance for Hv_dens, Cv_dpm and the interaction Mn_dpm:FF0219, they differed by some margin in both parameters for the individual terms FF0219 and especially Mn_dpm. This led to Mn_dpm being identified as highly significant by the WEI and BCCGo models while being insignificant for the IG the IGAMMA and the LOGNO models (Tab.2). In the WEI model, the homogeneity of ticks decreased by about 15% (±0.03) when Hv_dens increased by a standard deviation of 12.6 (WEI: t(7, 29) = -4.883, *p*< .001) and by about 10% (±0.03) when Cv_dpm increased by a standard deviation of 19.8 (WEI: t(7, 29) = -3.839, *p*< .001). All models showed the interaction between Mn_dpm and FF0219 to be significant (Tab.2, WEI: t(7, 29) = 3.278, *p* = .003; IG: t(7,29) = 3.058, *p*= .005; IGAMMA:

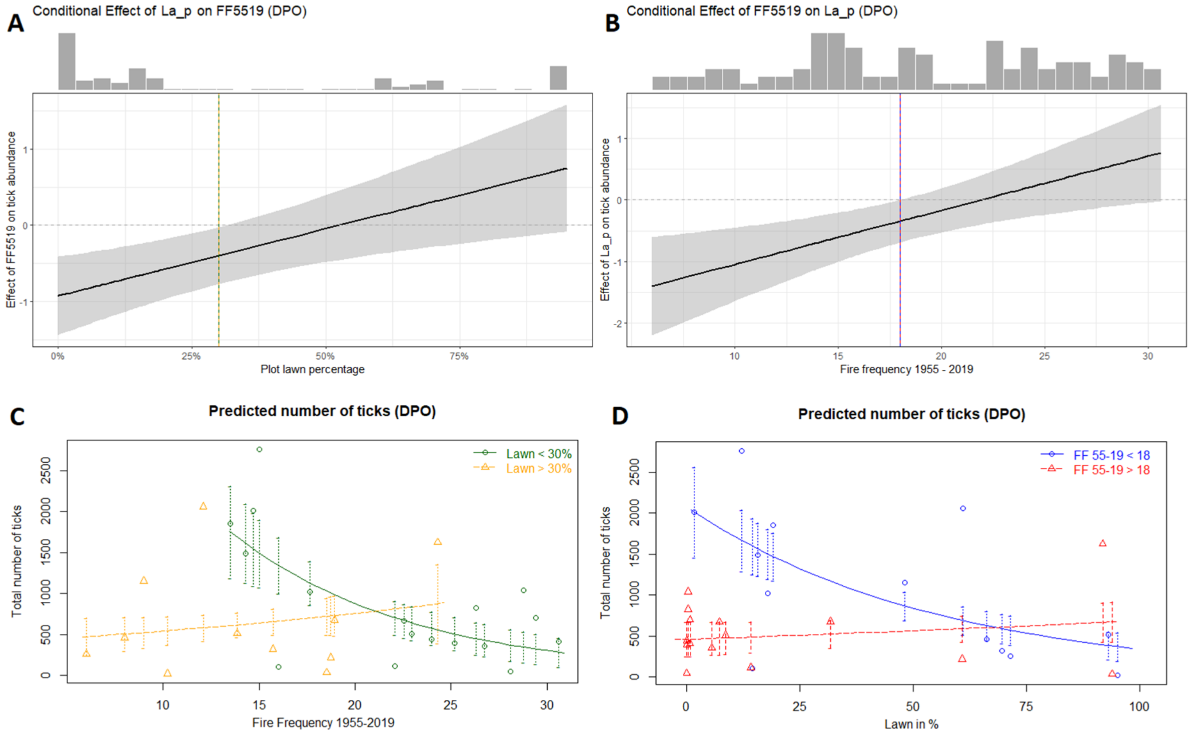


*Figure 4. The conditional effect and confidence intervals of lawn percentage on long-term fire frequency (A) and vice versa (B) for their significant interaction as identified in a double Poisson model (DPO, t (5,28) = 2.988, p = .007**) with a histogram added (top). C and D show the tick abundance (TTA) against the gradient of FF5519 (C) and La_p (D) with the other variable categorized at the thresholds indicated by the vertical lines in A and B. Points are observed TTA, horizontal lines are the predicted TTA as returned by the DPO model and the vertical, dotted lines show the confidence interval of the fit at the points of observation.*

t(7,29) = 2.971, *p*= .007; LOGNO: t(7,29) = 2.981, *p*= .006; BCCGo: t(8,29) = 3.579, *p*= .001). Both, the interaction found for TTA and CVT are indirectly connected as the average grass biomass is significantly connected to lawn coverage (Fig.5, t(4,30) = 3.376, *p*= .002**).

Table 2. Coefficients for the intercept and the variables average DPM (Mn_dpm), fire frequency 2002-2019 (FF0219), herbivore density (Hv_dens), heterogeneity in DPMs (Cv_dpm) and the interaction Mn_dpm:FF0219 with standard error in brackets and significance level as returned by the WEI, IG, IGAMMA, LOGNO and BCCGo models for the heterogeneity in tick distribution (CVT). Lower part shows goodness of fit statistics including ΔGAICc ZM that indicates the difference in GAICc to a zero model with only a random intercept fitted.

	WEI	**IG**	**IGAMMA**	**LOGNO**	**BCCGo**
Intercept	5.44***	5.36***	5.29***	5.34***	5.35***
	(0.04)	(0.04)	(0.05)	(0.04)	(0.14)
Mn_dpm	0.14**	0.07	0.03	0.05	0.17***
	(0.04)	(0.05)	(0.05)	(0.05)	(0.04)
FF0219	-0.26***	-0.20***	-0.19**	-0.20***	-0.28***
	(0.04)	(0.05)	(0.05)	(0.05)	(0.04)
Hv_dens	-0.16***	-0.17***	-0.18***	-0.18***	-0.14***
	(0.03)	(0.04)	(0.04)	(0.04)	(0.03)
Cv_dpm	-0.10***	-0.08*	-0.09*	-0.09*	-0.11***
	(0.03)	(0.03)	(0.04)	(0.04)	(0.02)
Mn_dpm:FF0219	0.11**	0.13**	0.13**	0.13**	0.10**
	(0.03)	(0.04)	(0.05)	(0.04)	(0.03)
Num. obs. (df)	29 (7)	29 (7)	29 (7)	29 (7)	29 (8)
Nagelkerke R2	0.67	0.57	0.54	0.55	0.58
Δ GAICc ZM	-17.42	-9.84	-7.34	-8.36	-8.92
Gen. AICc	313.72	314.12	315.71	315.73	315.93

$^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$

The effect of short term fire frequency (FF0219) on CVT was negative but decreases until it becomes negligible at an average grass biomass (Mn_dpm) above approximately 18 (Fig.5 A). On the other hand, the effect of grass biomass on CVT is increasingly positive at fire frequencies above approximately 2.5 (Fig. 5 B). To visualize this effect the respective variables were again categorized, albeit this time at their 1st and 4th quartile as there were not enough measurements above/below the thresholds of 18 in Mn_dpm and 2.5 in FF0219 to produce reliable predictions, which makes these exact thresholds unreliable (Fig.5 C, D). The overall effect of FF0219 on CVT is negative but considerably more so on plots within a range of 2.6 – 4.5 in Mn_dpm (Fig.6 C, green). In contrast, CVT

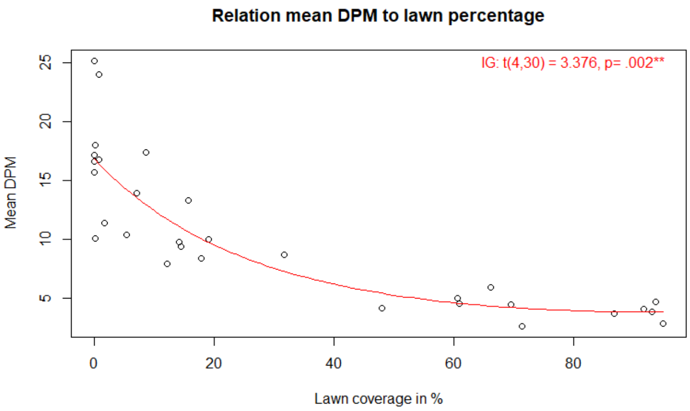


Figure 5. Observed (points) and predicted (line) relation between average grass biomass (Mean DPM) and lawn coverage on the sampled plots. Relation is significant in an inverse Gaussian (IG) model (upper right).

is generally lower on plots with a lower average grass biomass and increases on plots with higher biomass. This increase is sharper and more variable in mid fire frequencies above one than in higher fire frequencies above six. However, the CVT on plots that did not burn at all is considerably higher compared to the other plots with a low biomass, which disappears when it burned once (Fig.6 D, blue). The overall highest heterogeneity was found at lower fire frequencies in the last 17 years while lower heterogeneity were more likely on plots with low average mean DPM, independent of fire frequency with the notable exception of plots that did not burn at all (Fig.5).

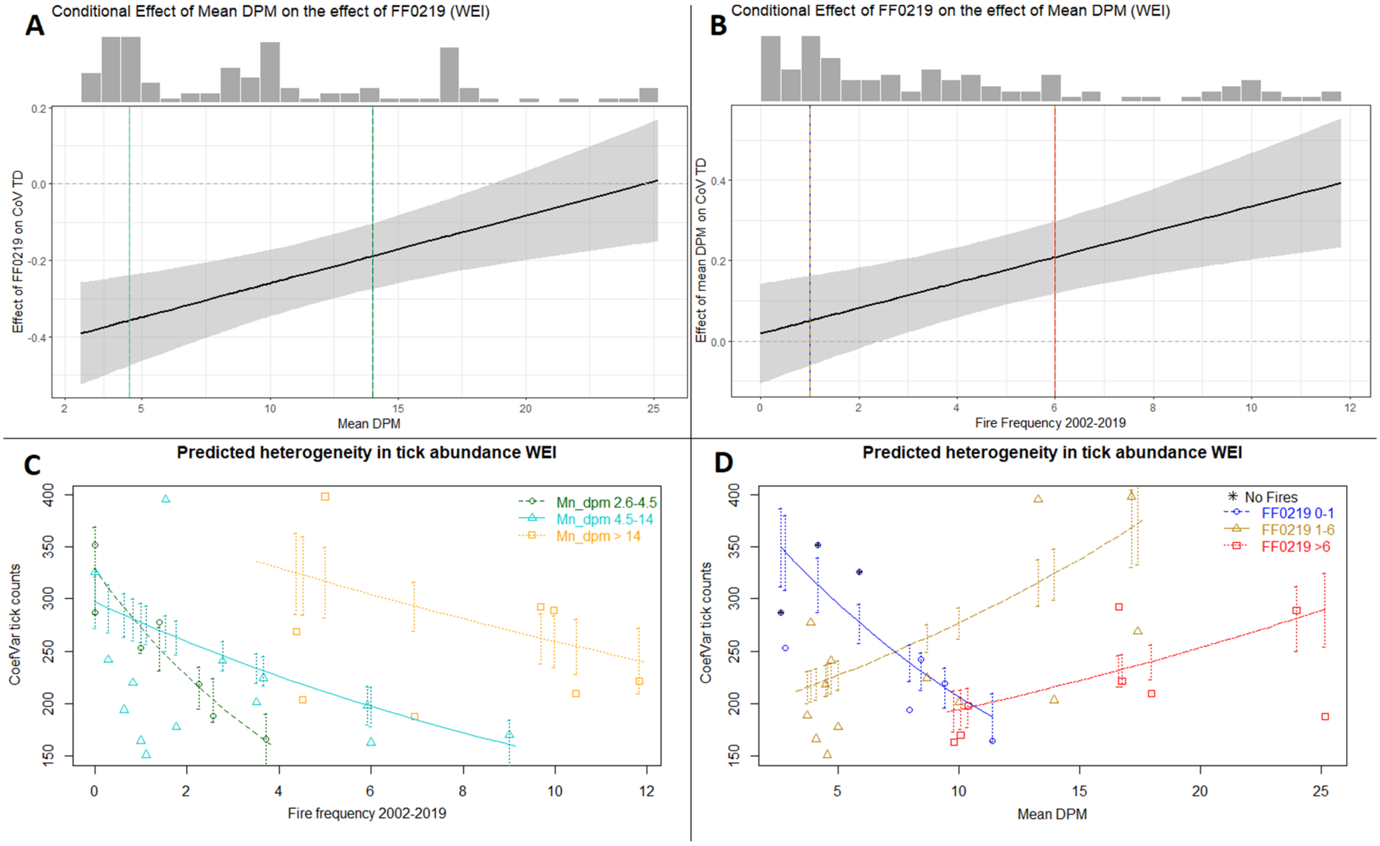


*Figure 6. The conditional effect of average DPM (Mean DPM) on short-term fire frequency 2002-2019 (A) and vice versa (B) for their significant interaction as identified in a Weibull model (WEI, t(7,29) = 3.278, p = .003**) with a histogram added (top). C and D show the tick distribution heterogeneity (CVT) against the gradient of FF0219 (C) and Mean DPM (D) with the other variable categorized at the thresholds indicated by the vertical lines in A and B. Points are observed CVT, horizontal lines are the predicted CVT as returned by the WEI model and the vertical, dotted lines show the confidence interval of the fit at the points of observation.*

4. Discussion

This study investigated how the interaction between fire frequency and grassland structure affects tick abundances on a landscape level. To achieve this, I tested if tick abundance decreased in areas with increasing proportional amounts of lawn or increasing fire frequency and if the lowest abundances are found in areas with the highest amount of grazing lawn and the highest fire frequencies. In addition, I assessed the effect of both factors on the heterogeneity of tick distribution throughout the landscape. Although not the main purpose of this study, the underlying assumption was based on observations that fire frequency and lawn coverage are closely linked, with previous studies postulating that fires cannot spread through areas with a lawn coverage of more than 30% due to it acting as a natural fire barrier (Archibald 2008; Archibald and Hempson 2016; Donaldson et al. 2018). The study presented here did not find such a clear threshold. While both short- and long-term fire frequencies showed a steep decrease when lawn coverage increased to 20%, there was no point after which either the long- or short-term fire frequencies uniformly dropped to their lowest values (appendix, Fig. A1). This could however be a result of the relatively crude method of calculation. Both the historic annual fire records and the satellite data are unlikely to be spatially explicit enough to establish if a grazing lawn really burned, or just the bunch grass surrounding it. However, it indicates the structural changes in grassland over time, as grazing lawn can turn into bunch grass and vice versa (Cromsigt and te Beest 2014). For example plot 8 showed high lawn coverage and a relative low short-terms fire frequency while the long-term fire frequency was relatively high which suggests that the area turned into grazing lawn only recently. Therefore it should be noted that the fire frequencies are long-term measurements while the lawn measurements and tick abundances represent the current state, which complicates the interpretation.

The tick abundance within an area did not universally decrease when lawn coverage or fire frequency increased, which partially rejects hypotheses one and two. It did decrease with increasing lawn coverage in areas with fire frequencies below approximately 18 fires in the last 64 years and with increasing fire frequency when lawn coverage was below approximately 30% (Fig. 4). Neither were the lowest tick abundances universally found in areas with very high lawn coverage or high fire frequency, which rejects hypothesis three. While the tick abundances were on average low in both circumstances, they were equally low at other points along the gradient of fire frequency and lawn coverage. However, the highest tick abundances were found in areas that combine a low amount of grazing lawn with a low long-term fire frequency (Fig.4). Therefore indeed, tick abundances are lower in areas with high lawn coverage and independent of fire frequency. On the other hand, tick abundances are indeed lowered to an equally low level by high fire frequencies in bunch grass areas. While all four models tested here agreed in the significance of this interaction, it should be acknowledged that two of them (GEOM and NBI) were not better in explaining the tick abundance than a random model with a ΔGAICc ZM of less than -2 (albeit the NBI model being close with -1.72,

Tab.1). Additionally, the tick distribution was more homogenous on plots with high lawn coverage, and therefore low grass biomass, but only if it burned at least once in the last 17 years.

In general, ticks can be found in three “states”. Either feeding on a host, or free on the ground where they either inactive or actively look for a new host (quest) (Madder, Horak, and Stoltsz 2014). Tick drags exclusively sample questing ticks (Mays, Houston, and Trout Fryxell 2016). Finding lower abundances of questing ticks could indicate a higher mortality for them in areas with a high amount of grazing lawn or high fire frequency. Multiple studies showed lower numbers of ticks in areas with shorter grasses (Medlock et al. 2012; Yawa et al. 2018). As other studies were able to demonstrate that the numbers of questing ticks are considerably lower after dry and hot days, this could be due to higher exposure in these conditions (Burtis et al. 2016). Furthermore, it was shown that burning reduces tick abundances, which is most likely due to their direct death through combustion and the reduction/elimination of their refugia (Fyumagwa et al. 2007; Polito et al. 2013; Gleim et al. 2014). However, the time until tick numbers after fire events return to their pre-burn level (or even above this) differs considerably between studies, ranging from one to more than three years (Fyumagwa et al. 2007; Adams et al. 2013; Goodenough et al. 2017). The results presented here could offer an explanation for this as the effect of fire on tick abundances depends on grassland structure. Intriguingly however, neither this study, nor the study of Goodenough et al. (2016) found a significant effect of time since last burn on tick abundances. While they noted that the number of ticks sampled from plots of different rotational burning regimes in another protected area in South Africa were lower on plots that burned the year before, they found equally low numbers on plots that burned more than three years ago. In contrast, the study presented here found no such pattern and with the by far highest number of ticks (3819) on plot 2 that, although excluded from all analysis due to sampling differences, burned only 221 days ago (appendix, Tab. A1). Additionally, they found a significant interaction between fire and individual plots which was attributed to heterogeneity in local environmental factors, one of which as this would study suggests, could be grassland structure (Goodenough et al. 2017). This potentially indicates that differences in mortality due to fire is not acting alone in determining the abundances of questing ticks in bunch grass dominated areas. The influence of fire on tick abundances could be an indirect effect based on fire and grassland induced changes in herbivore density and activity. While the study presented here did not find a significant effect of herbivore density on tick abundance, this could be due to the nature of the proxy. As it was a long term density calculated from annual, transect based game censuses, important small spatial and temporal differences, especially between lawns and bunch grass areas, are most likely missed. However, the herbivore density considerably homogenized the distribution of ticks throughout plots, showing that there are connections between the two. Other studies showed that the density of herbivores and how much time they spend in an area is higher on grazing lawns and in freshly burned areas (S. Archibald 2008; Donaldson et al. 2018). Therefore over time, areas that are either grazing lawns or burn frequently could have a higher availability of new hosts than areas that lack both over the same time, although this would still need to be demonstrated. This could translate into lower amounts of questing ticks in these areas as they quickly find new hosts and are therefore not collectable via tick drags. Consequently, high abundances of questing ticks in high bunch grass, low fire frequency areas could be a consequence of them accumulating due to the lack of hosts. This would be supported by experiments in Kenya that showed that within 13 months the exclusion of large herbivores lead to higher tick abundances, as potentially less ticks transfer from questing to hosts (Titcomb et al. 2017; 2018). Additionally, although it is hard to distinguish cause and effect, certain herbivores like African buffalo (*Syncerus caffer*) are more likely to frequent areas of taller grass and at the same time show a high level of infestation with ticks when compared to other species (Fyumagwa et al. 2007; Donaldson et al. 2018). The magnet effect that attract more herbivores into freshly burnt areas could in this regard offer an explanation for the disconnection between the abundances of questing ticks and time since the last burn as the increased turnover of hosts quickly re-stabilizes their numbers (Archibald et al. 2005). To further investigate these mechanisms, the relationship between long and short-term fire frequencies and grazing lawns should be established with a higher resolution to clearly establish the pattern between the three. Furthermore, it should be assessed how temporal patterns in herbivore movement and activity in relation to environmental parameters of the landscape influence the abundance of questing ticks and their own level of tick infestation.

The results of this study have more general implications for fire ecology as well. Beale et al (2018) showed in a study across African savannahs that while pyrodiversity had an increasing effect on the biodiversity of birds and mammals, this effect was notably stronger in wet savannahs (>650 mm/year). Regarding tick abundance, we find a similar pattern in which the effect of a singular factor of pyrodiversity, the fire frequency, depends on another environmental variable, the grassland structure. When Bowman et al. (2016) conceptualized pyrodiversity as an extension of a food web with fire competing with herbivores for vegetation, they emphasized the need for detailed studies of spatio-temporal mosaic of fire with particular species guilds to avoid the often contradicting conclusions linking bio- to pyrodiversity. The study presented here shows that sampling of ticks in only one grassland type would have influenced the conclusion about the effect of fire on ticks. Additionally our results strongly support the notion, that the interaction between fire and biotic parameters is not clear cut and that to predict the impact of fire several other environmental parameters have to be considered. These parameters need to be integrated into future studies, especially concerning sampling strategies, when the effect of pyrodiversity on individual taxa, or biodiversity as a whole, is investigated. As fire frequency changes tick abundance and heterogeneity depending on grassland structure, further research will be needed if other pyrodiversity parameters like seasonality and intensity are similarly affected.

Burning is the most common strategy to control tick populations beside acaricides, but only a continuous higher fire frequency might be effective to reliably decrease the number of ticks and even have no effect at all on certain grassland structures like grazing lawns (Gleim et al. 2014). In places where they occur, grazing lawns are most likely strongly linked to the presence of large herbivores in their formation and maintenance (Cromsigt and te Beest 2014). Therefore a decrease in large herbivores and potential following decrease in grazing lawns will lead to an increase in tick abundances if the fire frequency in the area is low.

Acknowledgements

Although not the type to typically write acknowledgements as I find them often a bit too cheesy, I want to thank Enzemvelo KZN Wildlife and especially their staff in Hluhluwe-iMfoflzi for their cooperation to enable this study. Additional thanks to Joris and Liza for their support and constructive criticism.

References

Abades, Sebastián R., Aurora Gaxiola, and Pablo A. Marquet. 2014. 'Fire, Percolation Thresholds and the Savanna Forest Transition: A Neutral Model Approach'. Edited by Osvaldo Sala. *Journal of Ecology* 102 (6): 1386–93. https://doi.org/10.1111/1365-2745.12321.

Adams, Jonathan, Chris Edmondson, Damien Willis, and Robert Carter. 2013. 'Effects of Prescribed Burning on Small Mammal, Reptile, and Tick Populations on the Talladega National Forest, Alabama'. *In: Guldin, James M., Ed. 2013. Proceedings of the 15th Biennial Southern Silvicultural Research Conference. e-Gen. Tech. Rep. SRS-GTR-175. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 123-126.* 175: 123–26.

Akinwande, Michael Olusegun, Hussaini Garba Dikko, and Agboola Samson. 2015. 'Variance Inflation Factor: As a Condition for the Inclusion of Suppressor Variable(s) in Regression Analysis'. *Open Journal of Statistics* 05 (07): 754–67. https://doi.org/10.4236/ojs.2015.57075.

Archibald, and Hempson. 2016. 'Competing Consumers: Contrasting the Patterns and Impacts of Fire and Mammalian Herbivory in Africa'. *Philosophical Transactions of the Royal Society B: Biological Sciences* 371 (1703): 20150309. https://doi.org/10.1098/rstb.2015.0309.

Archibald 2008. 'African Grazing Lawns—How Fire, Rainfall, and Grazer Numbers Interact to Affect Grass Community States'. *Journal of Wildlife Management* 72 (2): 492–501. https://doi.org/10.2193/2007-045.

Archibald, S., W. J. Bond, W. D. Stock, and D. H. K. Fairbanks. 2005. 'Shaping the Landscape: Fire–Grazer Interactions in an African Savanna'. *Ecological Applications* 15 (1): 96–109.

Archibald, Sally, and Gareth P. Hempson. 2016. 'Competing Consumers: Contrasting the Patterns and Impacts of Fire and Mammalian Herbivory in Africa'. *Philosophical Transactions of the Royal Society B: Biological Sciences* 371 (1703): 20150309. https://doi.org/10.1098/rstb.2015.0309.

Archibald, Sally, Caroline ER Lehmann, Jose L. Gómez-Dans, and Ross A. Bradstock. 2013. 'Defining Pyromes and Global Syndromes of Fire Regimes'. *Proceedings of the National Academy of Sciences* 110 (16): 6442–6447.

Beale, Colin M., Colin J. Courtney Mustaphi, Thomas A. Morrison, Sally Archibald, T. Michael Anderson, Andrew P. Dobson, Jason E. Donaldson, Gareth P. Hempson, James Probert, and Catherine L. Parr. 2018. 'Pyrodiversity Interacts with Rainfall to Increase Bird and Mammal Richness in African Savannas'. Edited by Margaret Mayfield. *Ecology Letters* 21 (4): 557–67. https://doi.org/10.1111/ele.12921.

Bonnet, Olivier, Hervé Fritz, Jacques Gignoux, and Michel Meuret. 2010. ‘Challenges of Foraging on a High-Quality but Unpredictable Food Source: The Dynamics of Grass Production and Consumption in Savanna Grazing Lawns: The Dynamics of Grass Consumption in Grazing Lawns’. *Journal of Ecology* 98 (4): 908–16. https://doi.org/10.1111/j.1365-2745.2010.01663.x.

Bowman, David M. J. S., George L. W. Perry, Steve I. Higgins, Chris N. Johnson, Samuel D. Fuhlendorf, and Brett P. Murphy. 2016a. ‘Pyrodiversity Is the Coupling of Biodiversity and Fire Regimes in Food Webs’. *Philosophical Transactions of the Royal Society B: Biological Sciences* 371 (1696): 20150169. https://doi.org/10.1098/rstb.2015.0169.

Burtis, James C., Patrick Sullivan, Taal Levi, Kelly Oggenfuss, Timothy J. Fahey, and Richard S. Ostfeld. 2016. ‘The Impact of Temperature and Precipitation on Blacklegged Tick Activity and Lyme Disease Incidence in Endemic and Emerging Regions’. *Parasites & Vectors* 9 (1): 606. https://doi.org/10.1186/s13071-016-1894-6.

Cromsigt, Joris P. G. M., and Mariska te Beest. 2014a. ‘Restoration of a Megaherbivore: Landscape-Level Impacts of White Rhinoceros in Kruger National Park, South Africa’. Edited by Peter Bellingham. *Journal of Ecology* 102 (3): 566–75. https://doi.org/10.1111/1365-2745.12218.

Donaldson, Jason E., Sally Archibald, Navashni Govender, Drew Pollard, Zoë Luhdo, and Catherine L. Parr. 2018a. ‘Ecological Engineering through Fire-Herbivory Feedbacks Drives the Formation of Savanna Grazing Lawns’. Edited by Cheryl Schultz. *Journal of Applied Ecology* 55 (1): 225–35. https://doi.org/10.1111/1365-2664.12956.

Fyumagwa, Robert D., Victor Runyoro, Ivan G. Horak, and Richard Hoare. 2007. ‘Ecology and Control of Ticks as Disease Vectors in Wildlife of the Ngorongoro Crater, Tanzania’. *South African Journal of Wildlife Research* 37 (1): 79–90. https://doi.org/10.3957/0379-4369-37.1.79.

Giglio, Louis, Luigi Boschetti, David P. Roy, Michael L. Humber, and Christopher O. Justice. 2018. ‘The Collection 6 MODIS Burned Area Mapping Algorithm and Product’. *Remote Sensing of Environment* 217 (November): 72–85. https://doi.org/10.1016/j.rse.2018.08.005.

Gleim, Elizabeth R., L. Mike Conner, Roy D. Berghaus, Michael L. Levin, Galina E. Zemtsova, and Michael J. Yabsley. 2014a. ‘The Phenology of Ticks and the Effects of Long-Term Prescribed Burning on Tick Population Dynamics in Southwestern Georgia and Northwestern Florida’. Edited by Kelly A. Brayton. *PLoS ONE* 9 (11): e112174. https://doi.org/10.1371/journal.pone.0112174.

Goodenough, Anne E., Alison N. Harrell, Rachel L. Keating, Richard N. Rolfe, Hannah Stubbs, Lynne MacTavish, and Adam G. Hart. 2017a. ‘Managing Grassland for Wildlife: The Effects of Rotational Burning on Tick Presence and Abundance in African Savannah Habitat’. *Wildlife Biology* 2017 (1): wlb.00318. https://doi.org/10.2981/wlb.00318.

Hempson, Gareth P., Catherine L. Parr, Sally Archibald, T. Michael Anderson, Colin J. Courtney Mustaphi, Andrew P. Dobson, Jason E. Donaldson, Thomas A. Morrison, James Probert, and Colin M. Beale. 2018. ‘Continent-Level Drivers of African Pyrodiversity’. *Ecography* 41 (6): 889–99. https://doi.org/10.1111/ecog.03109.

Herkenrath, Tim. n.d. ‘How Does White Rhino Respond to Fires During Dry Season?’ SLU Umea. 2019:6. https://stud.epsilon.slu.se.

Johnson, Christopher N., Lynda D. Prior, Sally Archibald, Helen M. Poulos, Andrew M. Barton, Grant J. Williamson, and David M. J. S. Bowman. 2018. ‘Can Trophic Rewilding Reduce the Impact of Fire in a More Flammable World?’ *Philosophical Transactions of the Royal Society B: Biological Sciences* 373 (1761): 20170443. https://doi.org/10.1098/rstb.2017.0443.

Kelly, Luke T., Lluís Brotons, and Michael A. McCarthy. 2017. ‘Putting Pyrodiversity to Work for Animal Conservation: Pyrodiversity and Animal Conservation’. *Conservation Biology* 31 (4): 952–55. https://doi.org/10.1111/cobi.12861.

Lock, J. M. 1972. ‘The Effects of Hippopotamus Grazing on Grasslands’. *The Journal of Ecology* 60 (2): 445. https://doi.org/10.2307/2258356.

Madder, Maxime, Ivan Horak, and Hein Stoltsz. 2014a. ‘Tick Identification’. *Faculty of Veterinary Science University of Pretoria*, 58.

Martin, R.E., and D.B. Sapsis. 1992. ‘Fire as Agents of Biodiversity: Pyrodiversity Promotes Biodiversity’. *Proceedings of the Symposium on Biodiversity in Northwestern California*, 150–57.

Mays, S. E., A. E. Houston, and R. T. Trout Fryxell. 2016. ‘Comparison of Novel and Conventional Methods of Trapping Ixodid Ticks in the Southeastern U.S.A.’ *Medical and Veterinary Entomology* 30 (2): 123–34. https://doi.org/10.1111/mve.12160.

Medlock, J.M., H. Shuttleworth, V. Copley, K.M. Hansford, and S. Leach. 2012. ‘Woodland Biodiversity Management as a Tool for Reducing Human Exposure to *Ixodes Ricinus* Ticks: A Preliminary Study in an English Woodland’. *Journal of Vector Ecology* 37 (2): 307–15. https://doi.org/10.1111/j.1948-7134.2012.00232.x.

Naimi, Babak, Nicholas A. S. Hamm, Thomas A. Groen, Andrew K. Skidmore, and Albertus G. Toxopeus. 2014. ‘Where Is Positional Uncertainty a Problem for Species Distribution Modelling?’ *Ecography* 37 (2): 191–203. https://doi.org/10.1111/j.1600-0587.2013.00205.x.

Oksanen, Jari, Roeland Kindt, Pierre Legendre, Bob O’Hara, Gavin L. Simpson, Peter Solymos, M. Henry H. Stevens, and Helene Wagner. 2008. *Vegan: Community Ecology Package*. http://cran.r-project.org/, http://vegan.r-forge.r-project.org/.

Parr, Catherine L., and Alan N. Andersen. 2006a. ‘Patch Mosaic Burning for Biodiversity Conservation: A Critique of the Pyrodiversity Paradigm’. *Conservation Biology* 20 (6): 1610–1619.

Polito, Victoria J., Kristen A. Baum, Mark E. Payton, Susan E. Little, Samuel D. Fuhlendorf, and Mason V. Reichard. 2013. ‘Tick Abundance and Levels of Infestation on Cattle in Response to Patch Burning’. *Rangeland Ecology & Management* 66 (5): 545–52. https://doi.org/10.2111/REM-D-12-00172.1.

R Core Team. 2019. ‘R: A Language and Environment for Statistical Computing.’ R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Rigby, R. A., and D. M. Stasinopoulos. 2005. ‘Generalized Additive Models for Location, Scale and Shape,(with Discussion)’. *Applied Statistics* 54: 507–54.

RStudio Team. 2018. ‘RStudio: Integrated Development for R.’ RStudio, Inc., Boston. http://www.rstudio.com/.

Titcomb, Georgia, Brian F. Allan, Tyler Ainsworth, Lauren Henson, Tyler Hedlund, Robert M. Pringle, Todd M. Palmer, et al. 2017. ‘Interacting Effects of Wildlife Loss and Climate on Ticks and Tick-Borne Disease’. *Proceedings of the Royal Society B: Biological Sciences* 284 (1862): 20170475. https://doi.org/10.1098/rspb.2017.0475.

Titcomb, Georgia, Robert M. Pringle, Todd M. Palmer, and Hillary S. Young. 2018. ‘What Explains Tick Proliferation Following Large-Herbivore Exclusion?’ *Proceedings of the Royal Society B: Biological Sciences* 285 (1878): 20180612. https://doi.org/10.1098/rspb.2018.0612.

Waldram, Matthew S., William J. Bond, and William D. Stock. 2008. ‘Ecological Engineering by a Mega-Grazer: White Rhino Impacts on a South African Savanna’. *Ecosystems* 11 (1): 101–12. https://doi.org/10.1007/s10021-007-9109-9.

Yawa, M., N. Nyangiwe, V. Muchenje, C. T. Kadzere, T. C. Mpendulo, and M. C. Marufu. 2018. ‘Ecological Preferences and Seasonal Dynamics of Ticks (Acari: Ixodidae) on and off Bovine Hosts in the Eastern Cape Province, South Africa’. *Experimental and Applied Acarology* 74 (3): 317–28. https://doi.org/10.1007/s10493-018-0234-2.

Appendix

Table A1: Plot location within HiP and environmental variables investigated in the study

Plot Information						Ticks				Fire				Grassland structure						Additional Covariates		
Plot	Date	Centroid_LAT (DD.ddddd°)	Centroid_LON (DD.ddddd°)	Drag Sum	Plot coverage (m)	Immatures	Adults	TTA	CVT	FF5519	FF0219	DSLB	DSLB_cat	Mean_DPM	Variance_DPM	SD_DPM	La_p (%)	Bu_p (%)	Ratio_lb	Tree_mn	H_trees	Hv_dens
1	190424	-28.16566	31.96914	35	680	442	1	443	188.2819	15.88571	2.57143	2078	1-19	3.69403341	7.846782496	2.8012109	86.8	10.66	76.41	23.597561	1.30965796	28.25004
2	190429	-28.08379	32.05655	35	285	3813	6	3819	120.4678	29.48571	8	221	<1	15.6864286	122.2403166	11.0562343	0	100	-100	21.2560976	1.06546547	56.13769
3	190430	-28.18749	31.92878	35	350	106	8	114	162.8577	22.05714	6	219	<1	9.7797619	50.02715507	7.0729877	14.14	83.37	-67.15	55.5	0.81585316	57.75128
4	190502	-28.0999	32.02891	35	350	495	15	509	268.5219	22.97143	4.37143	2054	1-19	17.4080952	131.1604116	11.4525286	8.56	90.71	-81.49	46.9285714	1.23965939	36.61225
5	190506	-28.08312	32.10885	35	350	422	20	442	187.8991	23.97143	6.94286	1722	1-19	25.1797619	101.0457708	10.0521525	0	99.76	-99.52	34.5	1.06671819	57.00177
6	190507	-28.09168	32.02063	35	350	641	29	670	203.3336	22.57143	4.51429	2055	1-19	13.9285714	41.85526764	6.46956472	7.16	92.36	-84.76	37.475	0.92247555	37.98908
7	190509	-28.21472	31.94425	35	350	405	7	412	221.5942	30.62857	11.82857	223	<1	16.7511905	43.76789834	6.61573113	0.72	98.8	-97.61	20	1.08800402	43.26712
8	190513	-28.25538	31.70427	35	350	1621	3	1624	166.1138	24.31429	3.71429	2120	1-19	4.08095238	4.266700761	2.06559937	91.77	6.78	85.09	30	1.0528743	88.93198
9	190514	-28.24202	31.81101	35	350	22	0	22	253.2722	10.22857	1	NA	>19	2.79642857	2.586741391	1.60833497	95.06	2.86	92.26	13.125	0.66156324	60.95732
10	190516	-28.07930	32.13708	35	350	664	37	701	289.0706	29.42857	9.97143	213	<1	23.9916667	87.28930986	9.34287482	0.72	98.56	-97.13	31.6463415	0.94224402	76.684
11	190520	-28.28654	31.74033	35	350	36	0	36	241.0291	18.51429	2.77143	5003	1-19	4.69761905	5.738896466	1.75829932	93.8095238	1.19047619	87.9880952	23.5714286	0.86067753	55.91062
12	190521	-28.31762	31.73790	35	350	508	4	512	277.3787	13.85714	1.4	5718	1-19	3.84642857	4.005595806	1.45195578	93.0952381	2.85714286	86.5856009	12.2560976	0.62464358	58.71635
13	190523	-28.15965	31.98390	33	330	1743	4	1747	201.3767	13.51429	3.51429	2076	1-19	10.0059524	55.43731532	6.08781179	19.047619	68.8095238	-43.7193878	34.075	1.23497138	25.72129
14	190527	-28.31500	31.90042	35	350	320	0	320	217.9950	15.71429	2.25714	2066	1-19	4.45454545	10.98473948	2.1600696	69.6172249	23.923445	42.7422678	18.5238095	1.12767934	58.91138
15	190528	-28.31485	31.78541	35	350	1489	1	1490	395.1385	14.28571	1.54286	6467	1-19	13.2857143	49.10313672	5.73129252	15.7142857	79.5238095	-60.7709751	38.4761905	1.34280654	26.57855
16	190530	-28.21669	32.01867	35	350	1038	2	1040	169.9741	28.77143	9	219	<1	10.0607143	17.13651977	3.27183673	0.23809524	98.8095238	-97.6326531	48.047619	1.22676386	45.58185
17	190603	-28.22944	31.77004	35	350	459	1	460	325.2120	8	0	NA	>19	5.875	11.02312053	2.32083333	66.1904762	31.1904762	34.0833333	22.4761905	1.33261914	66.09979
18	190604	-28.27876	31.81880	35	350	1150	3	1153	352.1156	9	0	NA	>19	4.12857143	7.592021821	2.06394558	48.0952381	43.3333333	4.3537415	44.3571429	1.52626553	27.97819
19	190605	-28.19520	32.03561	35	350	670	6	676	224.2805	18.94286	3.65714	1694	1-19	8.65952381	44.53296397	5.2344898	31.6666667	60.2380952	-26.2585034	46.5714286	1.39428278	45.03791
20	190607	-28.20709	31.95278	35	350	45	1	46	398.2650	28.08571	5	221	<1	17.1404762	38.14012388	4.72431973	0	99.7619048	-99.5243764	36.7619048	1.34476516	40.45255
21	190608	-28.35103	31.71375	35	350	217	0	217	177.7124	18.74286	1.77143	2094	1-19	4.99047619	6.793465166	2.05655329	60.7142857	35.952381	23.9365079	41.3571429	1.3468396	78.00942
22	190609	-28.24358	31.92012	35	350	825	2	827	209.7255	26.31429	10.45714	216	<1	17.9785714	102.7930958	7.01857143	0.23809524	98.3333333	-96.6938776	43.1904762	1.45187662	32.13299
23	190610	-28.24443	31.99308	35	350	354	0	354	197.8981	26.74286	5.91429	217	<1	10.3666667	25.49769292	3.88206349	5.47619048	90.7142857	-81.9909297	61.4761905	0.72228705	45.32619
24	190612	-28.2717	31.94607	35	350	388	2	390	292.5821	25.17143	9.68571	1705	1-19	16.622619	32.54519121	4.45213152	0	100	-100	47.0952381	0.92147106	37.08716
25	190613	-28.25562	31.75316	35	350	257	1	258	287.1563	6	0	NA	>19	2.60357143	4.62230225	1.29416667	71.4285714	15	48.7704082	38.7380952	1.59707876	51.25109
26	190619	-28.41129	31.91091	35	350	102	2	104	219.5458	16	0.82857	NA	>19	9.39285714	17.77011592	3.31683673	14.5238095	82.3809524	-65.7568027	27.1190476	1.27831567	48.29685
27	190620	-28.37754	31.97264	35	350	1020	2	1022	241.7388	17.62857	0.28571	NA	>19	8.40119048	19.85357853	2.87646825	17.8571429	80.2380952	-61.1927438	42.6666667	1.37141788	84.06026
28	190620	-28.39644	31.96478	35	350	2009	0	2009	164.3134	14.71429	1	NA	>19	11.3857143	23.28643028	3.53931973	1.66666667	98.0952381	-96.1989796	36.7142857	1.26671917	82.42016
29	190621	-28.35900	31.93779	35	350	2060	0	2060	150.9720	12.08571	1.11429	NA	>19	4.52761905	5.870022957	1.9158322	60.952381	33.0952381	26.1989796	18.1904762	1.0858813	93.47796
30	190622	-28.40778	31.94258	35	350	2756	3	2759	193.8364	15.02857	0.62857	NA	>19	7.93928571	26.81432407	3.80629252	12.1428571	81.1904762	-64.4444444	23.5714286	1.00035025	72.58235

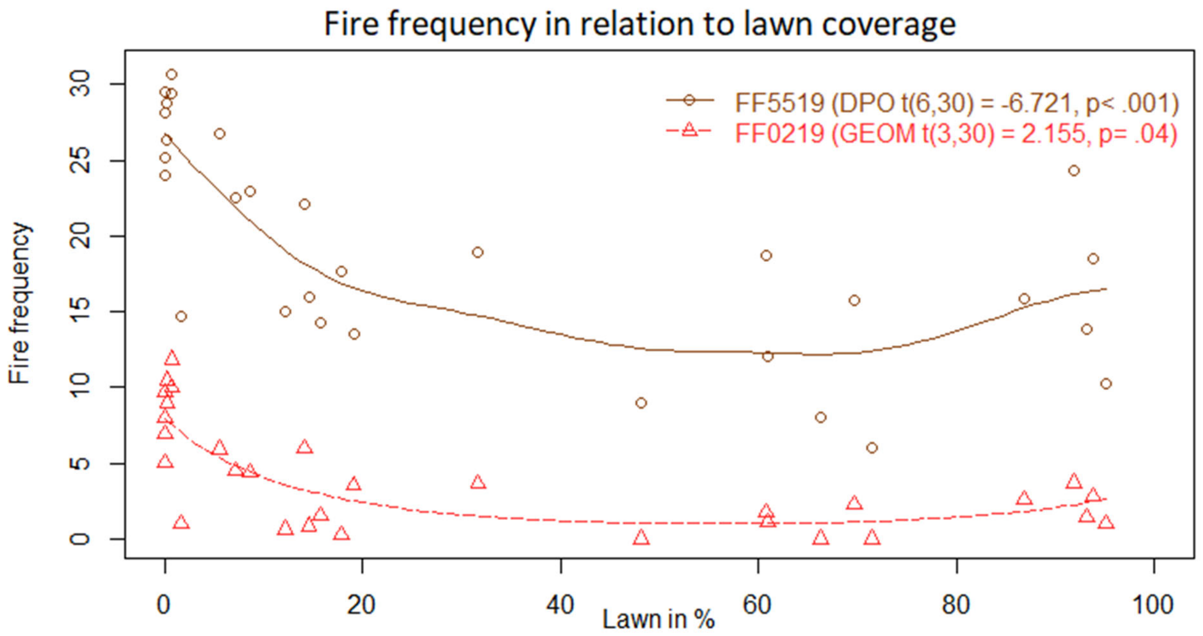


Figure A1: The long-term (FF5519) and short-term (FF0219) fire frequency of the plots in relation to lawn coverage (in %). Lines are predictions from a double Poisson (DPO) model for FF5519 and a geometric (GEOM) model for FF0219 and are significant (legend upper right). Points show the observed values from the 30 plots.

Latest issue number in our series Examensarbete/Master's thesis

2020:3	Movement ecology of ungulate communities – effect of species densities and habitat selection Author: Linda Zetterkvist
2020:4	Luckhuggning med friställning av asp och sälg – påverkan på epifytiska lavar Author: Maria Michold
2020:5	Dietary preferences of Golden eagles (Aquila chrysaetos) in Sweden – A camera trap approach Author: Tomas Melin
2020:6	Slaughter weight in relation to calving date – can area quality compensate for being born late? Author: Sanna-Maja Breiman Wistbacka
2020:7	Downstream migration and survival of Atlantic salmon (Salmosalar L.) kelts and fallbacks when passing a hydropower plant Author: Frans Byström
2020:8	Nocturnal moths use of novel habitats – A case study on a power line in a forest-mire mosaic in boreal Sweden Author: Oskar Lövbom
2020:9	Not everything that glitters is gold: Does linear infrastructure create an ecological trap for Golden Eagles? Author: Michelle Etienne
2020:10	Comparative movement behaviour and habitat selection of semidomestic herbivore: Central-place grazing versus free-range grazing in Reindeer (Rangifer t. tarandus) Author: Muhammad Fawad Sharif
2020:11	How does species density affect activity patterns of three sympatric ungulate species in a Scandinavian boreal forest? Author: Linda Zetterkvist
2020:12	The importance of Ecoparks for saproxylic beetles – A study on general ecological hypotheses in differently managed landscapes Author: Albin Larsson Ekström
2020:13	Restoration strategies in boreal forests – Prescribed burning and gap cutting effects on plant diversity and community composition Author: Clara Espinosa Del Alba
2020:14	Moose movement speed and home range during the rutting season Author: Irene Hjort
2020:15	The direct and indirect relation between ungulates on small mammals Author: Michael Wentzel

The entire list of published numbers can be found at www.slu.se/viltfiskmiljo