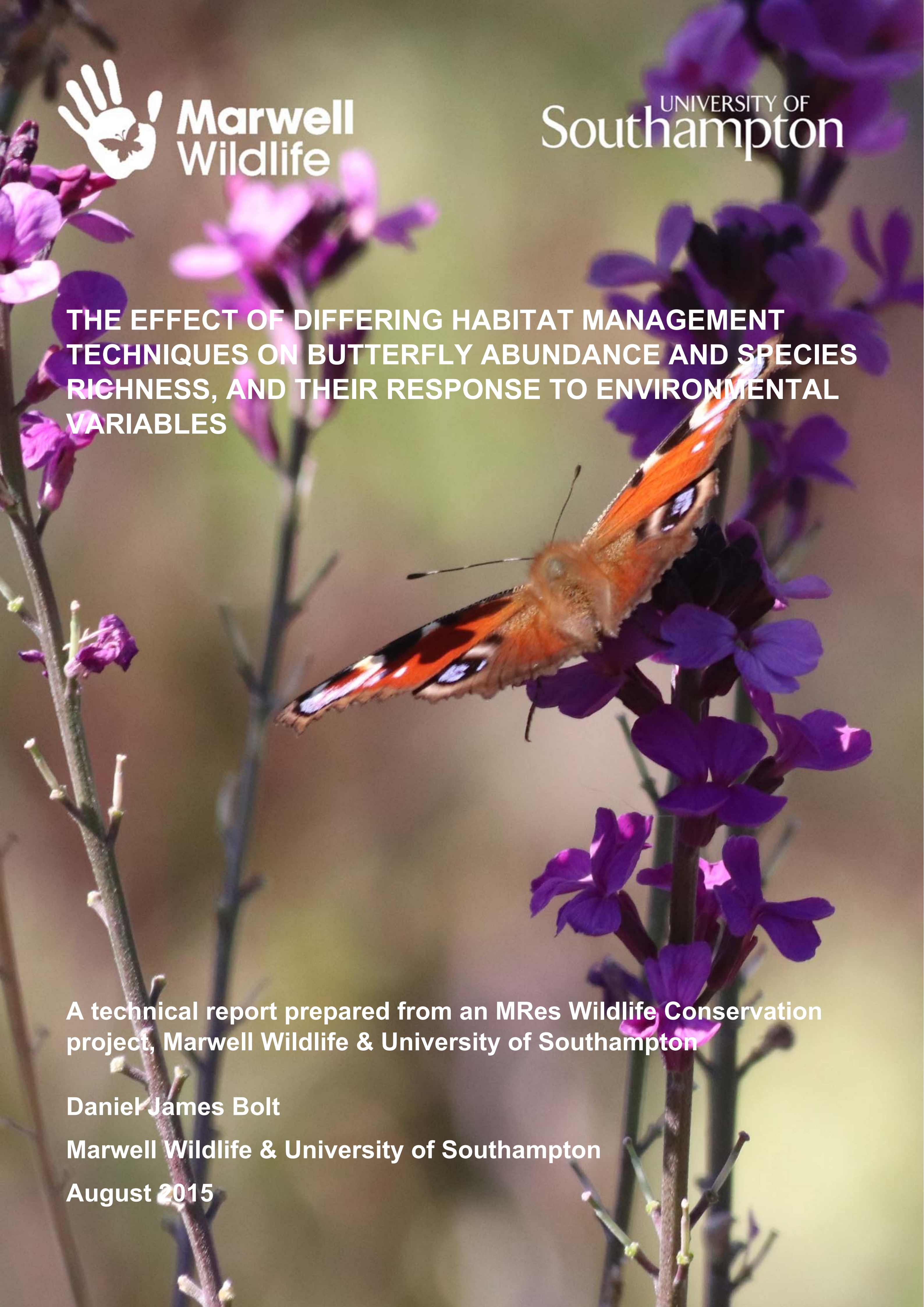

THE EFFECT OF DIFFERING HABITAT MANAGEMENT TECHNIQUES ON BUTTERFLY ABUNDANCE AND SPECIES RICHNESS, AND THEIR RESPONSE TO ENVIRONMENTAL VARIABLES

A technical report prepared from an MRes Wildlife Conservation project, Marwell Wildlife & University of Southampton

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Abstract

1. In this study the question of butterflies short term response to fluctuating environmental conditions, within habitats of differing management regimes is addressed through the monitoring of abundance and species richness in paired grassland and woodland habitats. Temperature, cloud cover and wind speed were measured and their influence on butterfly abundance assessed.

2. Structural measurements with the habitats were measured to examine whether these influenced the abundance and species richness of butterflies within these habitats.

3. It was found that habitats managed with biodiversity goals in mind provided higher species richness and abundance than those without. They also appear to dampen the short-term effects of environmental fluctuation, potentially providing greater resilience to extinction risk in these areas.

4. Canopy openness within the woodland was positively associated with higher abundance. But in the grassland, the effects of structure were less clear, with other factors possibly having a greater influence on butterfly abundance.

5. It is recommended that further efforts to create an open structured woodland should be encouraged through increased coppice rotation and continued logging of European larch. Grassland management for biodiversity is successful and the current management plan should be maintained, whilst further research efforts could more precisely ascertain the relative contribution of habitat structure to this success.

Contents

Introduction

Declines in native wildlife communities were considerable throughout the 20th century, more than 100 species went extinct in the UK, including 7% of dragonflies, 5% of butterflies and 2% of both fish and mammals (Laycock et al. 2009). Since the 1960s there have been severe decreases in key taxa, including 28% of plant species, 54% of bird species and 71% of butterfly species (Thomas et al. 2004). The main cause of these declines has been habitat fragmentation and degradation (Thomas et al. 2004). But the UK remains a stronghold for a significant number of species threatened with extinction, possessing internationally important populations of bats and bryophytes, and around 10% of the world's species of bumblebees. Britain has a diversity of important habitats, including the largest patches of calcareous grassland in Europe (Lawton et al. 2010), 18% of the world's heathland (Lawton et al. 2010), 9% – 15% of Europe's peatland (Littlewood et al. 2010) and hay meadows of global conservation importance (Lawton et al. 2010). There are very few habitats (some sea shores and coastal cliffs being the exceptions) within the UK that have not been shaped for thousands of years by human intervention. As a result, many of the most species rich habitats of greatest conservation importance in the UK have had, and will continue to require, human management (Lawton et al. 2010).

Management of Habitats

Ensuring that the management of semi-natural habitats is being carried out in such a way that it maximises biodiversity is of vital importance for the preservation of key taxa (Dawson et al. 2011; Stuhldreher & Fartmann 2014). If appropriate management is not carried out, then habitats can quickly deteriorate (Sutherland 2004). Butterflies are particularly sensitive to this. The High Brown Fritillary (*Fabriciana adippe*) has disappeared from 94% of its previous locations, whilst the Marsh Fritillary (*Eurodryas aurinia*) and Heath Fritillary (*Mellicta athalia*) have disappeared from 63% and 92% of their ranges respectively (Sutherland 2004), with the evidence suggesting that this is chiefly down to the deterioration of previously suitable habitats (Sutherland 2004). These cases demonstrate that often it is not enough to simply declare a specific area protected, but that the habitat then needs to be appropriately managed. Within this we need to be aware of a particular habitat structure that is required. Having a focal species or taxa to conserve in a managed habitat is of benefit, as you will be able to specify the structure and microclimate that is required within this (Dover 1996; Miller & Hobbs 2007). For example, many species of butterfly, especially in woodland habitat, require an early successional structure, which can be acquired through regular coppicing (Sutherland 2004; Fuller & Peterken 2004) providing them with a suitable ratio of shelter and sunlight.

The timing of particular management techniques is also of importance. The cutting of fields and meadows can be beneficial for plant biodiversity as it helps prohibit the domination of certain grass species (Ausden & Treweek 2004), but if carried out at the wrong time of year, it may destroy eggs and larvae of invertebrates, decimating the population and possibly leading to local extinctions (Sutherland 2004). Even the time of day that a field is cut could have negative consequences for populations, with previous research suggesting that early morning cuts on a field could increase butterfly mortality, as temperatures are too cold for adult butterflies to be able to escape machinery (Dover et al. 2010).

Structural Diversity

Habitats that are managed to increase biodiversity often set out to increase or diversify structural heterogeneity. A structurally diverse habitat provides more niches for species to exploit, with a more varied microclimate and suitable hiding and nesting sites (Kuuluvainen et al. 1996) able to accommodate a wider array of species (Macarthur & Macarthur 1961; Tews et al. 2004). For example, a low intensity grazing grassland system providing a varied sward height resulting in a variety of niches has been shown to result in higher species richness and abundance of butterflies and grasshoppers (Jerrentrup et al. 2014; Wallis De Vries et al. 2007). However several studies have yielded contradictory results of increased biodiversity with structural heterogeneity. A meta-analysis carried out by Tews et al (2004) suggests that the success of this is dependent upon the species or taxonomic group in question, the scale that it is looked at, and the structural variable in question. For example, the creation of woodland rides and clearings constitute positive structural heterogeneity for bird species (Greenberg & Lanham 2001) and butterflies (Spitzer et al. 1997). But the same structures have been found to represent negative habitat fragmentation for some species of beetle (Rainio & Niemelä 2003). When carrying out habitat restoration for conservation goals, it is important to be aware of the potential effects for all species, and to select a method of monitoring that will represent a wide array of taxa.

As well as this it is important to understand how the habitat that is being managed fits in to the wider landscape. It has been shown that a switch to organic farming is most effective for increasing butterfly abundance and species richness in a homogenous in landscape, whereas in a heterogeneous landscape, the overall benefits conferred to butterfly abundance is much more marginal, as the wider structural heterogeneity is already positively affecting their numbers (Rundlöf & Smith 2006).

Status of Grassland and Woodland Habitats within the UK

Chalk Grassland

Chalk grassland has some of the highest plant and invertebrate species richness and diversity within the UK. The shallow, nutrient-poor calcareous soils upon which it grows result in a combination of rare grasses and herbs (Ausden & Treweek 2004; Wilkie et al. 2014; Wilson et al. 1995), in particular it is known to be important habitat for species rich assemblages of vascular plants, butterflies and grasshoppers (Ausden & Treweek 2004; Poschlod & WallisDeVries 2002). Chalk grassland is considered to be of national conservation importance (Burnside et al. 2003; Haines-Young et al. 2006; Redhead et al. 2014; Poschlod & WallisDeVries 2002). This habitat formed around 6000 years ago as a result of forest clearances by humans, and remained due to low intensity grazing (Cox & Barneveld 2000; Wilkie et al. 2014). Today it is still reliant on specific grazing or mowing regimes. There were once extensive areas of this diverse habitat in the UK, but there is now estimated to be only 40,000 – 50,000 hectares remaining (Haines-Young et al. 2006). This still represents a globally important proportion of chalk grassland (Lawton et al 2010; Wilkie et al. 2014). Its decline is continuing, and it is suggested that this can be due to either the complete halting of management, resulting in eventual succession to woodland, or alternatively through the conversion to intensive agricultural use and nutrient enrichment through the use of fertilisers (Haines-Young et al. 2006). In order to preserve existing chalk grasslands and successfully restore degraded ones, it is important to understand the success of current management practices upon diversity, and which elements are driving the success or failure of these practices.

Woodland

The amount of woodland coverage in the UK is approximately 3.08 million hectares, representing around 12% of the total landscape (FAO 2010). Large swathes of this are coniferous plantation woodland, with low tree and structural diversity (Fuentes-Montemayor et al. 2012). The lack of structural diversity, such as from veteran trees, a wide vertical spread of foliage, dead wood, and forest gaps has resulted in a lower diversity of wildlife (Mason 2007; Peterken 1993; Tews et al. 2004). Semi-natural ancient woodland, an area that has been wooded continuously for at least the past 400 years (Parker et al. 2010; Peterken 1996), is more structurally diverse, but only 1.2% of this habitat remains. The decline of ancient semi-natural woodland has been halted and woodland habitat in Europe is actually increasing, but species diversity of these habitats is decreasing (Streitberger et al. 2012). Approximately 47% of woodlands within the UK are undermanaged, or not managed at all (Defra 2013). Most of those that are being managed, are being done so with modern practices that have altered their structure, from habitats with a variety of different successional stages, including open patches, to dense, even aged stands, resulting in a reduction of niches and subsequent loss in biodiversity (Streitberger et al. 2012). The loss of practices, such as grazing cattle in woodland and coppicing lead to lower structural heterogeneity, and mean that modern forests are losing species richness (Streitberger et al. 2012).

Butterflies

Butterflies have been shown to be good indicators of the biodiversity of a habitat, and provide a sensitive measure of habitat alterations, responding with fluctuations in abundance more rapidly to slight alterations than many other species (Boggs & Watt 2003; Fartmann 2006; Fox et al. 2011). They are poikilothermic animals, with the level of activity that they are able to carry out being closely determined by the weather (Roy & Sparks 2000). Alterations in plant structure, and dependence on particular plant species both at a larval and adult life history stage can influence these changes (Boggs & Watt 2003). Butterflies are a conspicuous taxa, diurnal, with a phytophagous life cycle (Boggs & Watt 2003; Roy & Sparks 2000). These traits mean that they are an accessible group to carry out research on in the field.

In order to be able to assess the efficacy of habitat management through creating structural heterogeneity, key species or taxa can be monitored that will reflect the type of structure being created, and are representative of an increase in biodiversity levels on the whole. Several studies have adopted taxonomic groups as indicators of structural complexity and habitat quality. Birds have been employed as an indicator of structural heterogeneity in forest landscapes (Segura et al. 2014; Zellweger et al. 2013). Butterfly species have also been shown to be indicators of structural heterogeneity within forested habitats due to their conspicuous plasticity to environmental change (Hamer et al. 2003; Hill et al. 1995; Spitzer et al. 1997). Although these studies have examined the effects of logging for commercial reasons and not with regard to direct conservation goals, this project can relate to these studies, as selective logging has been carried out in the sites being monitored. However this has been carried out for conservation reasons, and so provides a unique angle on the effects of this process on butterfly species assemblage and abundance. In a stand that has been logged for commercial reasons, it will have been done so with a goal of maximising commercial yield by homogenising within stand variance (Kuuluvainen et al. 1996). Whereas the logging at the site in question here has been carried out in an attempt to restore native trees to the area and to open up patches within the woodland to increase biodiversity (Wilkie et al. 2014). Butterfly population numbers are a good indicator of the health of the majority of terrestrial insects, which compose approximately two thirds of the species on this planet (Thomas 2005). So monitoring changes in butterfly abundance should give a good overall indication on the biodiversity of the habitats in question. Indeed such projects are being carried out on an international level (Van Swaay et al. 2013).

Butterflies and Weather

There has been previous research examining the effect of environmental factors on butterfly fluctuations over timescales of several years. These have shown that butterflies tend to increase in abundance during hot, dry summers, and that wet conditions early in one year correlate with increased numbers the following year (Pollard 1988; Roy et al. 2001). The UK Butterfly Monitoring Scheme has set out to collect data on butterfly numbers on a weekly basis every year from April to September. This provides a robust long term dataset examining how butterfly abundance is changing over time. However surveys are only carried out when weather conditions are considered conducive to providing the most amount of butterflies. This does not show how butterflies react in the short term to weather conditions that can fluctuate at any time during a season.

The interaction between weather conditions and habitat structure is an interesting one, as in the UK climate change has caused an increase in average Spring-Summer temperatures which is expected to be beneficial to species such as butterflies (Roy & Sparks 2000), many of which are at the northern edge of their range and are temperature limited. Most butterfly species are shifting their range further north and uphill, but at the same time the populations in the centres of their ranges are failing (Hardy et al. 2014). This means that abundances are still currently in decline due to a decrease in suitable habitats, and where these habitats do remain they are often too fragmented, so that those which are poor dispersers are unable to take advantage of them (Warren et al. 2001). A recent study has shown that the presence of Glanville fritillary (*Melitaea cinxia*) is more dependent upon the correct habitat structure than ambient temperature, and that these habitat structures have a microclimate warmer than the surrounding temperature (Curtis & Isaac 2014).

Project Aims

This project sets out to examine the influence of habitat management practices, aimed at enhancing the conservation potential of woodland and grassland, on the diversity of butterfly species and abundance. This will be done through regular surveying of transects within the habitats, the monitoring of environmental fluctuations and the measuring of habitat structure. It will quantify the structural heterogeneity of these habitat types, and identify the impacts that this may have on an order of animals that are particularly sensitive to environmental changes (Fartmann 2006; Fox et al. 2011; Jonason et al. 2010). The short term response of butterflies to environmental variables is not often studied, with datasets over several years generally preferred (Hardy et al. 2014; Pollard 1988; Roy et al. 2001; Van Swaay et al. 2013). This project will provide fine scale data on short term butterfly abundance fluctuations in response to environmental change. It will establish whether differing habitat management techniques influence their response.

The success or failure of the management of habitats is not often quantified, slowing the advancement of our knowledge in this area (Sutherland 2004). This study will provide tangible evidence of whether management practices that have been put in place for grassland and woodland habitats surrounding Marwell Zoo have conferred benefits to local wildlife, and determine whether this management is influencing butterfly response to environmental fluctuations.

Project Hypotheses

H1: There will be a difference in butterfly abundance and species richness between habitats with differing management practices.

H2: There will be a difference in butterfly response to environmental variables between habitats with differing management practices.

H3: There will be a difference in butterfly abundance and species richness between habitats with differing structure.

These hypotheses will be tested through the following objectives:

- Assess the population of butterfly species in woodland and grassland through regular counts along transects.
- Monitor the species richness found in each transect.
- Measure environmental conditions at the beginning of each transect.

- Assess habitat structure in woodland and grassland habitats.

Materials and Methods

Management Practices at Marwell

Marwell Wildlife owns a network of woodland and grassland surrounding Marwell Zoo, shown in Figure 1, situated on the edge of the South Downs National Park. Approximately 29 hectares of this is ancient broadleaved woodland, although Horsham Copse has been partly replaced by European larch (*Larix decidua*). Grasslands cover approximately 20 hectares and are predominantly chalk grasslands (Wilkie et al. 2014).

The woodlands have undergone a comprehensive management plan from 2010 – present, gradually remove the sections of European larch and encourage the return of broadleaf species. Creating greater structural heterogeneity through practices such as coppicing and the opening up of glades and rides to increase light levels to benefit ground flora and invertebrates, whilst being able to sustainably harvest its products (Parker et al. 2010).

Two woodland copses are being surveyed in this study; Horsham Copse and Pound Copse. Horsham Copse has been subject to a more intensive management programme. European larch has been thinned throughout the entire northern section from 2010 – 2013. In the southern section, an area of 0.914 hectares was cleared of European larch and re-planted with broadleaved trees during the winter of 2014 - 15. During 2010 glades were opened up around five mature oaks within the copse. Coppicing is also being carried out on long rotation.

Pound Copse has undergone less intensive management, with some thinning being carried out of conifers and sycamores within the copse, and some coppicing and rhododendron management.

The grasslands within the Marwell grounds are being managed to restore them to species rich assemblages of calcareous habitat and diversify the vegetation structure. Sward height heterogeneity within grasslands has been found to be beneficial to providing high levels of butterfly abundance (Jerrentrup et al. 2014). This is being managed whilst still being able to generate products such as fodder for animals within the zoo (Wilkie et al. 2014).

Two fields will be surveyed within the study; West Copse Field and Hurst Farm Field. These were sown with the same hay mix in 2011, comprising of 8 species of fine grass and 4 herb species in order to generate a hay product whilst providing suitable invertebrate foraging resources and habitats for wildlife within the landscape. Both of these sites are cut once a year around mid-July.

West Copse Field has no fertiliser added to it. The edge habitat between the grassland and woodland sites have been managed to create a scalloping scrub border with plant species such as blackthorn (*Prunus spinosa*) and bramble (*Rubus*). This scrub should provide valuable invertebrate nest and foraging resources, and serve to ensure a smooth connection between the two habitat types (Parker et al. 2010; Wilkie et al. 2014). The east side of this field borders Horsham copse. It possesses wide field margins cut on a 3 year rotational cycle in order to leave margins with varying sward height levels. The top section of West Copse Field was not sown with the hay mix and has had nothing added to it. During the previous winter (2014-15) this section was cut and collected and has been allowed to grow back.

Hurst Farm Field has more commercial management practices carried out upon it. Fertiliser is added to this field every other year, generally a nitrogen, phosphorus, and potassium mix of 20:40:20. This field was last fertilised in April 2015 as well as having silt added in November 2014. Hurst Farm Field does not possess field margins. One side of the field runs directly adjacent to Pound copse.

Butterfly Transects

Nine transects were walked in total; through the middle of West Copse Field (WCF), along its border with Horsham Copse (WCFB), two through Horsham Copse (HC1, HC2), along the bridleway of Horsham Copse adjacent to West Copse Field (HCRi), through the middle of Hurst Farm Field (HFF), along its border with Pound Copse (HFFB), through the middle of Pound Copse (PC), and along its border to Hurst Farm Field (PCRo). Transects walked are shown in Figure 1. GPS co-ordinates of the start and end points of transects are given in Table S1 of the Appendix.

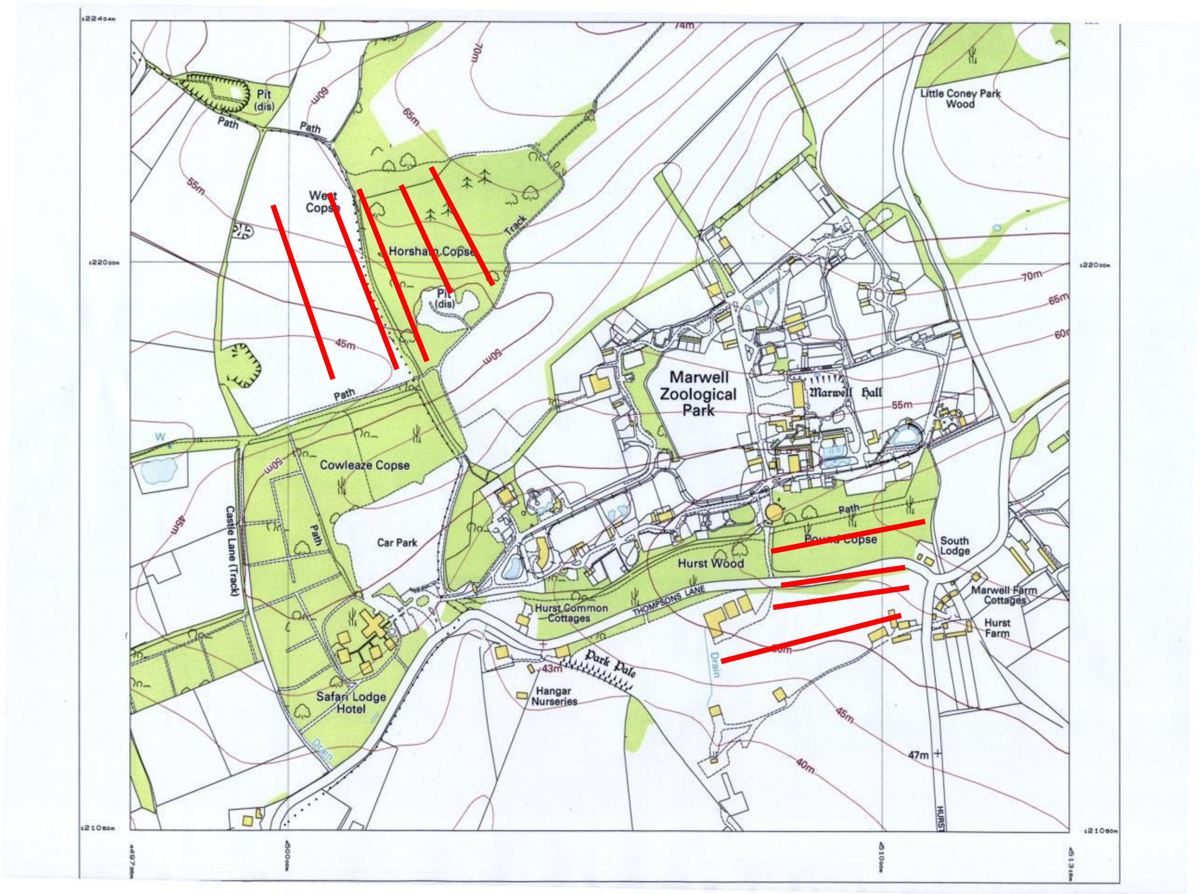

Figure 1. Map of grounds surrounding Marwell Zoo. Green sections represent woodland. White sections represent grassland. Transects are denoted by the red lines. Horsham Copse and West Copse Field are in the North West section. Pound Copse and Hurst Farm Field are in the South East section.

Each transect was walked three days a week, from the 20/04/2015 to 13/07/2015, resulting in a total of 37 survey days for each transect. At the beginning of each transect temperature in degrees centigrade, average wind speed in metres per second, and an estimation of the percentage cloud cover were taken. Temperature and wind speed were measured using a portable Kestrel 3000 weather station.

Transects were walked at an even pace. Any butterflies observed up to 5 metres either side of the transect line were logged to species level with the aid of a Collins gem Butterflies identification book. If the species of the butterfly could not be discerned whilst it was at rest or on the wing, then it was caught using a butterfly net so that it could be examined more closely, and released.

Structural Measurements

Grassland

Structural measurements were taken along the grassland transect at 50 m intervals. The sward height was measured in millimetres using a metre stick. A point quadrat was used within a 1x1 m quadrat. 50 pins, approximately 1.5 mm in diameter, were dropped down through the point quadrat and the number of times vegetation made contact with the pin was logged. This was separated into total grass contacts, total herb contacts and total vegetation contacts.

The measurements were taken 3 times throughout the survey period, with the structural measurements in the intervening period being interpolated from these. Hurst Farm Field was cut prematurely, so the final structural measurements for this field were unable to be taken along transects. As a result, measurements were taken from sections of grassland around the field that were considered to be representative of what the vegetation would have been like along transects.

Woodland

Structural measurements were taken along the woodland transects at 50 m intervals. Canopy openness of transects was calculated with the use of a densiometer. A densiometer possesses a convex mirror with a graticule etched upon it resulting in 96 separate points. The number of these points which possessed open sky is logged. This was carried out in 4 directions at each interval; North, South, East and West. Each result was multiplied by 1.04 in order to get a percentage of coverage. The openness for each point was then calculated from the average value of the 4 points.

At each of the intervals the vertical structural heterogeneity of foliage cover was calculated with the use of a telescopic pole 7 m in length. The pole was partitioned into 0.5 m sections and a cylinder 50 cm in radius was imagined around the pole. The sections were grouped into height strata defined by the height that vegetation layers were usually found within the deciduous woodland. The strata were split as follows; 0 to 1 m, >1 to 2 m, >2 to 3 m, >3 to 5 m and >5 to 7 m. The presence or absence of live foliage in each of these sections, and total number of sections containing foliage within each strata, was noted and proportions calculated. This was used to calculate a modified Foliage Height Diversity (FHD) Index as used and described in detail by Berger & Puettmann (2000). The mean FHD for each transect was then calculated.

Statistical Analysis

Environmental and structural measurements were analysed separately as the structural measurements were necessarily speculative. Transects were divided between COPSE with COPSE HORSHAM inclusive of Horsham Copse and West Copse Field, and COPSE POUND inclusive of Pound Copse and Hurst Farm Field (If copse is written in capitals, this will always refer to both the woodland and neighbouring grassland, whereas if it is in lower case, it will refer simply to the woodland). Another categorical variable, Transect Type, was also used. Transects were divided into Grassland (transects that passed through the middle of the grassland, Edge (transects that passed along the edge of the grassland habitat, and Woodland (transects situated within the woodland). This included transects within the woodland that were moving along the edge of the grassland habitat, as it was judged that these were not sufficiently different from transects within the centre of the woodland to classify separately.

The influence of temperature, wind, cloud cover, COPSE and Transect Type upon butterfly abundance, along with any two-way interactions between these variables was tested using a zero-inflated poisson (ZIP) method. This allows for data with many zero points and also with a few very high data points resulting in the variance being greater than the mean (over dispersion) (Atkins & Gallop 2007; van Iersel et al. 2000). This was calculated in the program R 3.2.0. The same analysis was also carried out upon species richness.

For the structural variables, woodland and grassland habitats were analysed separately as the variables measured are different from one another. A ZIP or zero-inflated negative binomial (ZINB) analysis was used on this data. The decision to choose one model over the other was based on the plotting of residual vs fitted data points and on the lowest result from the Akaike Information Criterion (AIC).

All models were simplified as much as possible, removing the most insignificant results based on their *p*-values, with interaction coefficients being removed first. This was carried out until no insignificant results were left or the AIC value started to increase.

Results

A total of 5,740 butterflies and 23 separate species were counted during the survey period. The total species list, and which transects they were observed on are listed in Table S2 in the Appendix. West Copse Field yielded the most butterfly observations, whilst the most species were seen at West Copse Field Border. The total frequencies and species richness for each transect over the survey period is shown in Table 1.

Table 1. Total butterfly frequency and species richness for each transect. The sum total across all transects is shown at the bottom

Transect	Number of Butterflies	Number of Species
West Copse Field	2320	14
West Copse Field Border	2001	21
Horsham Copse Ride	221	14
Horsham Copse 1	250	14
Horsham Copse 2	121	13
Hurst Farm Field	356	10
Hurst Farm Field Border	371	13
Pound Copse Road	38	5
Pound Copse	60	9
Total for all transects	5740	23

Butterfly Abundance

During ZIP analysis on environmental variables, COPSE and Transect Type, the two-way interactions between the environmental variables were excluded due to insufficient data and these interactions not being of primary focus in this project. The interaction between COPSE and cloud cover was also removed to simplify the model further as this did not give a significant result. This yielded multiple effects of the predictor variables on butterfly abundance, as well as interactions between the variables from the poisson model portion of the analysis, as shown in Table 2. Table 3 shows that the logistic model yielded very few significant interactions. The one variable found to have an effect in both models was temperature. The model estimates that the proportional rate of butterfly abundance will increase greater in POUND when compared to HORSHAM, as shown by the estimate (1.51).

Table 2. Results of poisson section of zero-inflated poisson analysis on butterfly frequency.

Variable	Estimate	Std. Error	z score	Pr(>|z|)
Temperature	0.25	0.01	34.26	<0.001
Wind	0.85	0.05	17.66	<0.001
Cloud Cover	0.01	0.001	7.88	<0.001
Transect Type Grassland	-0.20	0.29	-0.67	0.51
Transect Type Woodland	-0.003	0.40	-0.01	0.99
COPSE POUND	1.51	0.27	5.56	<0.001
Temperature:Transect Type Grassland	0.03	0.01	2.34	0.02
Temperature:Transect Type Woodland	-0.07	0.02	-4.12	<0.001
Temperature:COPSE POUND	-0.11	0.01	-9.32	<0.001
Wind:Transect Type Grassland	-0.52	0.07	-6.92	<0.001
Wind:Transect Type Woodland	-0.30	0.10	-2.87	0.004
Wind:COPSE POUND	-0.90	0.09	-9.88	<0.001
Cloud Cover:Transect Type Grassland	0.01	0.001	7.22	<0.001
Cloud Cover:Transect Type Woodland	0.001	0.002	0.53	0.59
Transect Type Grassland:COPSE POUND	-0.51	0.09	-5.94	<0.001
Transect Type Woodland:COPSE POUND	0.24	0.13	1.81	0.07

Table 3. Results of logit model section of zero-inflated poisson analysis on butterfly frequency.

Variable	Estimate	Std. Error	z score	Pr(>|z|)
Temperature	-0.67	0.21	-3.20	0.001
Wind	0.72	0.95	0.75	0.45
Cloud Cover	0.01	0.01	1.29	0.20
Transect Type Grassland	0.75	4.81	0.16	0.88
Transect Type Woodland	-3.92	3.52	-1.11	0.27
COPSE POUND	0.86	2.43	0.36	0.72
Temperature:Transect Type Grassland	0.09	0.26	0.35	0.73
Temperature:Transect Type Woodland	0.39	0.21	1.85	0.06
Temperature:COPSE POUND	0.10	0.12	0.86	0.39
Wind:Transect Type Grassland	1.16	1.16	1.01	0.32
Wind:Transect Type Woodland	-0.86	0.97	-0.88	0.38
Wind:COPSE POUND	0.004	0.92	0.004	0.20
Cloud Cover:Transect Type Grassland	-0.02	0.02	-1.26	0.21
Cloud Cover:Transect Type Woodland	0.01	0.02	0.86	0.39
Transect Type Grassland:COPSE POUND	0.30	1.45	0.21	0.84
Transect Type Woodland:COPSE POUND	-0.60	1.32	-0.45	0.65

There was an interaction between temperature and Transect Type for the poisson model but this was still marginally non-significant in the logistical model. This interaction was with the Woodland Transect Type, which had a trend of being cooler than the Grassland and Edge Transects. None of the of the other predictor variables within the logistical model were shown to have an effect.

All of the other variables within the poisson model yielded significant results, either individually or in interactions with other predictors. Wind and cloud cover were both shown to have an effect upon butterfly frequency. Figure 2, showing the interaction of copse type and transect type on butterfly numbers, suggests that whilst the Edge and Grassland transects of HORHSAM have a positive effect upon butterfly abundance compared to those of POUND, there is not a significant difference between the Woodland transects of the two copses. Figure 3 shows butterfly abundance consistently higher in HORSHAM than POUND throughout the temperature ranges, and still maintaining good abundances below 20˚C.

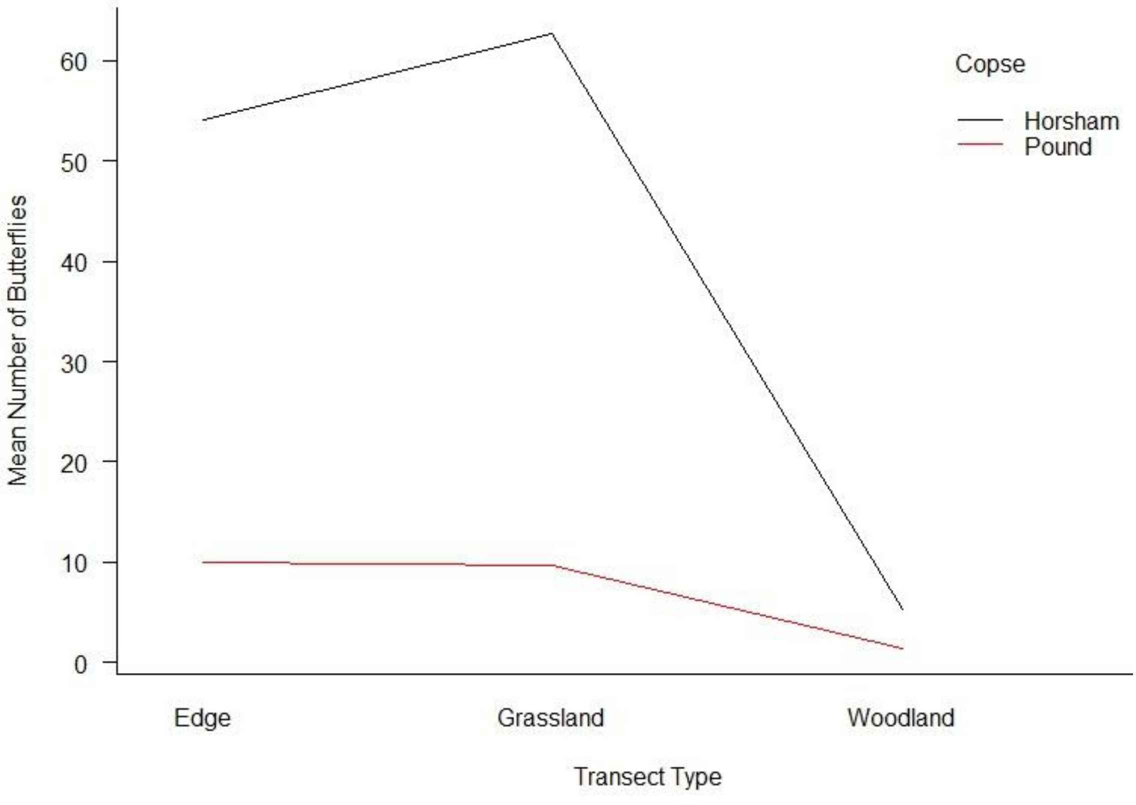

Figure 2. Interaction plot of mean butterfly abundance and copse type with transect type.

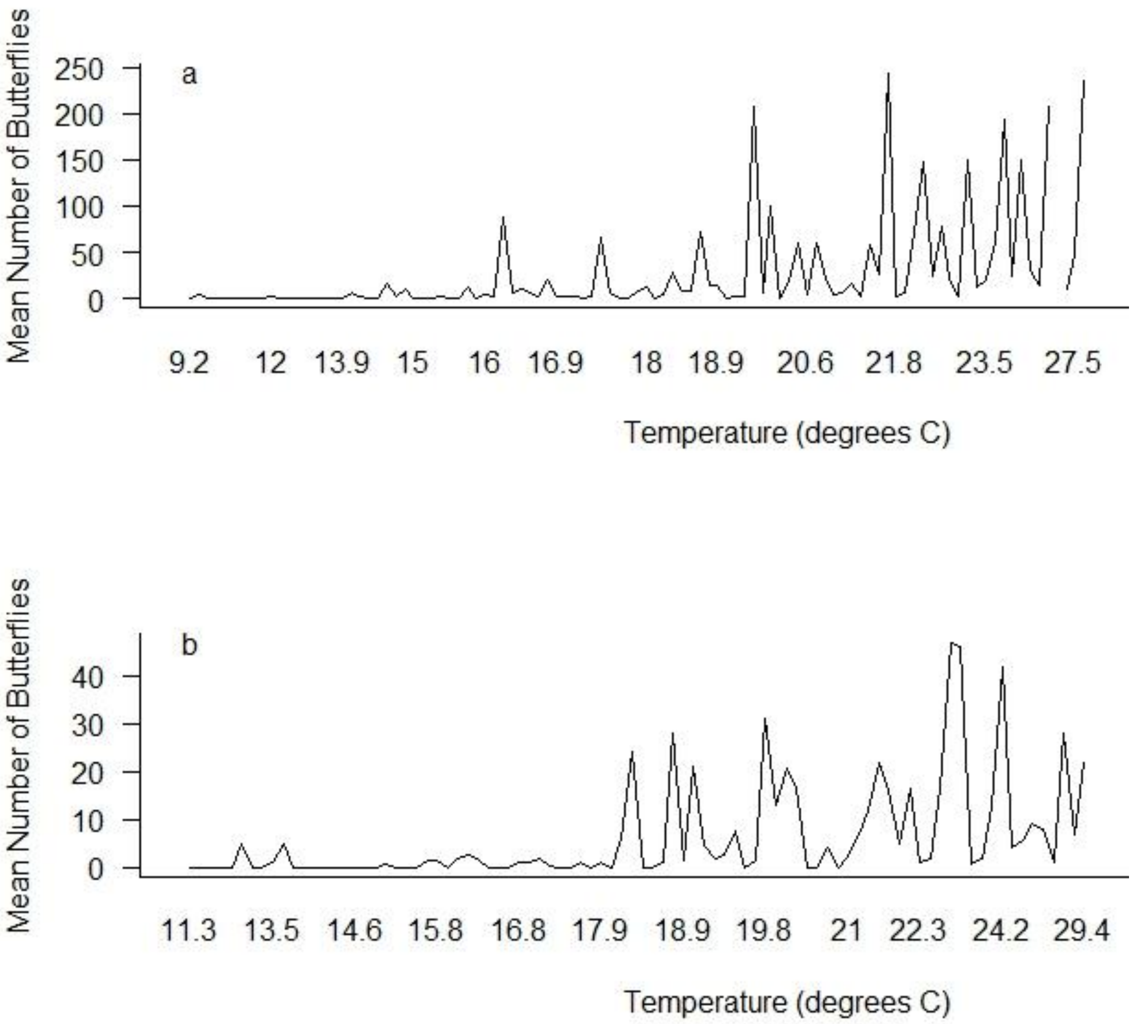

Figure 3. Mean butterfly abundance in response to increasing temperature for (a) HORSHAM and (b) POUND.

Species Richness

ZIP analysis was carried out upon the species richness of each transect and the environmental and habitat variables. The resulting model was simplified to remove all two-way interactions that were not significant to 5% and culminated in the removal of Wind as a variable as this was not significant either in interactions or on its own. The results of these are shown in Tables 4 and 5. Temperature and COPSE were found to have an impact upon butterfly species, with HORSHAM possessing more species than POUND and the number of species observed increasing with rises in temperature. It was also found that Edge transect types provided more species than either Grassland or Woodland transect types. The poisson model analysis also showed an interaction between temperature and Transect Type, with temperature being consistently lower in the Woodland transects compared to the Grassland and Edge transects. In the logistic section of the analysis COPSE was found to predict zero counts of butterflies. The interaction of COPSE and Transect Type on species richness is shown in Figure 4, demonstrating the higher species richness of HORSHAM over POUND, and of Edge transects over Grassland and Woodland, but with Woodland having lowest species richness. This also shows the lack of interaction between COPSE and Transect Type. Figure 5 shows the fluctuations of species richness for each transect type with changes in temperature.

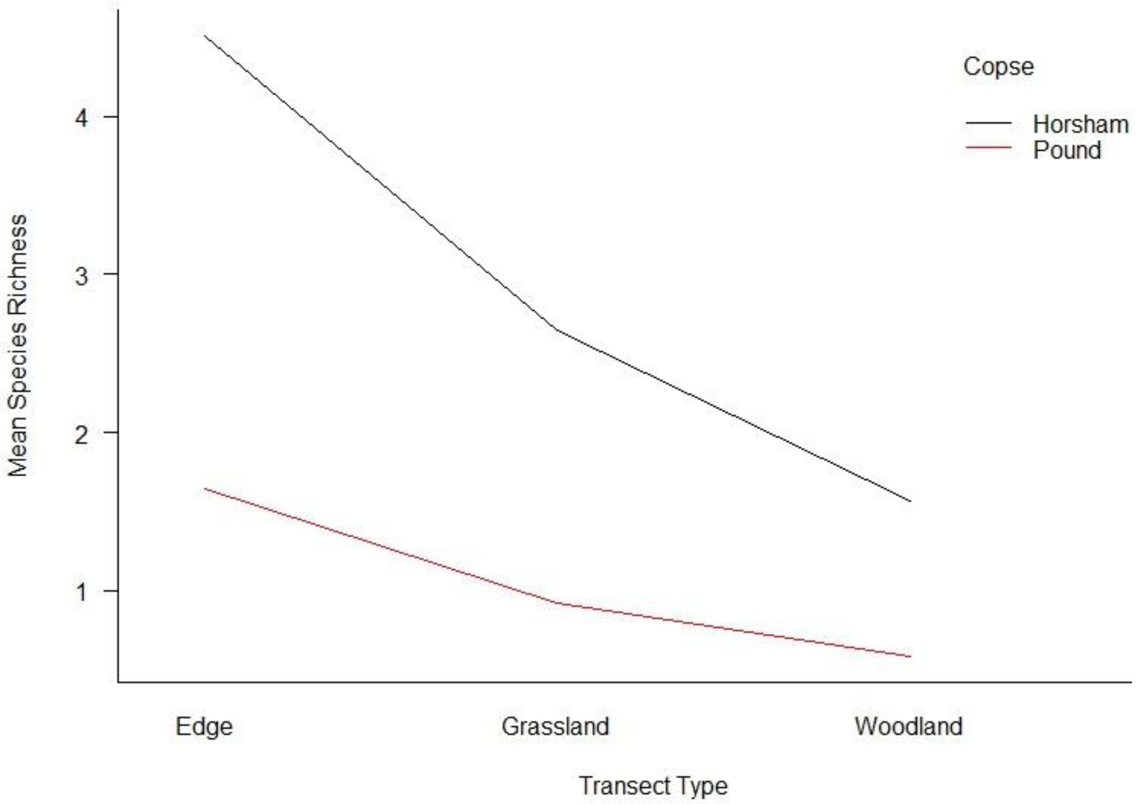

Figure 4. Interaction plot of butterfly species richness and copse type with transect type.

Table 4. Results of poisson model part of zero-inflated poisson analysis on butterfly species richness

Variable	Estimate	Std. Error	z score	Pr(>|z|)
Temperature	0.07	0.02	3.39	<0.001
Cloud Cover	-<0.001	0.002	-0.03	0.98
Transect Type Grassland	-2.55	0.97	-2.64	0.01
Transect Type Woodland	-0.61	0.73	-0.83	0.41
COPSE POUND	-0.90	0.11	-8.19	<0.001
Temperature:Transect Type Grassland	0.08	0.04	1.96	0.05
Temperature:Transect Type Woodland	-0.008	0.03	-0.27	0.80
Cloud Cover:Transect Type Grassland	0.008	0.004	1.91	0.06
Cloud Cover:Transect Type Woodland	-0.001	0.004	-0.38	0.71

Table 5. Results of logit model part of zero-inflated poisson analysis on butterfly species richness

Variable	Estimate	Std. Error	z score	Pr(>|z|)
Temperature	-1.10	0.36	-3.04	0.002
Cloud Cover	0.04	0.03	1.39	0.16
Transect Type Grassland	3.14	9.17	0.34	0.73
Transect Type Woodland	-9.47	5.34	-1.77	0.08
COPSE POUND	2.38	0.72	3.29	0.001
Temperature:Transect Type Grassland	0.06	0.65	0.09	0.93
Temperature:Transect Type Woodland	0.71	0.37	1.91	0.06
Cloud Cover:Transect Type Grassland	-0.04	0.05	-0.84	0.38

Cloud Cover:Transect Type Woodland	0.01	0.04	0.28	0.78

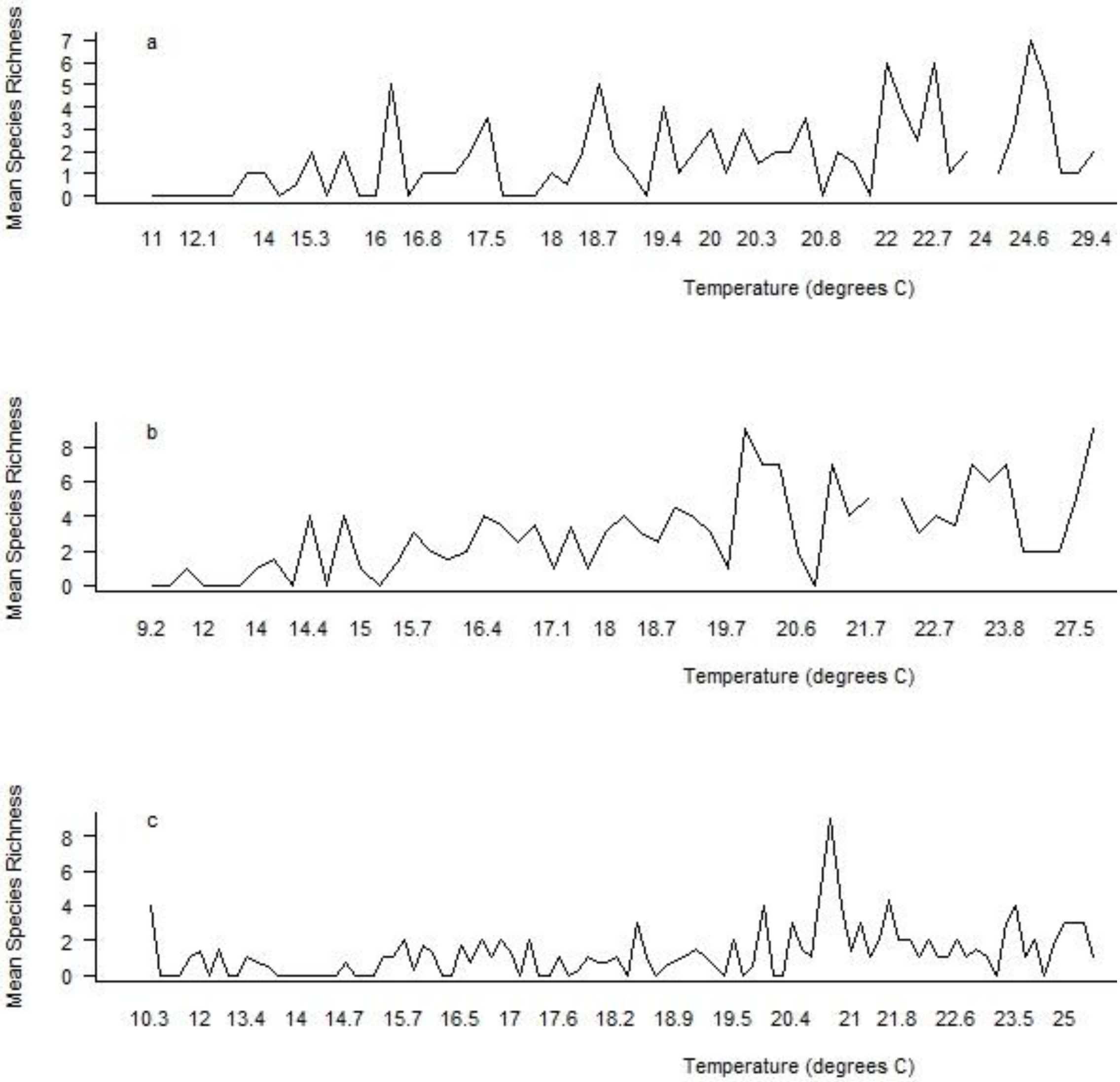

Figure 5. Mean species richness in response to increasing temperature for (a) Grassland, (b) Edge and (c) Woodland.

Structural Variables

Grassland

ZIP analysis was carried out upon butterfly abundance and structural variables for woodland and grassland. Within the poisson model for grassland structure, total vegetation point contacts and sward height were found to have an effect upon butterfly abundance. Total vegetation point contacts had a negative effect upon abundance, whilst sward height had a slightly positive effect. There was no interaction between herb point contact, total vegetation point contact and sward height. Conversely, in the logistic section of the model, herb point contact was found to effect butterfly abundance, with a strong negative effect, suggesting that the absence of herbs made it more likely for there to be zero butterfly observations, whilst the estimate in the logistic section for total vegetation contacts suggests that the chances of observing zero butterflies increases with increasing sward height. The results of the analysis are detailed in Tables 6 and 7. Figure 6 shows butterfly abundance in relation to (a) the mean total vegetation and (b) herb contact of the grassland transects. West Copse Field and West Copse Field Border have the highest butterfly abundances, but not necessarily the highest total vegetation and herb point contacts.

Table 6. Results from poisson section of analysis of grassland structural variables on butterfly abundance.

Variable	Estimate	Std. Error	z score	Pr(>|z|)
Herb Point Contact	4.05	1.35	3.00	0.002
Total Vegetation Point Contact	-2.15	0.25	-8.79	<0.001
Sward Height	0.009	0.001	8.86	<0.001
COPSE POUND	-1.20	0.24	-4.93	<0.001
Herb Point Contact:Total Vegetation Point Contact	-0.72	0.70	-1.02	0.31
Herb Point Contact:Sward Height	-0.002	0.001	-1.34	0.18
Total Vegetation Point Contact:Sward Height	<0.001	<0.001	195.96	<0.001
Total Vegetation Point Contact:Copse Pound	0.66	0.19	3.44	<0.001
Sward Height:COPSE POUND	-0.002	0.001	-2.47	0.01

Table 7. Results from logit section of analysis of grassland structural variables on butterfly abundance.

Variable	Estimate	Std. Error	z score	Pr(>|z|)
Herb Point Contact	-22.58	12.81	-2.01	0.04
Total Vegetation Point Contact	4.28	2.74	1.56	0.12
Sward Height	-0.006	0.02	-0.42	0.67
COPSE POUND	1.18	2.30	0.40	0.69
Herb Point Contact:Total Vegetation Point Contact	8.28	4.76	1.74	0.08
Herb Point Contact:Sward Height	-0.009	0.03	-0.29	0.77
Total Vegetation Point Contact:Sward Height	-0.005	<0.001	-5.08	<0.001
Total Vegetation Point Contact:COPSE POUND	-1.96	2.60	-0.75	0.45
Sward Height:COPSE POUND	0.009	0.01	0.69	0.49

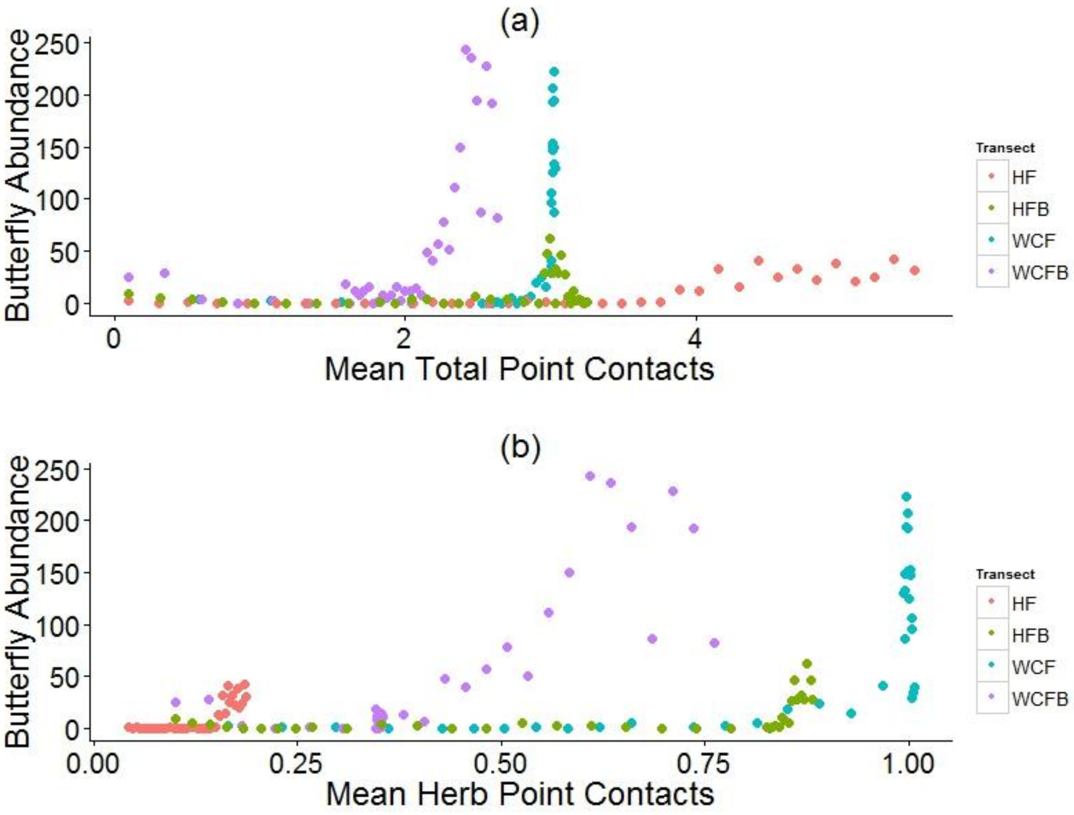

Figure 6. Grassland and Edge transects and butterfly abundance in relation to (a) mean total vegetation point contacts and (b) mean total herb point contacts.

The same analysis was carried out upon number of species observed in the grassland transects, the results of this are detailed in Tables 8 and 9. Individually the structural variables did not have an effect on species richness. POUND did have a negative effect. There were interactions between total and herb point contacts, herb point contact and COPSE, and sward height and COPSE. Figure 7 shows the lack of a relationship between (a) total vegetation point contact or (b) total herb point contact on butterfly species richness.

Table 8. Results from poisson section of analysis of grassland structural variables on butterfly species richness.

Variable	Estimate	Std. Error	z score	Pr(>|z|)
Herb Point Contact	4.14	3.50	1.18	0.24
Total Vegetation Point Contact	0.21	0.57	0.36	0.72
Sward Height	-0.001	0.002	-1.02	0.28
COPSE POUND	-1.24	0.47	-2.64	0.01
Herb Point Contact:Total Vegetation Point Contact	-3.54	9.40	-3.76	<0.001
Herb Point Contact:Sward Height	0.006	0.004	1.82	0.07
Herb Point Contact:COPSE POUND	4.75	1.80	2.64	0.008
Total Point Contact:Sward Height	0.001	<0.001	497.64	<0.001
Sward Height:COPSE POUND	-0.004	0.002	-2.16	0.03

Table 9. Results from logit section of analysis of grassland structural variables on butterfly species richness (continued on to next page).

Variable	Estimate	Std. Error	z score	Pr(>|z|)
Herb Point Contact	-0.39	40.17	-0.01	0.99
Total Vegetation Point Contact	-5.76	14.58	-0.40	0.69
Sward Height	0.09	0.13	0.66	0.51
COPSE POUND	7.49	6.30	1.20	0.51
Herb Point Contact:Total Vegetation Point Contact	33.22	41.20	0.81	0.42
Herb Point Contact:Sward Height	-0.18	0.33	-0.55	0.58
Herb Point Contact:COPSE POUND	-26.16	27.56	-0.95	0.34

Total Point Contact:Sward Height	-0.03	0.02	-1.28	0.20
Sward Height:COPSE POUND	0.01	0.04	0.34	0.74

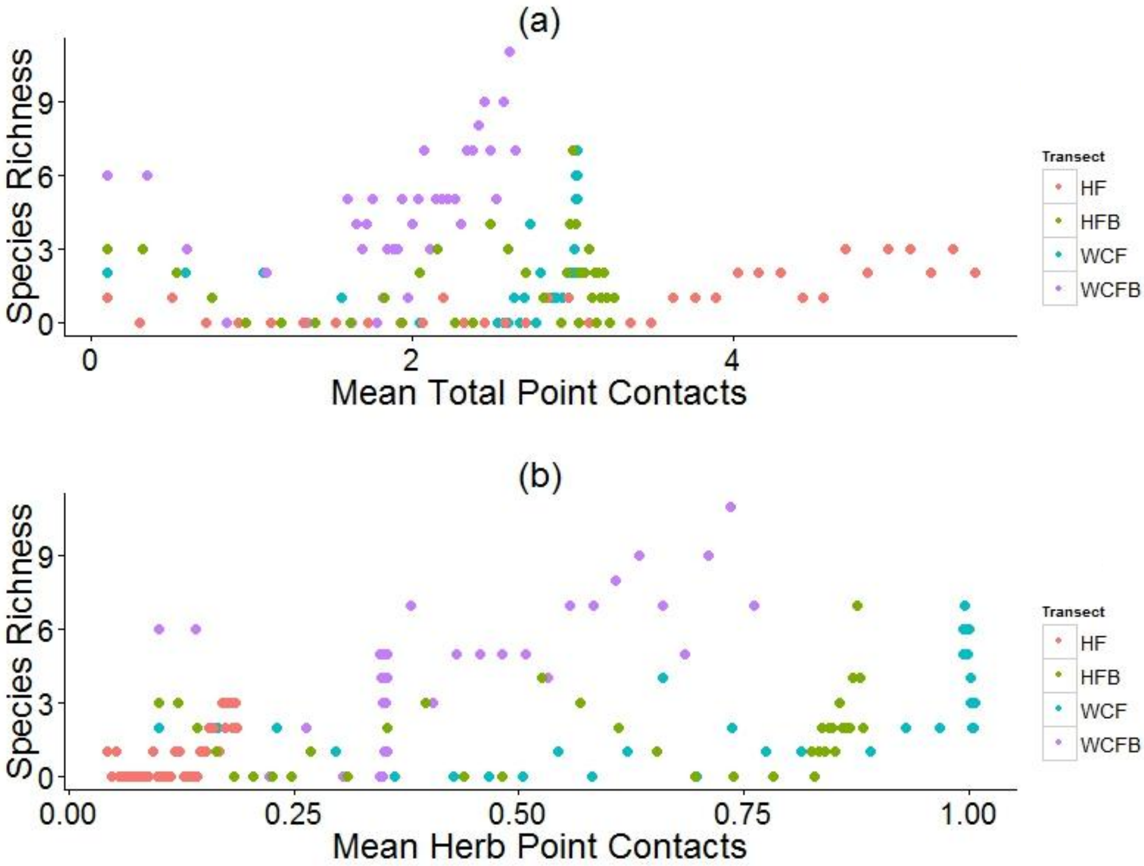

Figure 7. Grassland and Edge transects and butterfly species richness in relation to (a) mean total vegetation point contacts and (b) mean total herb point contacts.

Woodland

For the woodland structural variables, a ZINB model was used as this provided a better fit for the data. This showed that canopy openness, FHD and COPSE had an effect upon butterfly abundance, whilst there were interactions between FHD and Canopy Openness, and FHD and COPSE. The results from the analysis are detailed in Tables 10 and 11. Figure 8 (a) shows HC1 possessing a lower FHD than the other transects, but with higher butterfly abundance than most of the other transects, whilst (b) shows that HC1 and HCRi have higher levels of canopy openness as well as higher butterfly abundance.

Table 10. Results from poisson section of analysis of woodland structural variables on butterfly abundance.

Variable	Estimate	Std. Error	z score	Pr(>|z|)
Canopy Openness	0.87	0.25	3.52	<0.001
Foliage Height Diversity	23.67	7.31	3.24	0.001
COPSE POUND	9.43	3.90	2.42	0.02
Canopy Openness:Foliage Height Diversity	-1.45	0.45	-3.20	0.001
Foliage Height Diversity:Copse Pound	-16.94	7.20	-2.35	0.02

Table 11. Results from logit section of analysis of woodland structural variables on butterfly abundance.

Variable	Estimate	Std. Error	z score	Pr(>|z|)
Canopy Openness	-0.11	2.29	-0.05	0.96
Foliage Height Diversity	-25.76	69.59	-0.37	0.71
COPSE POUND	-7.84	26.23	-0.30	0.77
Canopy Openness:Foliage Height Diversity	1.57	4.05	0.39	0.70
Foliage Height Diversity:COPSE POUND	35.11	48.75	0.72	0.47

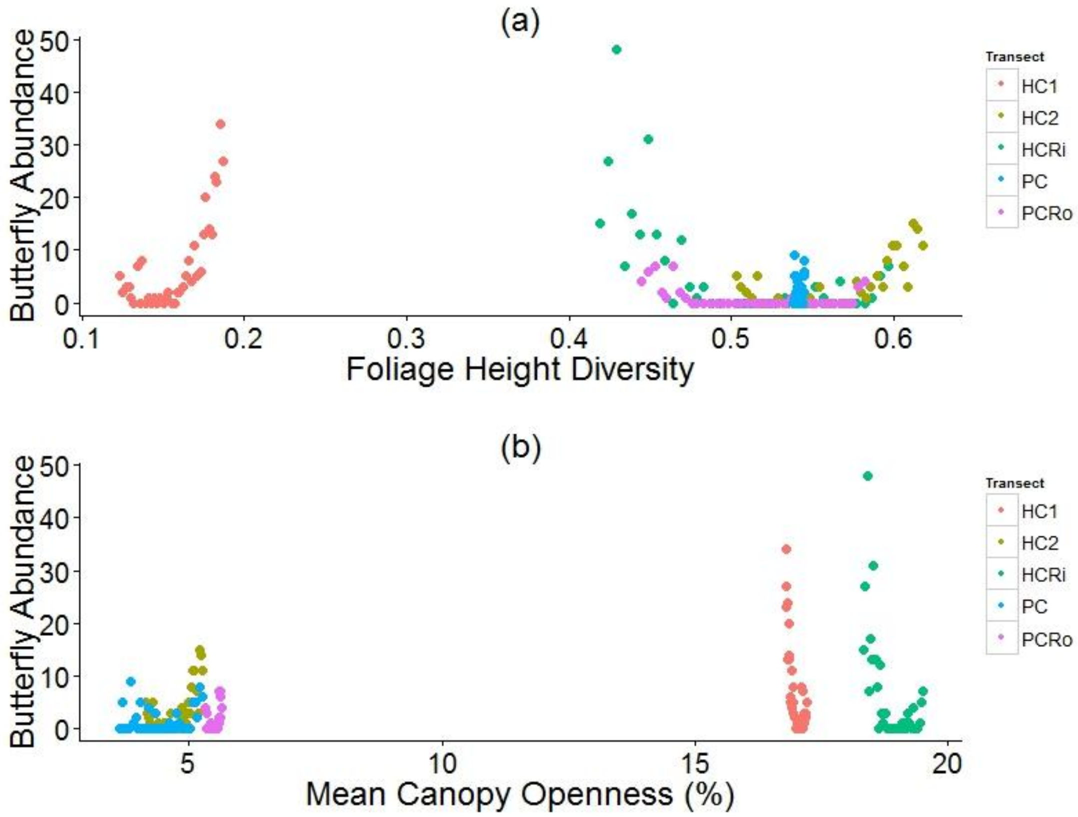

Figure 8. Woodland transects and butterfly abundance in relation to (a) FHD and (b) mean canopy openness

A ZINB analysis was carried out on species richness and the woodland structural variables. Once this model was simplified removing the least significant results one at a time and AIC numbers checked, it was found that none of the structural variables had an effect upon species richness in the woodland. This is shown in Tables 12 and 13. Figure 9 shows the difference between transects in (a) FHD and (b) canopy openness as in Figure 7, but this time in relation to species richness. This shows the more even spread between transects in species richness.

Table 12. Results from poisson section of analysis of woodland structural variables on butterfly species richness.

Variable	Estimate	Std. Error	z score	Pr(>|z|)
Canopy Openness	0.03	0.02	1.65	0.10
COPSE POUND	-0.56	0.37	-1.52	0.13

Table 13. Results from binomial section of analysis of woodland structural variables on butterfly species richness.

Variable	Estimate	Std. Error	z score	Pr(>|z|)
Canopy Openness	1.12	0.87	1.29	0.20
COPSE POUND	15.42	11.17	1.38	0.17

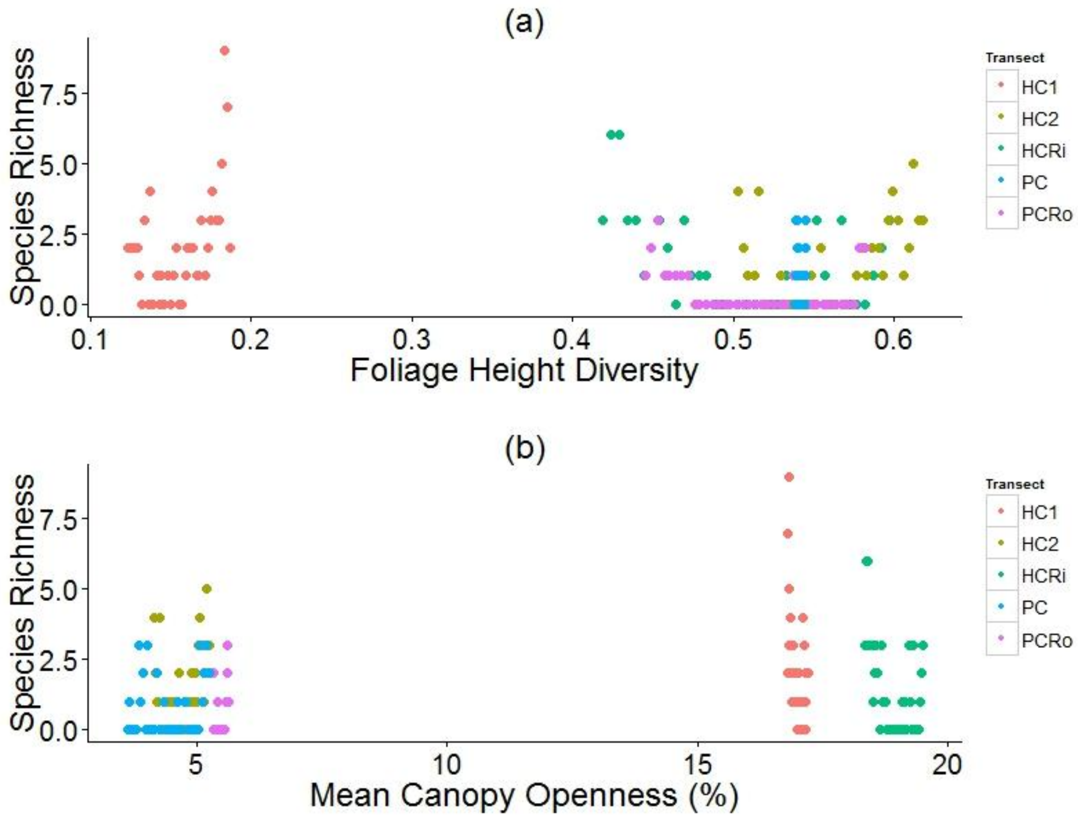

Figure 9. Woodland transects and butterfly species richness in relation to (a) FHD and (b) mean canopy openness

Discussion

This study set out to provide fine scale data on the response of butterflies to differing management practices, and assess if this impacted upon how they responded to fluctuating weather conditions. Overall butterfly abundance and species richness was higher in the sites that have been managed to increase biodiversity; West Copse Field and Horsham Copse, compared to Hurst Farm Field, which has been managed to produce a greater crop yield, and Pound Copse, which has been subject to less active management than Horsham Copse. Referring back to the first hypothesis, the assertion that the differing management practices would result in a difference in butterfly abundance and species richness can be accepted.

Environmental Drivers

Temperature was found to be the strongest environmental variable for both butterfly abundance and species richness. This is in line with our knowledge of butterflies being poikilothermic as highlighted in the introduction (Roy & Sparks 2000). Wind and cloud cover did have an effect upon overall abundance but not upon species richness. This suggests that the majority of species still maintained a certain level of activity when conditions became windier and cloudier, but overall abundance would decline. Previous research has suggested that many species of butterfly are not greatly affected by wind speed until it reaches above 5 on the Beaufort scale (Wikström et al. 2009), around 10 ms^{-1}. These wind speeds were never reached during this study, but the results suggest that the activity of butterflies is still affected by wind speeds below 10 ms^{-1}.

The model shows POUND having a significant positive estimate on species richness. This is counterintuitive as it is clear that species richness was higher in HORSHAM. This positive estimate is due to the complexity of the model and POUND's relationship to other coefficients. It is estimating that the proportional rate of increase in butterfly abundance is higher for POUND (inclusive of Pound Copse and Hurst Farm Field) than HORSHAM (inclusive of Horsham Copse and West Copse Field) with changing environmental conditions. This may be due to HORSHAM already possessing butterflies in greater numbers than POUND, and is possibly an indication of the healthier numbers in HORSHAM being less affected by environmental factors.

These environmental variables did interact differently with the different transect types. Again, this is to be expected as the increased vegetation cover of woodland transects resulted in cooler temperatures and less windy conditions. This highlights how climatic conditions can vary over a relatively small scale resulting in microclimates (Curtis & Isaac 2014;

Gardiner & Dover 2008). Wind had a greater adverse effect on Grassland transects than Woodland transects. Trees provide a taller, sturdier vegetation structure, sheltering the woodland habitat from wind. Having two habitats with differing microclimates directly adjacent to each other means that taxa such as butterflies could move from one habitat to another if conditions in the grassland were to become unfavourable. This has been shown before with butterflies sheltering from windy conditions on the leeside of hedgerows (Dover 1996; Dover et al. 1997).

The statistical analysis showed a more negative interaction between POUND and temperature and wind speed, than HORSHAM and the same environmental variables on butterfly abundance. There was no interaction between COPSE and these environmental variables on species richness. This partially upholds the second hypothesis outlined in the introduction, as there is a difference in response of butterfly abundance, but not species richness to environmental variables between patches with differing management plans. Again it seems that the proportional response of butterfly abundance in HORSHAM was smaller than the response of POUND. It is possible that the habitat management practices in West Copse Field and Horsham Copse have provided an environment in which butterflies are able to proliferate and better withstand changes in environmental conditions, which have been shown to be key drivers of their change in abundance in the past (Pollard 1988; Roy et al. 2001). Being present in greater numbers allows butterflies to be more resilient to environmental stochasticity and will act as a buffer for a population against local extinction (Hanski 1998). This study has demonstrated a difference in short-term response to environmental factors between habitats with differing management plans, and provides a positive assessment of the management practices in place in West Copse Field and Horsham Copse.

Vegetation Characteristics

Grassland

The differences in butterfly abundance between the Grassland and Edge transects of West Copse Field and Hurst Farm Field were particularly large. The edge habitat of West Copse Field also yielded 8 more species than that of Hurst Farm Field, and 21 of the 23 species observed in total. This is interesting, as the amount of herb point contacts observed was greater in Hurst Farm Field Border than West Copse Field Border. Although no specific floristic analysis was carried out, the number of herb point contacts could crudely act as a proxy for the abundance of possible nectar plants for the butterflies to feed upon. In this case we would expect Hurst Farm Field Border to be a preferable habitat to West Copse Field

Border, as butterflies are attracted to herb rich patches (Cole et al. 2014; Sparks & Parish 1995). The fact that this is not the case may be due to Hurst Farm Field not possessing buffer strips. It has been found in previous studies that once a hay meadow has been cut, butterfly abundance will significantly decline for most species, and it is suggested that the main cause of this is mortality rather than emigration (Dover et al. 2010). The presence of buffer strips within a meadow that are not cut during the same period have the potential to offer a refuge to butterflies after the cutting period, and allow populations to persist through to subsequent generations. West Copse Field possesses buffer strips cut on a three year rotation cycle, and this may be a reason that more butterflies were surveyed along its border than Hurst Farm Field Border, despite having lower herb point contacts. Furthermore, this rotational cycle of cutting provides a sward height heterogeneity within West Copse Field not found in Hurst Farm Field. As previous research has shown (Jerrentrup et al. 2014) a variety of sward heights on a horizontal level can contribute to high butterfly abundance and species richness, and may be part of the reason for the increased levels seen in West Copse Field.

The analysis of grassland structure shows that increasing sward height has a slightly positive effect on butterfly abundance. At the end of the survey period, a high average sward height was being provided both in Hurst Farm Field and West Copse Field. An increased sward height allows for greater vertical sward heterogeneity, and could provide a more heterogeneous structure with a variety of microclimates (Dennis et al. 1998). Hurst Farm Field possessed consistently taller sward heights, and also had the most total vegetation point contacts. But as Figure 7 (a) shows, Hurst Farm Field had lower species richness than the other field transects, and total vegetation contact had a negative effect upon abundance. As previous research has suggested (Jerrentrup et al. 2014), increased vertical microclimates were not having an effect on butterfly abundance in this study, and that other factors are resulting in the increased butterfly abundance and species richness observed in West Copse Field.

With regards to Hypothesis 3 then in terms of the grassland, it is clear that there is a difference in overall abundance and species richness between the fields, but it is not clear that differences in structure is having an effect. Other factors may be causing the increased numbers in West Copse Field, such as the presence of larval food plants (Pocewicz et al. 2009) and specific composition of nectar resources. From the surveying period it was clear that there were a lot more nectar resources in the centre of West Copse Field than Hurst Farm Field. This is interesting because, as noted in the methods, both fields were sown with the same hay mix at the same time. The high floral presence in West Copse Field is likely to be a key factor in the higher butterfly levels in West Copse Field, with these increased floral levels a result of the current and prior management practices for each field respectively. The policy of leaving West Copse Field unfertilised has allowed the herbs to remain and compete with grass species, and provided nectar resources for butterflies.

Woodland

Canopy openness did have a positive effect on butterfly abundance. As expected, the creation of open spaces allowing for greater penetration of sunlight resulted in more individuals (Greatorex-Davies et al. 1993; Warren & Thomas 1992). The analysis for the woodland structural variables predicts a stronger rate of increase in butterfly abundance for Pound Copse than Horsham Copse. This is seen with both the FHD and canopy openness. This may be due to the lower starting point of butterfly abundance in Pound Copse, but it does suggest that if more open spaces were created within Pound Copse, a significant increase in butterfly abundance could be observed, and it is known that many butterfly species that breed within woodland do require open habitat (Warren & Thomas 1992). The relationship between increased FHD and butterfly abundance in the woodland is unclear. The model suggests that as FHD increases beyond 0.55 butterfly abundance will also increase at a greater rate in Pound Copse. However, Figure 8 (a) shows that an increase in FHD is not necessarily resulting in higher butterfly abundance, in fact the highest numbers are found at lower FHD levels. The large positive estimate of FHD is a result of its association with other coefficients, suggesting that species richness will increase in Pound Copse with an increase in FHD. An examination of the data does not indicate that this would be case.

There was found to be no overall difference in butterfly abundance or species richness between the woodland transects of Horsham and Pound copse. This has been shown before in comparing logged and unlogged tropical forests (Hamer et al. 2003). Whilst there was a higher abundance of butterflies in Horsham copse, the relative magnitude of this was not much larger than Pound Copse. This suggests that further work could be carried out to open up the woodland habitat of both copses. The Silver-washed fritillary (*Argynnis paphia*), a species observed in Horsham Copse, thrives within freshly cut coppice, but needs this to adjoin older coppices where its larval food plant, violets, will grow (Warren & Thomas 1992).

The Silver-washed Fritillary is one species that was seen to emerge in strong numbers in Horsham copse towards the end of the survey period. Horsham copse appears to be a very good environment for them, possessing open spaces for the adults to fly in, the larval food plant common dog-violet (*Viola riviniana*), a favoured nectar source in bramble (Tudor et al. 2004), and tree stumps on which they can lay their eggs. The large amount of bramble in open sections of the woodland is likely to be a factor driving the strong presence of Silver-washed Fritillary as it has been noted that woodland specialists tend to have a reduced range of nectar sources that they feed upon (Tudor et al. 2004). This is a species that was previously in decline on a national level, but in recent years has shown signs of recovery (Fox et al. 2011). Its continued presence should be encouraged here to aid in its ongoing recovery. Time constraints meant that surveying could not continue throughout the entirety of the Silver-washed Fritillary's flight period, restricting full monitoring of this species.

The Landscape Context

The lower butterfly abundance of Hurst Farm Field Border may be due to where it sits in the wider landscape. Although butterflies are a mobile species, the relatively flower poor areas of Hurst Farm Field and Pound Copse may reduce butterfly visits to this edge habitat as they prefer to stay in a nearby flower rich habitat (Cole et al. 2014) such as West Copse Field. Within the wider landscape the Marwell grounds are surrounded predominantly by agricultural fields and smaller copses. The Marwell grounds form part of this multifunctional landscape, where any measures to promote biodiversity have to sit alongside more commercial interests. It has been shown that within agricultural landscapes butterfly species richness and abundance in one patch is affected by the farming practice in neighbouring patches and by the habitat heterogeneity of the landscape (Rundlöf & Smith 2006; Rundlöf et al. 2008). As such, the grassland of Hurst Farm Field and the woodland of Pound Copse may be negatively affecting butterfly abundance and species richness on a local scale for Hurst Farm Field Border. The butterfly abundance and species richness of neighbouring farmlands may also be affecting the sites that have been surveyed in this project; it is known that at least one of these farms is engaged in a governmental environmental stewardship scheme designed to give financial incentives for farmers to use measures to increase biodiversity on their farmland. Further research may be able to establish the influence of the surrounding landscape.

Species rich chalk grassland is now estimated to cover only 3% of the South Downs (Haines-Young et al. 2006). Much of the national park is engaged in agricultural land use creating a fragmented landscape (Burnside et al. 2003). The management practices in place in West Copse Field offer a way in which a species rich assemblage of invertebrates can be achieved whilst still being able to provide a commercial yield.

Within a fragmented landscape an organism's movement between suitable habitats will involve less favourable areas. The opening up of sections within the woodland provides corridors for species to move from one suitable habitat to another. This has been shown previously for species such as the Ringlet (Sutcliffe & Thomas 1996). It is important though that suitable habitats are not too far away from each other, as it has species such as the Pearl-bordered Fritillary (*Boloria Euphrosyne*) are not able to move to suitable habitats if the distance is too great. Even strong fliers like the Silver-washed Fritillary were seen not to connect with their nearest population 1 km away (Warren & Thomas 1992).

Implications and Recommendations for Management

The majority of the species recorded in this survey are classed as habitat generalists. Habitat generalists are less rare than habitat specialists, with only one species recorded here found on the UK BAP list, the Small Heath (*Coenonympha pamphilus*), and this individual was only recorded on one occasion. This suggests that the habitat management currently in place is providing suitable habitat for generalist species and allowing some, such as the Meadow Brown (*Maniola jurtina*), Marbled White (*Melanargia galathea*), Ringlet (*Aphantopus hyperantus*) and Common Blue (*Polyommatus Icarus*) to persist in large numbers. Currently these habitats are not providing the necessary conditions for specialists in the grassland habitats to thrive. For example the Adonis blue (*Polyommatus bellargus*) thrives in a grassland habitat that is close cropped and is known to be closely associated to habitats that are actively grazed (Dennis 2010). It is not known at this moment whether any grassland species with specific requirements are present in the surrounding landscape and able to colonise the grasslands should suitable conditions be created. Any changes in management practices for West Copse Field which may result in shortening the sward height of the majority of the field should be treated with caution at this point, as large numbers of generalist species are being well supported here and may be adversely affected by this.

If buffer strips are added to Hurst Farm Field, this will create more structural heterogeneity and areas that will remain uncut for several years. This should increase species richness in Hurst Farm Field. But abundance levels are unlikely to reach the levels of West Copse Field, whilst the herb levels within the field itself are so low. If future management would like numbers to be comparable to West Copse Field, a re-sowing of Hurst Farm Field and a cessation of fertilization will most likely be required.

A study of the surrounding environment would be of benefit in order to establish if there are specialist species nearby that could colonise West Copse Field should the right conditions be created. Until that point, the maintenance of the current management plan should be encouraged.

The maintenance of conditions conducive for the proliferation of the habitat specialist, Silver-washed Fritillary, should be encouraged in ongoing management of the woodland. The logging of European larch should continue, which will in turn open up more clearings. This should further encourage butterfly abundance levels to increase. There are sections of Horsham Copse where hazel has been allowed to grow for several years. The increased rotation of coppicing in these areas should contribute to the overall open structure of the woodland.

Silver-washed Fritillary's were not observed during the survey period in Pound Copse. However they were seen at low numbers outside of surveying, and with Silver-washed Fritillaries being strong fliers and the known presence of a close-by population in Horsham copse, a stronger population could be established in Pound copse through the creation and maintenance of open spaces there. This could be achieved through more regular coppice rotation.

Evaluation of the method

The surveying of butterflies 3 days a week over a 3 month period provided fine scale information on butterfly response to environmental variables, and indicated that those in West Copse Field and Horsham Copse responded better to these variables than butterflies in Hurst Farm Field and Pound Copse. It was able to show that management measures for increasing biodiversity have been successful, particularly in the grassland habitat. Intensive surveying of an indicator taxa, such as butterflies, can provide a good indicator for land managers as to the relative success of their work.

The structural variables that were carried out did also provide insights into their effect, but time constraints and a lack of manpower meant that the results are speculative. Grassland habitat in particular rapidly changes in structure during the summer months, and so for this method to be more effective more regular surveying, possibly on a weekly basis, would give more reliable results.

Suggestions for Further Research

The stability and resilience of a population to local extinctions is tied in whether how well it can deal with unfavourable conditions and take advantage of beneficial ones. This research has shown that there is a difference in response to environmental variables between similar habitats under different management regimes. The analysis of this could be taken further by assessing whether there is a specific difference in the lag response of butterfly numbers to these fluctuating environmental conditions. This could be achieved by carrying out a Granger-causality test on the time series of butterfly abundance and temperature, and comparing the differences between transects.

Understanding exactly where these habitats fit in the wider landscape would also be of further benefit. Future surveying of neighbouring lands could assess whether there are any butterfly species populations present which are not currently within the Marwell grounds, and whether these could potentially move into the grounds if the correct conditions were created. Similarly, establishing whether the populations within the Marwell grounds are part of a wider meta-population could help provide an idea of how resilient these current populations are to local extinctions.

A detailed floristic analysis of the grasslands surrounding Marwell would complement the analysis carried out in this study well. This would allow further insight into the relative contribution of butterfly abundance and species richness compared to the abundance and diversity of floral resources.

Conclusions

This study was successful in highlighting the differences in butterfly abundance and species richness between habitats of differing management practices. As an indicator species, the large presence of butterflies in West Copse Field suggests that biodiversity levels here are in good health. It has shown a difference in the short-term response of these habitats to environmental fluctuations, an area that has been little studied before.

The lack of a detailed floristic analysis within this study is a weakness. If this could have been carried out, then a greater idea of the overall effect of structure on butterfly abundance could be gauged.

Furthermore, the structural variables were necessarily speculative due to time constraints, and the results of the structural analysis should be treated with an element of caution. Despite this, this project has given an indication of the role that structure plays in the biodiversity of invertebrates, and if the above weaknesses could be remedied in the future, valuable insights could be made.

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Appendix

Table S1. GPS Co-ordinates for start and end of transects. Co-ordinates are in UTM UPS position format. All transects are in zone 30U.

Transect	Start Northing	Start Easting	End Northing	End Easting
WCF	0620175	5650471	0620075	5650885
WCFB	0620127	5650879	0620271	5650503
HCRi	0620298	5650510	0620154	5650887
HC1	0620273	5650830	0620332	5650695
HC2	0620426	5650713	0620331	5650855
HFF	0620801	5650040	0621152	5650143
HFFB	0620907	5650138	0621135	5650181
PCRo	0621123	5650194	0620919	5640157
PC	0621141	5650263	0620897	5650197

Table S2. Butterfly species recorded and transects in which they were recorded.

Common Name	Scientific Name	Transects Recorded
Small Skipper	*Thymelicus sylvestris*	WCF, WCFB, HFF, HFFB
Essex Skipper	*Thymelicus lineola*	WCFB
Large Skipper	*Ochlodes Sylvanus*	WCF, WCFB, HFFB
Brimstone	*Gonepteryx rhamni*	WCF, WCFB, HCRi, HC1, HC2, HFF, PCRo, PC
Large White	*Pieris brassicae*	WCF, WCFB, HCRi, HC1, HC2, HFF, HFFB, PCRo, PC
Small White	*Pieris rapae*	WCF, WCFB, HCRi, HC1, HC2, HFF, HFFB, PC
Green-veined White	*Pieris napi*	WCF,WCFB, HCRi, HC1, HC2, HFF, HFFB, PCRo, PC
Orange Tip	*Anthocharis cardamines*	WCFB, HCRi, HC2, HFFB, PCRo
Small Copper	*Lycaena phlaeas*	WCF
Common Blue	*Polyommatus Icarus*	WCF, WCFB, HFF, HFFB
Holly Blue	*Celastrina argiolus*	WCFB, HCRi, HC1, HC2, HFF, HFFB, PC
Red Admiral	*Vanessa atalanta*	HC1, HC2, PC
Painted Lady	*Vanessa cardui*	WCFB
Small Tortoiseshell	*Aglais urticae*	WCF, WCFB, HCRi, HC2
Peacock	*Aglais io*	WCF, WCFB, HCRi, HC1, HFFB, PC
Comma	*Polygonia c-album*	WCFB, HC1, HC2
Silver-washed Fritillary	*Argynnis paphia*	WCFB, HCRi, HC1, HC2
Speckled Wood	*Pararge aegeria*	WCFB, HCRi, HC1, HC2, HFFB, PC
Marbled White	*Melanargia galathea*	WCF, WCFB, HCRi, HC1, HFF, HFFB
Gatekeeper	*Pyronia tithonus*	WCF, WCFB, HCRi, HC1
Meadow Brown	*Maniola jurtina*	WCF, WCFB, HCRi, HC1, HC2, HFF, HFFB,

		PCRo, PC
Ringlet	*Aphantopus hyperantus*	WCF, WCFB, HCRi, HC1, HC2, HFF, HFFB
Small Heath	*Coenonympha pamphilus*	WCFB