The Effect of Habitat Condition and Vegetation on the Moth Communities of the Limestone Habitats at Hutton Roof and Farleton Knott Sites of Special Scientific Interest, North West England

Justine Patton

BSc (Hons)

This dissertation is submitted for the degree of MSc by Research, Ecology

March 2022

Lancaster Environment Centre, Lancaster University

Declaration

I declare that the work presented in this thesis is that of my own and has not been previously presented for any other assessment. The ideas explored in this work are entirely original and have been refined through supervisory discussions. Any photographs used belong to the author. The trait data used in chapter 4 is available through Butterfly Conservation (Cook *et al.,* 2021).

Justine Patton

Lancaster University, March 2022

Acknowledgements

First and foremost, I must thank my supervisors Dr Andy Wilby and Dr Rosa Menendez for their support throughout the whole process, from refinement of the sampling protocol to support throughout the statistical analysis. Your guidance was greatly appreciated, thank you.

Also, to Dan Blumgart who kindly passed on several of the UV LED bulbs, funnels and baffles he used during his PhD, they were gratefully received. They had very much come to the end of their life by the time I had finished with them. Thank you for providing such detailed instructions to go with them, they were needed as the timers were quite complicated. I removed them in the end.

Many thanks go to all the landowners of Hutton Roof and Farleton Knott that gave permission to survey their land; Jennifer Burrow (Commoners representative), Peter Jones (Cumbria Wildlife Trust), Martin Colledge (Forestry England), Craig McCoy (National Trust), Julian Olston (Dallam Tower Estate) and Jane Hopwood (Holme Stinted Pasture representative). Also, thank you to the Natural England team for their advice and overall consent to sample the reserves.

I am also indebted to Steve Palmer for supporting with the micro-moth dissection and identification, who selflessly offered his expertise. I would have struggled with the smaller specimens. I am glad there were plenty of interesting Gelechiids for you! And to Martin Tordoff for assisting with my request for moth records from Cumbria.

Most importantly, to my Son, Jacob, who (surprisingly!) barely grumbled at the long hours doing fieldwork in what can be quite a challenging landscape. He proved himself to be an invaluable assistant and took the hills, the heat, and the horseflies all in his stride. I am sincere when I say that nobody else could have done a better job.

Abstract

Moths in western Europe have seriously declined since the mid-20th century, mirroring the trends seen in other insect groups. The drivers of decline are multifarious, with agricultural intensification, habitat loss and degradation, eutrophication and climate change being key factors. In the UK, Sites of Special Scientific Interest (SSSI) protect some of the rarest flora, fauna, and geological features and are of high conservation value. The designation protects against damage and development through maintaining 'favourable' condition. This thesis aimed to investigate how habitat type (grassland vs pavement), habitat condition (declining, recovering, favourable) and vegetation composition affects the moth communities of Hutton Roof and Farleton Knott SSSIs, NW England, by assessing moth samples and data on vegetation along with existing macro-moth trait data. Observed levels of species richness, estimated measures of moth diversity, functional diversity, community composition and trait composition did not differ between habitat types or habitat condition. Instead, the moth community and trait composition differed between SSSI units and reserves, being driven by forb cover. More woodland macro-moth species were sampled at the grassland habitat despite the limestone pavement supporting taller, woody plants, suggesting the vegetation surrounding the grasslands is a key driver. The findings highlight advancing stages of succession from undermanagement: encroachment is not being actively managed, and a lack of rotational livestock grazing is promoting swards dominated by rank grasses. The increased grass cover in place of forbs negatively affected moth species richness. The macro-moth community was represented by many ubiquitous species, with a range of complementary generalist life-history traits. A number of specialist moths have been identified at both reserves, some of which are locally abundant. Bryophytes, lichens, and algae play an important role at the limestone pavement habitat; there is potential for them to provide a medium in which to pupate, a food source for larval stages, support for plant species to develop in an extreme environment and have a positive effect on estimated moth diversity. Condition assessments fail to acknowledge the value of bryophytes and lichens in a water and nutrient limited environment. This thesis highlights the limitations of condition assessments that focus on vegetation, supporting the need for the integration of additional taxa.

Contents

Page

List of figures

Page

List of tables

Page

Chapter 1
General Introduction

1.1 Global insect diversity

Insects are the most species rich taxon on Earth, comprising over half of all species currently described (Stork, 2018). Approximately one million species of insect have been described to date, whereas the true estimate of extant insect species is likely to be upwards of five million (Gaston & Hudson, 1994; Mora *et al.,* 2011). The Order Lepidoptera is one of the most speciose, with over 157,000 species being described globally, only second in magnitude to Coleoptera (387,000 species) (Stork, 2018). The evolutionary diversity of this hyperdiverse group occupies almost every available ecological niche (Grimaldi & Engel, 2005). Hypotheses reviewed by Mayhew (2007) suggest a number of possible mechanisms have contributed to their success relating to complex morphologies and broad ecological and reproductive diversification, in particular.

1.2 Loss of insect biodiversity

The complexities of insect life histories mean any losses in abundance or diversity may lead to reduced ecosystem functioning. Insects play central roles in many ecosystem services; they are important pollinators, which has played a key role in their diversification (Ollerton *et al.,* 2011), they play key roles in the cycling of nutrients (Swank *et al.,* 1981; Lovett & Ruesink, 1995), and form an important part of the food chain, most notably within the higher trophic levels (Martin *et al.,* 2013; Grass *et al*., 2017; Møller, 2019). Therefore, studies noting worrying declines in species richness, abundance and a shrinking of many species' geographical distribution provides justification for concern (Wenzel *et al*., 2006; Hallman *et al.,* 2017; Lister & Garcia, 2018; Møller, 2019; Wagner, 2020). Current assessments of biodiversity loss do not always fully consider insects due to a lack of available baseline data, but moves are being made to fill knowledge gaps. Trends observed for insects do not always follow suit with declines in other taxa (Clausnitzer *et al.,* 2009). The principal drivers of insect loss have been identified as habitat change, pollution, and climate change (Sánchez-Bayo & Wyckhuys, 2019). The knock-on effects of insect decline on higher trophic levels are also becoming evident, with the decline in insectivorous birds at both a local and global scale (Bowler *et al*., 2021; Møller, 2019).

1.3 Moth diversity in the UK

In the United Kingdom (UK), over 2500 moth species have been recorded; approximately 900 are macro-moths and over 1600 are micro-moths (Agassiz *et al*., 2013). Butterflies, the diurnal subgroup of the Order Lepidoptera, are represented by just 59 species in the UK (61 including migrants). The arbitrary split of the macro and micro-moths does not have any scientific backing and is more for convenience. Generally, the macros are larger than the mostly smaller micros, but overlap occurs, leading to some confusion regarding identification for those new to Lepidoptera. The larger moths are generally easier to identify with confidence and thus are studied in greater depth, which has led to a comprehensive understanding of their life histories having been developed (Waring and Townsend, 2017). The 900 species of macro-moth found in the UK span 19 lepidopteran families and encompass a vast ecological spectrum, making them well suited as a tool in studies of ecological change. Furthermore, they are an important fauna in understanding how habitat quality interacts with community structure and are an important indicator in the assessment of environmental quality (Mortelliti *et al.,* 2010). However, for the micro-moths, there are still major knowledge gaps in the life histories of even some of the commoner species.

1.4 Moth declines in the UK

Moths have experienced widespread declines, even for many common species, however, our understanding of why this is happening is limited (Fox, 2013; Fox *et al.,* 2013; Dennis *et al.,* 2019). Macro-moths form an important component of the biodiversity found within the UK and underpin the functioning of ecosystems. Their high levels of diversification and short generational overturn make them useful indicators of environmental change (Macgregor *et al.* 2015). The population trend for macro-moths in the UK is one dominated by decline (Conrad, 2006). Two-thirds of 337 widespread and common macro-moth species have declined over a 35-year period. Furthermore, 21% of these have declined more than 30% in a 10-year period (Fox *et al*., 2021). The *State of Britain's Larger Moths 2021* reported a 33% decrease in the total abundance of moths caught in the Rothamsted Insect Survey (RIS) light traps over the last 50-years, with 32% of 511 species decreasing in distribution over the same period (Fox *et al.,* 2021).

The declines mirror those reported in butterflies and surpass losses seen in birds and vascular plants (Thomas *et al*., 2004). There are some winners though, including both habitat generalist and specialist macro-moth species, which has been predominantly facilitated by a warming climate in the UK (Boyes *et al.,* 2019). Long-term RIS fixed trap data collected from sites across Britain have shown that moth biomass is higher now than it was in the 1960s (Macgregor *et al.,* 2019). However, biomass has declined from a peak in the 1980s, which is in-line with biomass and abundance declines reported in other studies (Fox *et al.,* 2021). The general consensus is that declines are widespread and not restricted to specialists, although more pronounced in moth species of open grassland and heathland (Coulthard *et al.,* 2019). It is, therefore, no surprise that these are some of the most threatened habitats in the UK (Lawton *et al.*, 2010).

1.5 Drivers of moth decline

The UK's countryside now consists of fragments of once larger areas of semi-natural habitats, which are frequently surrounded by intensively managed agricultural land and urban developments. Agricultural intensification, habitat loss, degradation, and fragmentation are cited as key drivers of biodiversity loss globally (Maxwell *et al.,* 2016), reducing connectivity between suitable habitats for species that remain (Conrad *et al.,* 2006; Fox. 2013). Habitat loss, including the deterioration of quality and the effects of fragmentation have already been shown to be a principal driver of butterfly declines throughout Europe, but little evidence has been collected to date to examine these effects on moths (Fox e*t al.,* 2013).

It is widely known that many moth species are attracted to light, particularly those emitting short-wave ultraviolet radiation (Brehm *et al.,* 2021). As the majority of moth species are crepuscular or nocturnal, the impact of light pollution is an important driver of decline to consider. Boyes *et al.* (2021) found strong evidence to suggest that artificial light sources do negatively affect the behaviour of both the adult and larval stages of moths. However, it is noted that the implications at the population level are still unknown. Ultimately, drivers of moth declines do not work in isolation, they act synergistically, often to greater effect than the individual driver (Fox *et al*., 2014).

1.6 Habitats and resources

Habitats are a fundamental unit in ecology, which are characterised by their distinctive communities of plants, animals and the physical environment (Lake *et al*., 2021; Dennis *et al*., 2006). Their origins are a result of complex factors including geology, geography and climate and are under constant evolution and are therefore extremely variable (Lake *et al*., 2021). Habitat is synonymous with distinct vegetation categories, however, such adherence suggests uniformity throughout space and time (Dennis *et al*., 2006). Instead, habitats can be considered along a continuum of vegetation types and structures, provisioning resources for invertebrate species; larval foodplants, nectar sources, shelter (Hanski & Ovaskainen, 2000; Dennis *et al*., 2013). The same resources can be provided in different habitat types and may occur as patches of different sizes within the matrix. A resource-based view of vegetation patchworks at the landscape level, rather than the limitations of vegetation within particular habitats, may be better for identifying species' needs throughout their life cycles, and enhancing connectivity should be key when considering conservation strategies (Hilty *et al*., 2006; Dennis *et al*., 2013). In the UK, Lepidopteran species such as High Brown Fritillary and *Anania funebris* have been found to have benefitted from the creation of woodland rides as clearance favours their larval foodplants and provides corridors between other larger, suitable areas within the landscape (Willott, 2017; Ellis *et al*., 2021).

The synergy between habitat destruction, fragmentation and climate change that serves to accelerate biodiversity loss simultaneously degrades and isolates habitat for those species that persist (Opdam & Wascher, 2003). In a human dominated world, large tracts of the landscape are inhospitable to many species. Therefore, smaller habitat patches within the matrix and corridors are vital for increasing landscape permeability. Maintaining a heterogenous landscape and removing barriers to habitat patches are key to increasing biodiversity (Dennis *et al*., 2012; Dennis *et al*., 2013).

1.7 Functional traits and functional diversity

Habitat loss and degradation, even at nature reserves, is threatening the resilience of ecosystems. The negative effects of increased land use intensity and abandonment of semi-natural grasslands on plants, moths and other insect groups have been well documented (Öckinger *et al*., 2006; Debinski *et al*., 2011; Socher *et al.,* 2011; Seibold *et al*., 2019), but this is not the case for limestone pavements. The biodiversity of calcareous grassland is highly dependent on how they are managed and the intensity of the management methods implemented (Poschlod & WallisDeVries, 2002). Management is therefore key to maintaining and safeguarding species-rich communities, which are essential for ecosystem functioning as biodiversity promotes both resilient and productive ecosystems (Mori *et al*., 2013; Duffy *et al*., 2017). Reductions in biodiversity and the resultant biotic homogenisation, decreases the ability of the ecosystem to respond to environmental perturbations (McKinney & Lockwood, 1999). Land use intensity and will dictate the structure of the plant community and therefore resource availability. As such, the moth communities of semi-natural habitats will be a product of the environment they inhabit (McGill *et al*., 2006; Perović *et al*., 2015). For example, reduced plant species richness has been found to replace species with specialist herbivorous diets with those with generalist diets and reduces overall species richness and abundance (Mangles *et al*., 2017; Siebold *et al.,* 2019). At the landscape scale, diversity of land cover type and patch size have been found to be a crucial factor in maintaining functionally diverse arthropod communities (Gámez-Virués *et al*., 2015) and at a local scale, by habitat quality (Knuff *et al*., 2020; Uhl *et al*., 2021).

Community wide changes in the value of particular traits, as measured by trait Community Weighted Means (CWM), can indicate how the trait composition of the community has responded to environmental change and identify which are the key environmental drivers of community change. The different functional aspects of moth communities can provide insight in to how they respond to disturbances within their environment and how that may affect ecosystem functioning (Suding *et al*., 2008). Functional diversity is an important determinant of the functionality of communities, which is likely also to convey resilience to environmental change (Uhl *et al*., 2021). Different measures of functional diversity tend to be used as they give complimentary insights into the filling of niche space by a community: Functional richness considers the amount of functional space filled by the community, but it is sensitive to outliers and does not consider abundances (Laliberté & Legendre 2010); both functional evenness and divergence consider species abundances, but not the dissimilarity of species within the available trait space (Laliberté & Legendre 2010); functional dispersion accounts for this by considering the species mean deviance form the mean and is weighted by abundance (Villéger *et al*., 2008); and Rao's quadratic entropy considers the proportion of dissimilarity between species abundances within the community (Botta-Dukát, 2005). Functional diversity measures can detect different facets of the moth community structure (Mouchet *et al*., 2010), identifying links between them and ecosystem functioning (Mason *et al*., 2005).

1.8 Sites of Special Scientific Interest

One of the key conservation policy mechanisms employed in the UK is the designation of Sites of Special Scientific Interest (SSSI). By definition, a SSSI is "*an area which, in the view of the statutory authority, is of particular interest because of fauna, flora, geological or physiographic features*" (Allaby, 2015). Sites that are designated a SSSI are legally protected by the Wildlife and Countryside Act, 1981 and are therefore a formal conservation designation. There are two types of SSSI: biological and geological, although the most extensive sites are generally notified for both. Following the guidelines set out by the Joint Nature Conservation Committee (JNCC), land is designated by Natural England (NE) if it believes it contains any of the aforementioned features that are particularly special or rare (Bainbridge *et al.,* 2013; Natural England, 2020). Once designated, rules must be followed to manage the land to maintain or achieve "favourable" condition.

There are 6705 SSSIs in Britain. The sites are managed by a wide range of individuals and organisations both in the public and private sector. As the designation intends to protect habitats and features that are seen as the most valuable, they do not form well connected and coherent ecological corridors and as a result are rarely situated next to one another (Rayment, 2011), but it is acknowledged that this is not the aim of the designation (Lawton *et al.*, 2010).

1.8.1 Designated features

SSSI status is designated in recognition of unique taxa or geomorphological features, protecting them from damage, development, and neglect. Tailored assessments are carried out regularly to ensure the quality of designated biological or geological features is upheld. The condition of SSSIs is traditionally determined through quantitative and qualitative vegetation assessments.

Calcareous grassland and limestone pavement habitats are uncommon but are widely distributed. With an area covering 49000 ha and just 2000 ha of each respectively in England, these quantities are significant in a global context and make them of high conservation value (Lake *et al*., 2020; JNCC, 2021). They are also some of the most-threatened. Agricultural intensification through the addition of fertilisers and increased ploughing of calcareous grasslands, has resulted in some of the most-rapid destruction and degradation of any habitat in Europe (Poschlod & WallisDeVries, 2002). What remains is a highly fragmented network left vulnerable to undermanagement and succession (Poschlod & WallisDeVries, 2002). Limestone pavements have not been free from exploitation and have been marred by quarrying and extraction for the horticultural trade (Ward & Evans, 1976; Natural England, 1988).

1.8.2 SSSI condition

SSSIs are categorised by their condition:

- **Favourable –** habitats are in a healthy state and are appropriately managed.
- **Unfavourable (recovering) –** recovery will occur over time if management is sustained.
- **Unfavourable (no change) –** not being conserved and will not reach favourable condition without changes to management and external pressure.
- **Unfavourable (declining)** - not being conserved and will not reach favourable condition without changes to management and external pressure, with condition becoming considerably worse.
- **Part destroyed or destroyed –** fundamental damage with permanent loss of special features and favourable condition cannot be achieved.

Favourable condition in many non-climax habitats is maintained predominantly through livestock grazing, with some clear-felling and scrub management to slow successional processes. As with much of the countryside, habitats are changing. A shift away from traditional land use has resulted in the increased need for practical management to conserve and maintain important habitats. Habitat loss through lack of management threatens to reduce biodiversity (Fahrig, 2001), but the remote nature of some sites presents challenges for effective management.

Habitat quality can be difficult to quantify in the field, however, quality may be estimated by the diversity and abundance of plant species, vegetation structure and potential nectar source availability for invertebrates (Summerville & Crist, 2004; Mortelliti *et al.*, 2010; Soga & Koike, 2012). Here, habitat quality has been determined using condition assessments of the SSSI units, being checked at least every six years on average. If the assessment finds that a site has declined in condition, then a Condition Improvement Process is started. This involves advice from Natural England on the work required to improve site condition (Natural England, 2020).

Reasons for not attaining favourable condition varies, with the outcome being influenced by the type and intensity of management implemented. For the grassland habitat, grazing intensity is noted as a strong determinant for not attaining favourable condition. Some SSSI units are over grazed by sheep, whilst others have not been grazed for some time, allowing successional processes to take hold. One of the key features of limestone habitats is their sparsely vegetated and open nature. Similarly for the limestone pavement where the feature is not as dominant, the scrubbing-over of the pavement is of real concern. At sites where pavement is extensive, some scrubbing over and succession to woodland is beneficial and adds to the heterogeneity of the habitat matrices and provides shelter for many species in a landscape that is extremely exposed.

SSSIs do protect most of the rare species in England and Wales, the majority of which occur in semi-natural habitats (Rayment, 2011). The main focus in achieving the protection of species is to obtain and maintain favourable condition. Without protection, many of these sites would have been subject to the effects of development, fragmentation, and other detrimental changes in land use.

The targets set out in DEFRA's (2019) 25-year environment plan should see over 75% of protected sites brought into favourable condition. Currently, less than 40% of the land area designated as SSSIs across England meet the desired favourable condition (Fig. 1.1). Farleton Knott and Hutton Roof currently have just over 40% of their SSSI units in favourable condition, which is marginally above the national average, but this is still strides away from the desired state. SSSI units are a division of land of varying size determined by habitat and/or management type, or tenure (Natural England, 2022).

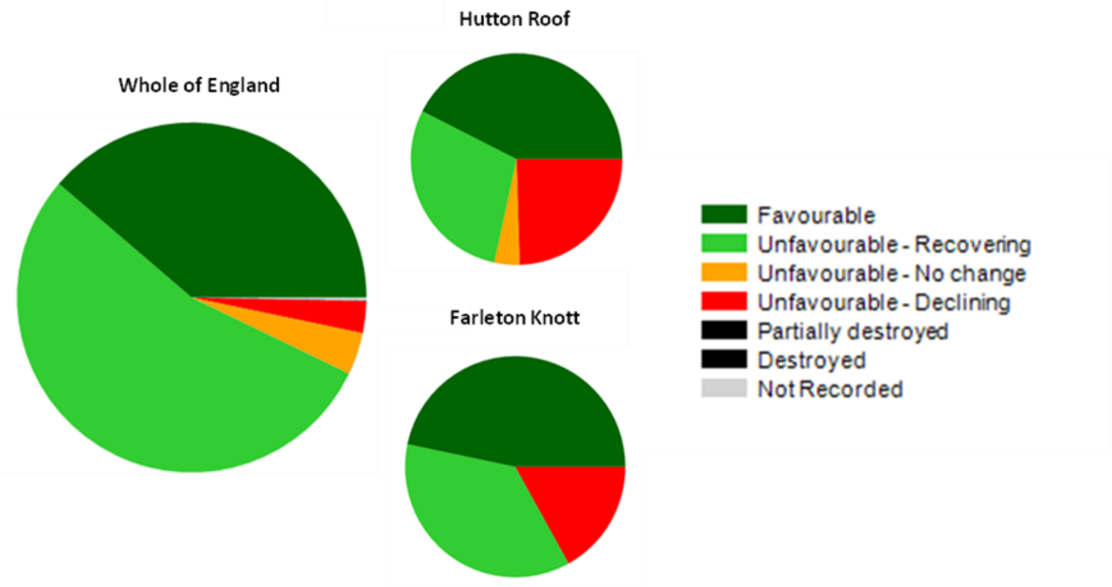


Figure 1.1 SSSI condition summary for the whole of England and the study sites, Hutton Roof SSSI and Farleton Knott SSSI showing the percentage area in hectares that falls into each category (Natural England, 2020).

1.9 Thesis aims

This study aims to assess the moth communities through the sampling of nocturnal Lepidoptera and vegetation of the limestone pavement and calcareous grassland habitats of Hutton Roof and Farleton Knott SSSIs in relation to the condition of the habitats as outlined by Natural England. Through the implementation of a sampling strategy across a range of conditions, the study will increase our understanding of how habitat condition and the vegetation composition of the pavement and grassland habitats within SSSIs influences moth community assemblages at the two reserves. The suitability of condition assessments that are currently in place will be considered and a more complete and up to date understanding of the moth community will be gained, which will ultimately be used to inform future management strategies. This will be explored over three chapters.

Chapter two details the sampling methods employed to collect the moth and vegetation data used in this study. Chapter three investigates if measures of observed and estimated moth diversity (based on taxonomic diversity) differ between habitat type and whether this is influenced by the condition of the habitat within the SSSI unit. Differences in vegetation composition are then assessed between habitat type and habitat condition and how moth diversity responds to each component of the vegetation. Ordination methods are then used to assess how the plant community affects the moth communities depending on habitat type and condition, but also if they differ between SSSI units and the reserves. Lastly, indicator species are identified for the habitat type and condition categories.

The fourth chapter then focuses on the functional traits and functional diversity of the macro-moth community, again, assessing differences between habitat type, habitat condition, and vegetation variables. Ordination methods are used to explore how the different plant community attributes contribute to the composition of the macro-moth community traits between habitat and condition categories, but also between the units and reserves.

In the final chapter, the key findings are brought together and used to determine if the condition assessments adequately reflect the moth community composition, providing recommendations for future research, management, and conservation.

Chapter 2

Methods

2.1 Overview

Sampling of vegetation and moth communities in limestone pavement and calcareous grassland habitats at Hutton Roof (SD553775) and Farleton Knott (SD543798) Sites of Special Scientific Interest (SSSI) took place between June 1st and August 31st, 2021. Ten SSSI units were selected for sampling out of fourteen in total across the two habitats (Fig. 2.1). Four SSSI units were not selected for sampling due to inaccessibility at two private sites (Clawthorpe Fell and Holme Park Quarry), a lack of key features in one (Park Wood) and an extreme inclined limestone pavement at another (The Rakes). The SSSI units were categorised as being in declining (three units), unfavourable (three units), or favourable condition (four units). Permission from all landowners was obtained prior to sampling and overall permission was provided by Natural England. Landowners further notified graziers of the planned operations in advance.

2.2 Study sites

The Carboniferous limestone hills of Hutton Roof and Farleton Knott are situated to the east of the Arnside and Silverdale Area of Outstanding Natural Beauty near Burton in Kendal, Cumbria (Fig. 2.1) and form part of the Morecambe Bay limestone series. Some of the best examples of limestone pavement in the UK can be found here. They are of an intermediate altitudinal position (140 – 270 m ASL) compared to those of nearby Gait Barrows National Nature Reserve in Lancashire (sea-level) and Ingleborough in Yorkshire (sub-alpine) (Natural England, 1988; Cumbria Wildlife Trust, 2019).

The reserves are protected by multiple statutory designations. Hutton Roof National Nature Reserve (NNR) is a site of Special Scientific Interest (SSSI), the pavements are Special Areas of Conservation (SAC) and many Local Nature Reserves (LNRs) surround these reserves. Farleton Knott SSSI also has NNR and SAC status and both Farleton Knott and Hutton Roof are included in the wider Morecambe Bay Pavements SAC (Natural England, 1988). The designations appropriated are in recognition of the unique geological and biological assemblages. Many SSSIs featured throughout the Morecambe Bay limestone series are relatively well connected. However, land that directly surrounds SSSIs is often degraded, which can have an indirect negative impact on them (DEFRA, 2019).

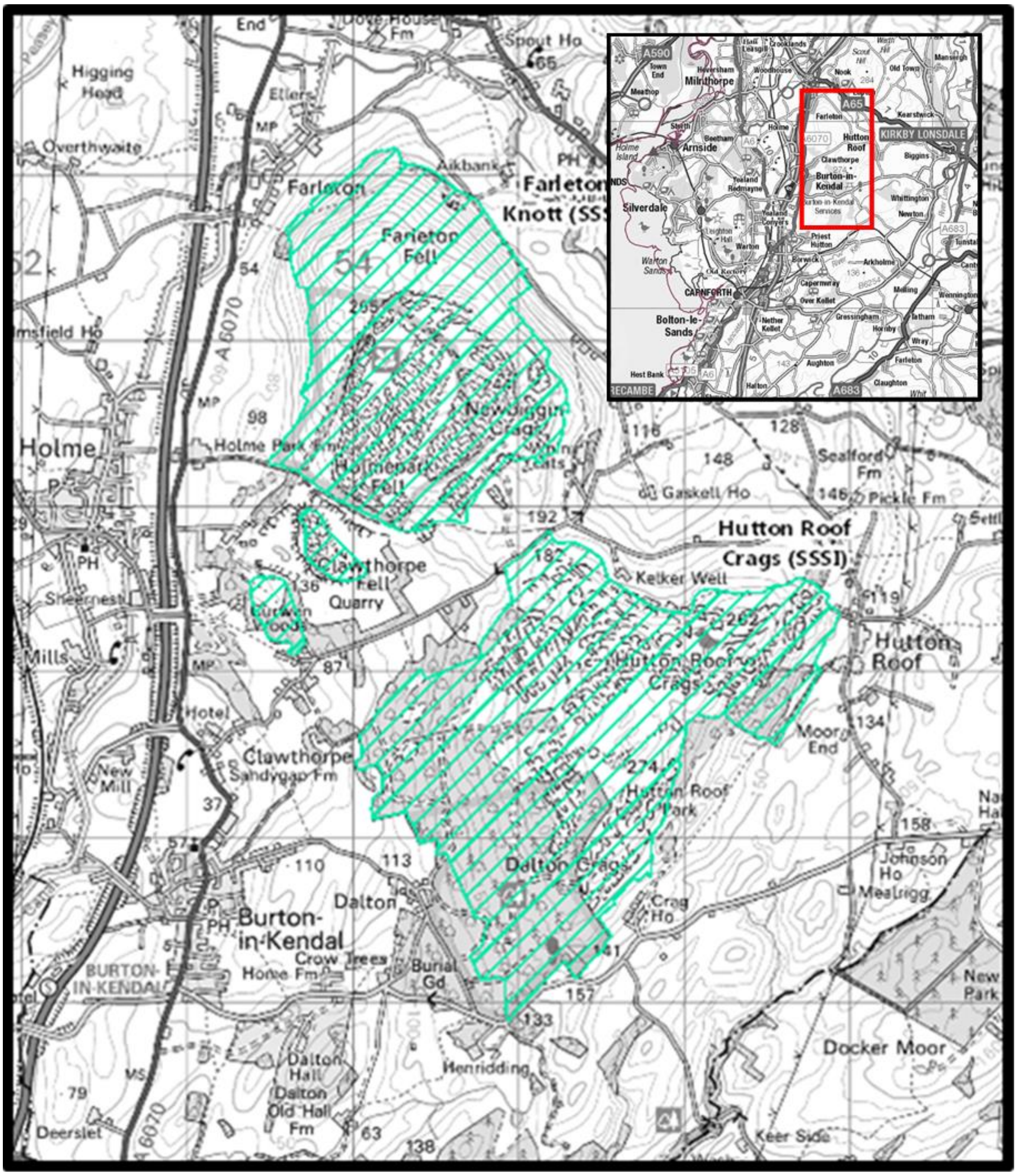


Figure 2.1 Highlighted in green, are the locations of the Hutton Roof and Farleton Knott Sites of Special Scientific Interest (Magic, 2021).

Hutton Roof and Farleton Knott are designated SSSIs principally for their limestone pavement and calcareous grassland habitats. The open limestone pavement with a mosaic of woodland, scrub and calcareous grassland characterises these sites (Natural

England, 1988). Despite separate designations, they do form a single ecological unit. Limestone pavement occurs extensively across both sites, comprising 103.8 ha of a total 391.7 ha land area at Hutton Roof and 103.2 ha of a total 290.7 ha at Farleton Knott, making it the dominant feature (Craven, 2012; Craven, 2013). The pavement ranges in inclination, structure, and vegetation cover, supporting unique plant communities within and around the clints, grikes, runnels and kamenitzas. Broken stone and rubble is frequent and indicates an industrial past until cessation in the 1960s of removal of pavement as rockery stone. Calcareous grassland is the second most extensive feature at 53.6 ha and 110.6 ha respectively and is generally dominated by *Sesleria caerulea* Blue Moor-grass. The precise extent of this feature is yet to be mapped due to the acknowledged complexities in separating pure stands of calcareous grassland from the pockets of heath and acid grassland (Craven, 2012; Craven, 2013). Other designations exist within other units in recognition of habitats such as Maple-Ash woodland and Juniper scrub, but these are limited in their extent and therefore not included in the study.

Hutton Roof and Farleton Knott are of high botanical interest, with the floral assemblages having been extensively and thoroughly documented (Ward & Evans, 1976). A national survey of limestone pavements ranked Hutton Roof second on the floristic index (Natural England, 1988). The mosaic of woodland, pavement, and grassland support rare and endemic species of fern, orchid, and tree. It is stated that the association the underlying geology has with the floral diversity is a key contributor to the invertebrate richness found at such sites (Natural England, 1988). However, the JNCC guidelines for the selection of non-montane rock habitats state that "*the invertebrate interest of limestone pavements is incompletely known*" (JNCC, 1989). Alongside being a stronghold for High Brown Fritillary, strong populations of Chestnut-coloured Carpet, Least Minor and Barred Tooth-striped can be found here.

Cumbria Wildlife Trust commissioned Liverpool Museum to survey the invertebrate biodiversity and assess the conservation value of Hutton Roof Crags in 2002, with a view to informing future site management (Knight, 2003). However, Lepidoptera were not targeted and instead the records amassed by Rev. J. Vine Hall, Neville Birkett and Jerry Briggs were referred to. Unfortunately, the majority come from outside the boundaries of the SSSIs and so it is difficult to say if certain species would also occur at the two reserves. Sampling the moth communities here will be invaluable in filling such a knowledge gap.

2.3 Sampling design

Within each of the ten selected SSSI units, four sites were sampled, two at limestone pavement habitat and two at calcareous grassland habitat (Fig. 2.2), with a minimum of 50 m between traps to minimise light interference. These two habitat types are the notified features of the SSSIs and also dominant features at both Hutton Roof and Farleton Knott. The total land area covered by the two reserves is 687 ha (Hutton: 396 ha, Farleton: 291 ha) so a pragmatic approach to sample site selection was taken. Areas of limestone pavement and calcareous grassland were initially identified using Natural England's Priority Habitat Inventory for England (Natural England, 2020). Once areas were identified, multiple visits to the reserves were required to confirm the suitability of each site. Walking through each unit, habitat patches were identified and grid references were obtained and mapped to ensure each site fell within the boundaries of the unit as there were oftentimes no visible boundaries on the ground. The units are occupied and managed by multiple landowners and organisations and range from being in favourable condition to un-favourable declining (Table 2.1).

Table 2.1 Details of the different sampling plots, including site and SSSI unit they belong to, habitat type and habitat condition, British OS grid coordinate, land owner and the order in which they were sampled.

Reserve	Unit number	Unit name	Unit area (ha)	Habitat type	Habitat condition	Site coordinate	Land owner
Farleton Knott	1	Holme Park Fell	116.6	Grassland	Favourable	SD54347940	National Trust
				Grassland		SD54167976	
				Pavement		SD54057976	
				Pavement		SD54557946	
Farleton Knott	2	Holme Stinted Pasture	10.9	Grassland	Favourable	SD54737921	Jane Hopwood
				Grassland		SD54597903	
				Pavement		SD54687908	
				Pavement		SD54667901	
Hutton Roof	3	Lancelot Clark Storth & Burton Fell	98.8	Grassland	Favourable	SD55257756	Cumbria Wildlife Trust
				Grassland		SD55017757	
				Pavement		SD55197790	
				Pavement		SD55127801	
Hutton Roof	4	Hutton Roof Commons	69.4	Grassland	Favourable	SD55537772	Common land
				Grassland		SD55627788	
				Pavement		SD56127797	

				Pavement		SD55887791	
Farleton Knott	5	Farleton Fell	96.3	Grassland	Recovering	SD54598005	Dallam Tower Estate
				Grassland		SD54038036	
				Pavement		SD54438013	
				Pavement		SD54368024	
Hutton Roof	6	Dalton Crags	100.3	Grassland	Recovering	SD55227655	Forestry England
				Grassland		SD55347704	
				Pavement		SD55137669	
				Pavement		SD55097666	
Hutton Roof	7	Crag House Allotment	15.3	Grassland	Recovering	SD55627695	Forestry England
				Grassland		SD55437692	
				Pavement		SD55497691	
				Pavement		SD55557680	
Farleton Knott	8	Newbiggin	49.3	Grassland	Declining	SD54877985	Common land
				Grassland		SD54757971	
				Pavement		SD54807943	
				Pavement		SD54957953	
Hutton Roof	9	Uberash Plain	33.7	Grassland	Declining	SD55317822	Common land
				Grassland		SD55117822	
				Pavement		SD55207801	
				Pavement		SD55237812	
Hutton Roof	10	Ploverlands	26.2	Grassland	Declining	SD55717723	Cumbria Wildlife Trust
				Grassland		SD55807724	
				Pavement		SD55647728	
				Pavement		SD55617714	

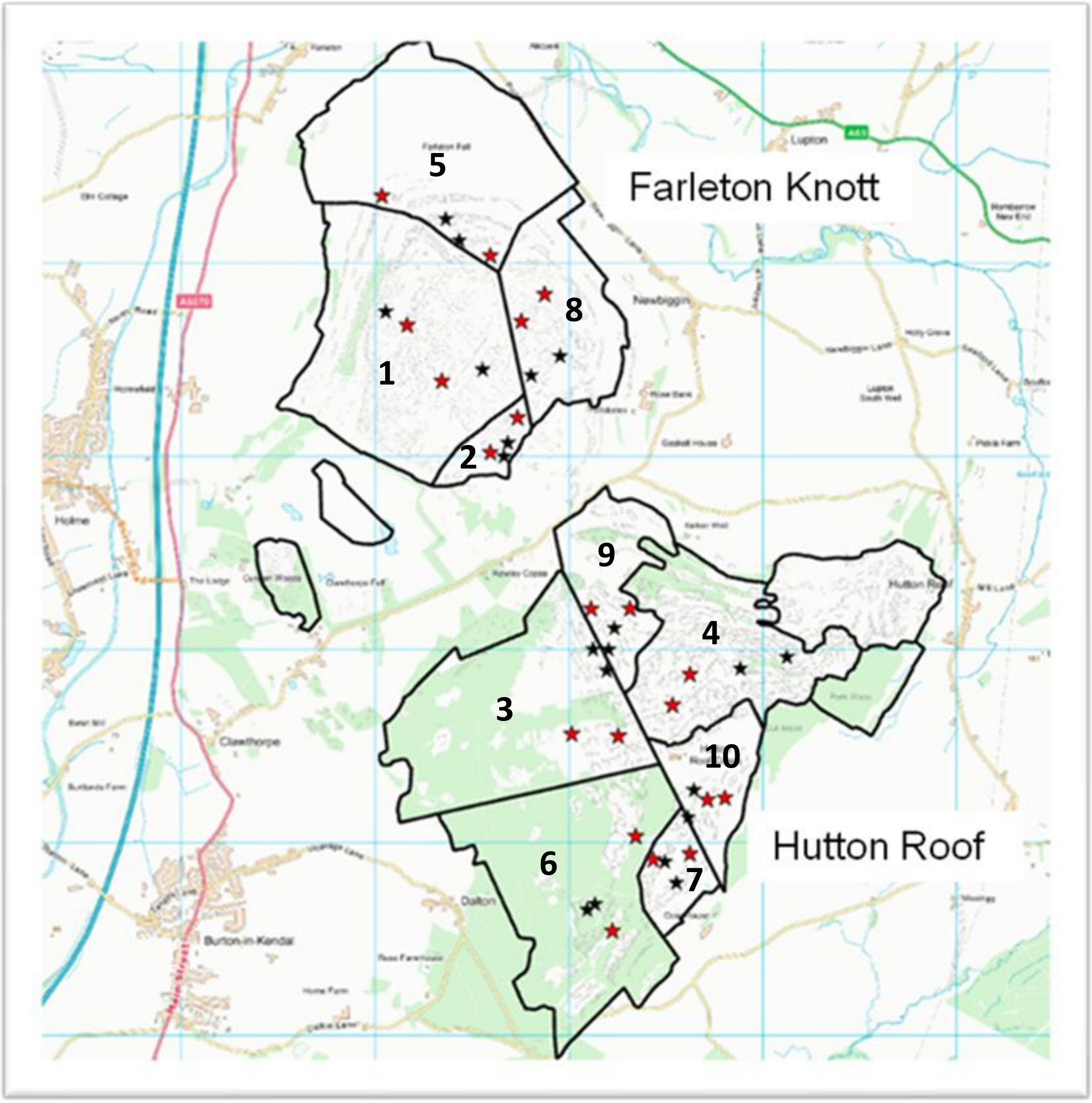


Figure 2.2 Map of the sampling sites within the SSSI units © ArcGIS Pro version 2.4.0 (Esri, 2020). Black lines delimit the boundaries of each unit, numbers are assigned to each unit (see Table 2.1), red stars represent calcareous grassland sites and black stars limestone pavement sites. SSSI units containing no numbers or stars within their boundaries were not sampled.

2.4 Moth sampling

Over 90% of moth species in the UK are nocturnal or crepuscular, therefore, moths were sampled using light traps, which are the most commonly used and effective method to survey nocturnal moths by exploiting their phototaxic behaviour. However, not all nocturnal moth species are equally attracted to light sources, with differences observed between species and families (Merckx & Slade, 2014). Four Heath traps with ultraviolet light emitting diode (UV LED) lights were used. The Heath trap (1965) is ideal for sampling remote habitats and so the trap bodies from Anglian Lepidopterist Supplies were used as they fold flat, improving portability (Fig. 2.3). Rain guards were cut from thin sheets of plastic and secured to the vane simply with an elastic band. The light source consisted of a strip of UV LEDs containing 30 LED units each within plastic casing (chip type 3528 SMD, 12 volts), with an output of less than 3W, each powered using 12V 12ah lead-acid batteries. The spectrum covered by the LEDs was in the range of 395 nm – 405 nm, peaking at 400 nm (Blumgart, 2020).

LEDs have been found to perform poorly when compared against more traditional light sources (van Grunsven *et al.,* 2014). However, it is suggested that if the spectrum is targeted correctly, as is the case here, then attractiveness can be improved (Gaston *et al.,* 2012). The focus on a specific spectrum emitted by the LED bulbs, shown to be particularly attractive to Lepidoptera, has provided results in species richness and abundance comparable to the high-powered mercury vapour bulbs (Infusino e*t al.,* 2017; Blumgart, 2020). On average, moths may be attracted from up to 30 metres away (Fry & Waring, 2001). The bulbs used in this study were found to have an average attractive radiance of 25 m in British woodland, with catch rates comparable to the 6W Heath traps (Blumgart, 2020). It has also been demonstrated that UV LEDs have a comparable catch rate to the 200W incandescent bulbs used in the Rothamsted Insect Survey moth traps (Infusino *et al*., 2017). Mercury Vapour bulbs (125 W) remain the most productive light sources for sampling nocturnal moths (Tikoca *et al*., 2016: Infusino *et al*., 2017), however, a mains power supply is required to run them and so are impractical for remote field work. As LED technologies improve, they are becoming more popular in the study of nocturnal invertebrates as they are cheap to make, compact and highly transportable given their limited power demands.

One SSSI unit, including all four sites within it, was sampled per visit due to the practicalities of vegetation sampling and setting and leaving moth traps over a large land area. Each unit was visited in a random order but alternating between condition (e.g., favourable, declining, then recovering) so two units of the same condition were not sampled consecutively. The majority of moth species in the UK are on the wing during the summer months (Jonason *et al*., 2014). Therefore, moths were recorded between June and August to capture as much community diversity as possible. Each SSSI unit was visited once per month, in June, July and August, totalling three visits to each unit over the sampling period. Visits were made when weather conditions permitted and not necessarily on consecutive nights, but each round was completed within the month timeframe. Two limestone pavement and two calcareous grassland sites were sampled within each of the 10 SSSI units, totalling 40 individual moth catches in each round of sampling (Table 2.1 & Fig. 2.2). Three visits to each of these sites within each SSSI unit were made over the recording period, equating to 120 individual moth trap catches.

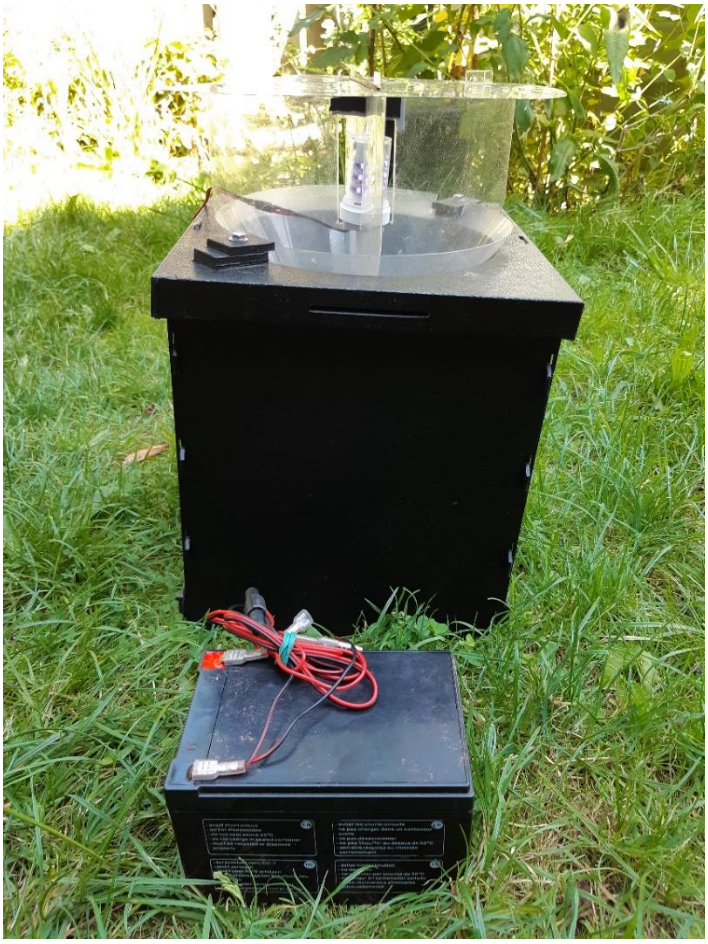


Figure 2.3 Light trap used to sample moths adapted from the original used by Blumgart (2020).

Moth activity is known to be affected by a number of variables. Nights that are warm and cloudy with light winds prove to be the most favourable for flight, whilst those that are cold and clear with a full moon are the least productive (Yela & Holyoak, 1997; Fry & Waring, 2001). In order to control these confounding variables, daily analysis of multiple local weather forecast sources (mainly BBC Weather, Met Office, and Accuweather) were used to set the required conditions for sampling: the risk of overnight rainfall was < 50%, minimum overnight temperature >10^{o}C and windspeeds of < 20 km/h (Merckx *et al*., 2009).

Moth traps were left out in suitable areas of habitat as close to dusk as possible as many species are crepuscular, returning at dawn to check them. Moths caught inside the trap as well as those found on the outside of the trap and immediate surroundings were all identified and counted, as some species rarely enter a trap (Fry & Waring, 2001). The majority of moths caught were identified to species level on site, though a small number of individuals were returned to the lab for identification (see section 2.3.1). Status was assigned to each species using “*A Review of the Status of Microlepidoptera in Britain*” by Davis (2012) for the micro-moths and a combination of “*A Field Guide to the Moths of Great Britain and Ireland,* Third edition*”* by Waring & Townsend (2017) and *“A Review of the Status of Macro-moth of Great Britain’* compiled by Fox *et al.* (2019) for the macros (Table 2.2).

Table 2.2 The national status criteria applied to the moth species (Davis, 2012; Fox *et al*., 2019).

Status	**Criteria**
RDB1	Occurs in 11 – 15 10 km squares - endangered
RDB2	Occurs in 11 – 15 10 km squares - vulnerable
RDB3	Occurs in 11 – 15 10 km squares - rare
Nationally Scarce A	Occurs in 16 – 30 10 km squares
Nationally Scarce B	Occurs in 31 to 100 10 km squares
Local	Occurs in 101 – 300 10 km squares
Common	Occurs in more than 300 10 km squares
Migrant	Occurs naturally in Britain but as a result of immigration only

All species records obtained during the sampling were incorporated to the national database, using the biological recording software, MapMate© version 2.4.0 (MapMate LTD, 2021), and shared with the Lancashire and Cumbrian County Moth Recorders and record collators. To ensure records were appropriately authenticated, local experts were consulted. This is an important process that ensures the quality and integrity of the national database is maintained (Randle, 2013). A local grading system for moths was used as a guide to identify the level of verification required for each species (Table 2.3).

Table 2.3 Moth grading system used for verification purposes and the criteria of each action (Randal, 2013; Langmaid *et al.,* 2016)

Grading Code	Description
A	Accepted without supported evidence, easily identified, common and already on the county list
P	Photo, easily confused species photo required
S	Specimen, specimen required for species not already on existing county lists
D	Dissection required as cannot be separated from similar species on morphology

2.4.1 Genitalia examination

Confirmation of a small number of species was required due to wear or difficulty differentiating from other species from external morphological features alone. The reproductive organs of moths are, as a general rule, unique to each species, the structures of which being analogous to a lock and key. This level of specificity is driven by sexual selection, avoiding any potential interspecific matings that would result in lost reproductive opportunity (Hosken & Stockley, 2004; Xu & Wang, 2010). Examination of genitalia characteristics through dissection is a vital process in the study of moths, with the provision of a voucher specimen being crucial for substantiating a record in many cases. For every ten individuals of a confusion species caught in a given trap, one was taken to be checked. The exception was with the Ear moth quadruplet as two species are smaller and the other two are larger, necessitating further investigation. All individuals of this group were therefore identified in the lab. A number of micro-moth species cannot be confidently identified without examination of the genitalia, and this requires greater experience to identify those which fall into the difficult to identify/confusion species category than for macro-moths. Any micro-moths retained were therefore dissected and identified by the local micro-moth expert, Stephen Palmer.

A standard procedure for dissection was followed by first freezing the specimen for a minimum of one hour prior to examination (mothdissection.uk). The abdomen was then removed and placed in a 10% potassium hydroxide (KOH) solution and heated for approximately 20 minutes, depending on the size of the specimen. The application of heat quickens the process of soft tissue removal from the hard structure of the genitalia. The remaining hard structure was cleaned using water and a small brush before positioning under the microscope, adjusting as necessary to reveal the identifying features.

2.5 Vegetation sampling

All vegetation sampling was carried out in each plot on the same day as the moth trap was set up in the first (June) and last trapping session (August). The vegetation at each site was sampled along two 30 m linear transects that intersected the site of the light trap. The length of the transect was determined by the attractive radius of the LED bulb. The protocol for recording the vegetation variables was based on methods used in the *Limestone Pavement Survey of Ireland* (Wilson & Fernández, 2013) and the priority habitat assessment guidelines followed by Natural England (JNCC, 2009). Eight vegetation variables (Table 2.4) were measured within nine 1 m x 1 m quadrats that straddled the transect line at 5 m intervals (Fig. 2.4).

Table 2.4 Details of vegetation variables recorded at each sampling site.

Variable	**Description**	**Measurement**	**Equipment**
Vegetation height	Any herbs, grasses, or woody species	Height in centimetres (cm)	Tape measure
Species of forb in flower	Herbaceous or woody species	Number of species	Tally from observations across quadrats
Cover of ferns	Pteridophytes excluding bracken, horsetail, and clubmosses	Percentage (%)	Visual estimation within quadrat
Cover of bare ground	Exposed surface geology/soil	Percentage (%)	Visual estimation within quadrat
Cover of forbs	No woody stems	Percentage (%)	Visual estimation within quadrat
Cover of woody plants	Woody stems	Percentage (%)	Visual estimation within quadrat
Cover of bryophytes	Mosses, lichens, and liverworts	Percentage (%)	Visual estimation within quadrat
Cover of grasses	Any Gramineous species	Percentage (%)	Visual estimation within quadrat
Negative indicator plant species	Plant species associated with poor habitat quality	Number of species	Tally from transect walk
Positive indicator plant species	Plant species associated with good habitat quality	Number of species	Tally from transect walk
Non-indicator plant species	Any other plant species observed during the transect	Number of species	Tally from transect walk

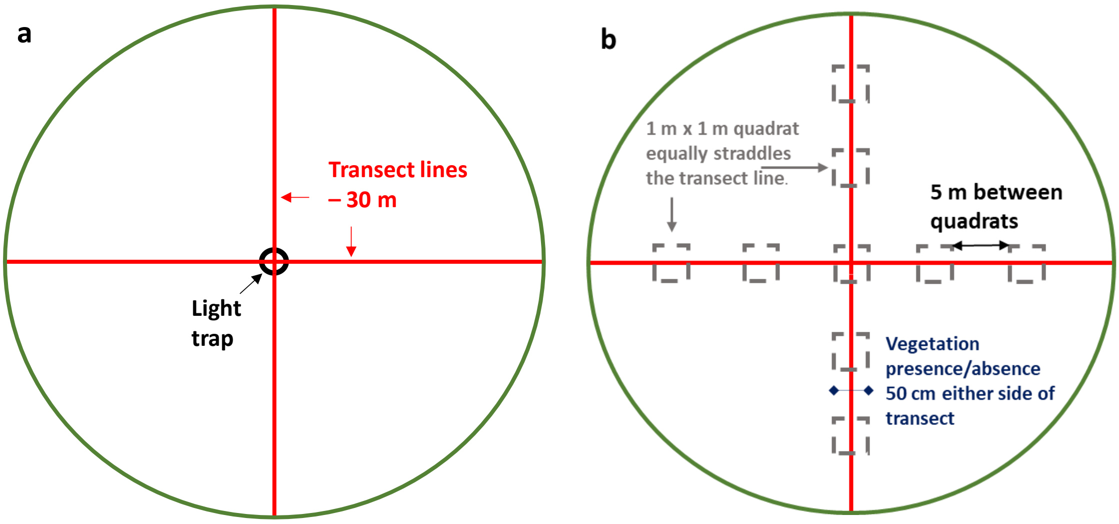


Figure 2.4 Transect protocol whereby a) two 30 m transects intersect the site of the light trap. Habitat assessments were made from north to south and east to west using presence/absence checklist approach for positive, negative, and non-indicator plant species 50 cm either side of the transect line with b) vegetation variables were measured at 5 m intervals along each transect line.

At designated sites, such as SSSIs, the habitat quality is assessed at regular intervals by Natural England. Reviews were last carried out at Hutton Roof and Farleton Knott in 2020 and 2014 prior to that and so are up to date and conditions range from being favourable to unfavourable-declining across the two reserves (Table 2.1). As part of this assessment, the presence/absence of site specific positive and negative indicator plant species is recorded. Therefore, similar data were collected at each sampling site in this study (Table 2.5). Natural England carry out SSSI assessments of the indicator species once in either June or July, so indicator species sampling was done on the second visit (July) to correspond with standard methods used in habitat condition assessment. Two checklists were compiled to reflect variations in plant community assemblages at Hutton Roof and Farleton Knott. Positive and negative indicator plant species are taken from the Common Standards Monitoring guidance for SSSIs and are characteristic of a habitat type, with positive indicators being typical of those in good condition, whilst negative indicator plant species are often indicative of habitats in poor condition (Smart *et al.*, 2010). This approach was designed to make a rapid assessment of the vegetation in the vicinity of each moth trap. Both transect lines at each sampling site were walked at a steady pace with a metre-long cane that straddled the transect line to provide an even recording boundary along each 30 m transect. The number of positive and negative indicator plant species were tallied, and any other plant or grass species (non-indicator plant species) observed on the transect were also noted.

Table 2.5 Positive and negative indicator plant species. Negative indicators were the same at both habitats and reserves. The positive indicators plant species differed by habitat type and reserve.

Negative indicator plant species
Arrhentherum elatius, Cirsium arvense, Cirsium vulgare, Cynosurus cristatus, Lolium perenne, Jacobaea vulgaris, Rubus spp., *Rumex* spp., *Urtica dioica*
Farleton Knott positive indicator plant species
Grassland
Asperula cynanchica, Campanula rotundifolia, Carlina vulgaris, Euphrasia spp., *Filipendula vulgaris, Galium sterneri, Gentianella spp., Helianthemum canum, Helianthemum nummularium, Hippocrepis comosa, Leontodon hispidus, Lotus corniculatus, Pilosella officinarum, Poterium sanguisorba, Scabiosa columbaria, Sesleria caerulea, Succisa pratensis, Thymus drucei*
Pavement
Carex digitata, C. ornithopoda, Convallaria majalis, Dryopteris submontana, Epipactis atrorubens, Geranium sanguineum, Gymnocarpium robertianum, Hypericum montanum, Juniperus communis, Melica nutans, Polygonatum odoratum, Taxus baccata, Thalictrum minus
Hutton Roof positive indicator plant species
Grassland
Asperula cynanchica, Carlina vulgaris, Campanula rotundifolia, Euphrasia spp., *Filipendula vulgaris, Galium sterneri, Gentianella* spp., *Helianthemum canum, Helianthemum nummularium, Hippocrepis comosa, Leontodon hispidus, Lotus corniculatus, Pilosella officinarum, Poterium sanguisorba, Scabiosa columbaria, Succisa pratensis, Thymus drucei*
Pavement
Arabis hirsuta, Asplenium viride, Convallaria majalis, Cystopteris fragilis, Dryopteris submontana, Epipactis atrorubens, Gymnocarpium robertianum, Hypericum montanum, Juniperus communis, Melica nutans, Melica uniflora, Polygonatum odoratum, Polystichum aculeatum, Taxus baccata, Thalictrum minus

Chapter 3

The Effect of Habitat Condition and Vegetation on Moth Diversity and Community Composition of Limestone Habitats

3.1 Abstract

In the UK, SSSIs provide protection to some of the best examples of floral and faunal assemblages, and periodic habitat assessment of these sites is key to judging the favourability of their condition. However, it is not clear that the condition assessments carried out by Natural England (NE), which are largely based on vegetation, reflect the health of the insect assemblages. Here, the effects of habitat type (grassland vs pavement) and condition (declining, recovering, favourable) on the species richness and community composition of moth assemblages at Hutton Roof and Farleton Knott SSSIs in NW England were assessed by collecting moth samples, alongside data on the vegetation. Levels of observed and estimated moth diversity were found to be similar between habitat types and condition categories. The cover of grass was found to have a significant negative effect on observed moth species richness, which may be linked to the reduced diversity of forbs that are potential larval hostplants for moths. Bryophyte cover had a positive effect on rarefied moth species richness and Simpson diversity of moths, which may be through its provision of water, which is a limiting resource in this extreme environment. The cover of forbs was significantly higher in grassland habitats compared with limestone habitats, as was the number of forb species in flower, particularly at sites in recovering and favourable condition. Additionally, ordination methods identified the cover of forbs as the primary driver of the moth community composition. Whilst little difference was observed in relation to the habitat type and condition categories, community composition varied significantly among SSSI units, with those at Farleton Knott SSSI hosting the most unique assemblages, which is likely due to the differences in scrub and woodland cover between the two reserves. Management will be key to improving the condition of those areas in decline and maintaining and enhancing those currently in favourable condition.

3.2 Introduction

Startling insect declines are becoming an ever more frequent headline in the media with suggestions of ecological collapse in the wake of dramatic reductions in abundances and biomass being reported (Hallman *et al.,* 2017; Sánchez-Bayo & Wyckhuys, 2019). Habitat destruction and deterioration, and atmospheric changes including pollution and climate change, are said to be the main drivers of insect decline (Butchart *et al.,* 2010; Potts *et al.,* 2010; Owens *et al.,* 2020; Boyes *et al.,* 2021; Fox *et.,* 2021). Due to their sensitivity and vulnerability to change, this hyperdiverse taxon are increasingly being used as indicators of change. The traits possessed by rarer species increase their sensitivity to the drivers of decline (Öckinger *et al.,* 2010; Kamp *et al.,* 2020), but we are now also noting declines in common species (Conrad *et al*., 2006). For example, the abundance of V-moth and Garden Dart, two once common species in the UK, declined by 54% in the last 10-years (Fox *et al*., 2021). In the UK, analysis of long-term moth data collected through the Rothamsted Insect Survey (RIS) found that the abundance of larger moths caught had declined by 33% over a 50-year period and that this trend was markedly stronger in the south (39%) than in the north (22%) (Fox *et al.,* 2021). The previous report in 2013 showed that 28% of moth species had experienced significant decreases in abundance but declines in the north were offset by gains elsewhere so net abundances had not changed over the 40-year recording period (Fox et al., 2013). Comparison between these reports suggests something has changed significantly in the last decade. Not only are species' abundances changing, but their distributions are also shifting. Analysis of the long-term distribution trends of >500 larger moth species using National Moth Recording Scheme (NMRS) data found that 44% of those species had decreased, with 32% showing significant long-term declines (Fox *et al*., 2021). It is likely that the breakdown of complex species networks will lead to wider ecological impacts such as trophic cascades, thus, further eroding biodiversity (Kehoe *et al.,* 2021). For example, insect declines have been found to mirror those observed in insectivorous birds in Denmark (Møller, 2019). Furthermore, Lepidopteran declines have also been linked to an increase in abundance of non-native, invasive plant species through a reduction in native plant species availability (Burghardt *et al*., 2010).

While general trends show declines across many species, there is evidence to suggest that some species have benefitted. Analysis of the national database of Odonata by Bowler *et al.* (2021) identified that more species of dragonfly and damselfly had significantly increased in range compared to those that had decreased. An assessment of the larger moths in the UK by Fox *et al.* (2021) noted that since the start of the twentieth century, 53 species of moth have experienced significant changes in their geographic range and have since become established in the UK. In the same assessment, slightly more species had significantly increased in distribution (37%) than decreased (Fox *et al*., 2021). The observed increases are suggested to be in response to a changing climate change, whilst habitat destruction and deterioration through land-use change are the principal driver of declines (Fox *et al*., 2021).

Moths are a diverse taxon with over 2500 known species in the UK (Agassiz *et al*., 2013). Not all habitats support equal levels of diversity, and our understanding of their biodiversity also varies. Limestone pavements are of high geological interest and the flora had been extensively documented in the past (Ward & Evans, 1976), but unlike calcareous grasslands, much less is known about other taxonomic groups, let alone the invertebrate communities found in this habitat, with the moth community being left largely unexplored. The literature is limited to a small number of studies on terrestrial gastropods (e.g., Baur & Baur, 1995; Fröberg, *et al*., 2011; Willis, 2011), with no record of systematic moth sampling, although opportunistic sampling does take place on an ad hoc basis (see Whittaker, 2020). This knowledge gap is recognised and yet it is still to be filled (JNCC, 2009). In the absence of high-quality data, it is often assumed that high levels of floral diversity equate to high levels of invertebrate diversity, which in some cases may be true (Jonas *et al*., 2002), but we are yet to understand to what extent the diversity of different taxonomic groups correlate (Brunbjerg *et al.,* 2018).

In the UK, a number of rare Lepidoptera are used as indicator species to guide conservation efforts and as biological markers reflecting the biotic state or condition of habitats (Levin, 2001). Indicators are often limited to butterfly species (e.g., the rare species of fritillary) despite butterflies accounting for less than 3% of the Order Lepidoptera. As moths have relatively high diversity with representatives in almost every habitat, they can be expected to better represent species diversity at a site or reserve, making them excellent indicators of environmental change (Thomas, 2005). However, there are a number of barriers to using moths as indicator species. The majority of species are either crepuscular or nocturnal in nature, introducing the need to use alternative methods for monitoring, which oftentimes requires working unsociable hours. The observer must also be able to identify the species and differentiate from any that may be similar, which means the experience necessary is much greater than with butterflies.

Calcareous grasslands are a semi-natural habitat that have developed over millennia at sites that were formally wooded limestone pavement but cleared for livestock grazing (Poschlod & WallisDeVries, 2002; Lake *et al.,* 2020). These thin, well drained soils are nutrient poor but support a diverse mosaic of grasses and forbs, with invertebrate diversity oftentimes mirroring that of the flora (van Swaay, 2002; Woodcock *et al*., 2005), however they are becoming increasingly threatened by agricultural intensification on one hand and abandonment on the other. Land that was once traditionally maintained through low-intensity grazing and hay making has either been replaced by high densities of stock or converted and so conservation management is geared towards the avoidance of either extreme (Poschlod & WallisDeVries, 2002; Valkó *et al*., 2016). The changing climate is also playing a role in altering calcareous grasslands. Warmer, wetter, winters are favouring plant species with longer growing seasons such as grasses, which are out-competing those plant species more adapted to the short, dry sward (Stevens *et al.,* 2006). The mean nitrogen level of calcareous grasslands in Germany has increased due to deposition from the atmosphere, resulting in a decrease in plant species richness (Diekmann *et al*., 2014), however, this negative relationship is not as yet observed in the UK (Maskell *et al*., 2010). In the short-term, abandonment can increase species richness through reduced grazing pressure and an increase in vegetation structure, but with time, successional processes reduce habitat quality resulting in a community shift, thus reducing habitat specialists (Kormann *et al.,* 2015; Ernst *et al.,* 2017; Mora *et al.,* 2021). Alongside shifts in plant community composition, Lepidoptera of calcareous grasslands are in decline in the UK and across Europe (Wenzel *et al*., 2006; Fox *et al.,* 2021). Moreover, some of the UK's most threatened species of Lepidoptera are reliant upon continued management if populations are to persist (Ellis *et al.,* 2019) and so a balance must be struck when managing reserves in order to support the requirements of as many species as possible.

Limestone pavements experience a similar suite of threats to calcareous grassland along the theme of exploitation and abandonment, but also destruction through both anthropogenic (rock extraction) and natural processes such as weathering and glaciation (Vincent, 1995). An industrial past is still evident in the UK, from Roman iron mines to the many lime kilns still preserved across the landscape. The impressive decorative clints found in the north west of the UK were favoured by the horticultural trade and numerous quarries, both abandoned and active, scar the landscape (Ward & Evans, 1976). Due to these threats and the rarity of the habitat, they are protected by Limestone Pavement Orders (LPOs) (Section 34, Wildlife and Countryside Act, 1981). Despite the preponderance of exposed rock, natural weathering processes allow vegetation to establish in deep grikes, supporting a shade-loving community of bryophytes, ferns and a suite of plant species typically associated with woodland floor, without which trees and shrubs would not be able to develop. Mosses have been found to play an important role in the facilitation of establishing other vegetation by providing a medium for water and nutrients to become available in a resource-limited environment (Sand-Jensen & Hammer, 2012). High grazing pressure has stripped many pavements of their bonsaistyle trees and shrubs, but at the other extreme, abandonment allows woodland to develop. Whilst some of the woodlands that develop on pavement are rare habitats in their own rights (e.g., ancient Maple-Ash woodland at Hutton Roof), allowing succession to play out across them all would result in the loss of unique species assemblages.

The conservation management of calcareous grassland and limestone pavement is heavily focussed on flora despite the recognition that this may not be beneficial for the effective conservation of other taxa (WallisDeVries, Poschlod, & Willems, 2002 and references within). However, vegetation still forms the cornerstone of assessing the condition of SSSIs despite a clear need for the integration of a wider range of taxonomic groups given that the response to management efforts can differ between taxa (Van Noordwijk *et al*., 2017). This highlights the possibility that SSSI condition assessments that focus almost entirely on the presence of particular plant species and aspects of vegetation structure, may be insufficient to preserve the high levels of biodiversity desired at protected sites, with species declines potentially going undetected by rigidly following this format. When we consider the lack of information available for limestone pavements, coupled with their rarity, a concerted effort is required to rectify this.

In this chapter the effects of habitat type (limestone pavement vs calcareous grassland) and habitat condition (declining, recovering, favourable) on the moth and vegetation communities are explored. Habitat in favourable condition is expected to support a more diverse moth community as the habitat quality has been assessed to be optimal. To elucidate the mechanisms behind the influence of habitat and condition on the moth community, a number of components that make up the vegetation structure were assessed to determine how it differs between the habitats and conditions, and how this affects moth diversity. Moth species indicators of habitat type and condition were identified and their potential to supplement SSSI condition assessments explored. This study will hopefully form the foundation for future research on the moth communities of limestone pavements. The following research questions are addressed:

1. Does habitat type and/or the condition affect vegetation structure?
2. Does vegetation structure affect moth diversity and composition?
3. Does habitat type and/or condition affect moth diversity and composition?
4. Are there any moth species indicative of the habitat type and condition?

3.3 Methods

3.3.1 Study site and experimental design

Sampling was carried out on the limestone outcrop of Hutton Roof and Farleton Knott SSSIs, in the north west of England (Figure 2.1). The reserves lie to the east of the Arnside and Silverdale AONB and form part of the Morecambe Bay limestone series. They form one geological unit, covering approximately 687 ha and are of a mid-altitudinal position ranging from 140 – 270 m ASL.

Ten SSSI units were sampled from the available fourteen. In each SSSI unit, two grassland and two pavement sites were sampled, totalling 40 sampled sites (Figure 2.2). The habitat condition of each unit, as classified by NE, fell into three categories: declining (3 units), recovering (3 units), and favourable (4 units).

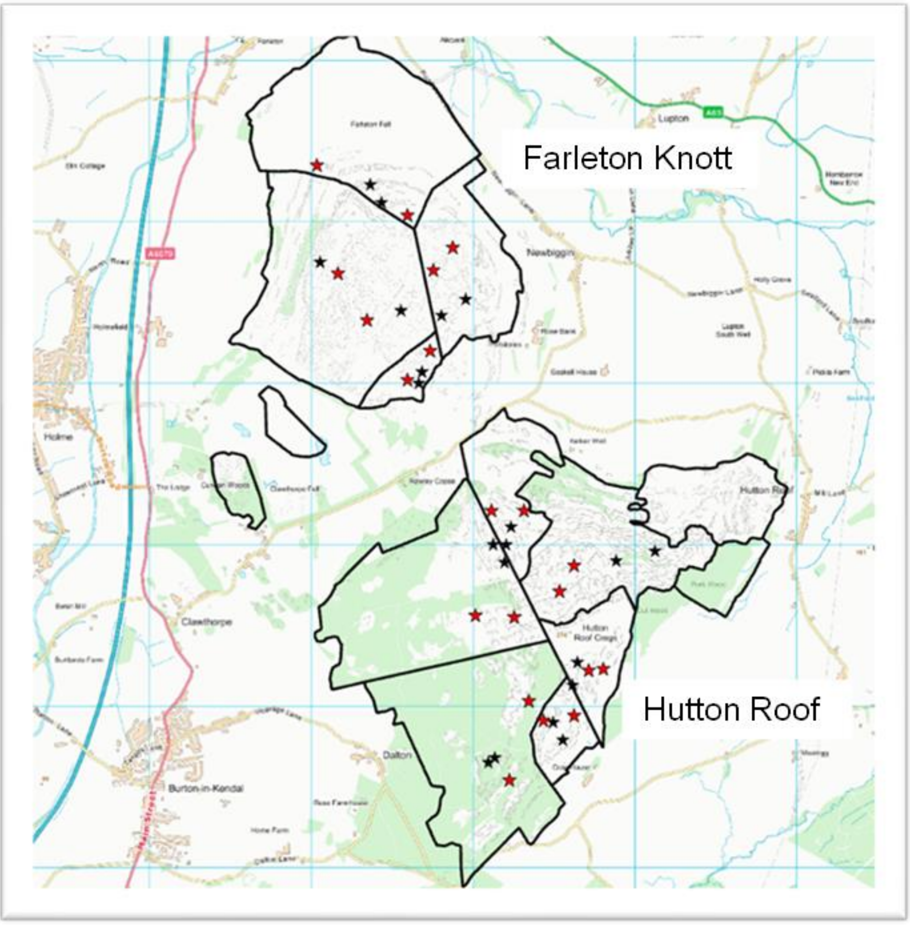


Figure 3.1. Map of the sampling sites within the SSSI units at Hutton Roof and Farleton Knott SSSIs © ArcGIS Pro version 2.4.0 (Esri, 2020). Black lines delimit the boundaries of each unit, red stars represent calcareous grassland sites and black stars limestone pavement sites. SSSI units containing no numbers or stars within their boundaries were not sampled.

At each sampling site, nine vegetation variables (Table 2.4) were measured within nine 1 m^2 quadrats at 5-metre intervals along two perpendicular 30-metre transects (Figure 2.4). Measurements were averaged for each site. A further three vegetation variables were recorded by walking each transect, recording the presence/absence of plant species listed by NE as positive and negative indicators of quality, noting any other plant species (forb, grass, woody) not on the list within a 1 m wide strip that straddled the transect (Table 2.5). Indicator species lists differed for Hutton Roof and Farleton Knott (see Chapter 2 for more details).

Nocturnal moths were sampled in June and July 2021. Each site was sampled once per month, covering one unit per night when weather conditions permitted. A single UV LED light trap (Figure 2.3) was left in the centre of the vegetation sampling transect at each of the four sites within a unit and checked at dawn the following morning. Moths were identified on site with any difficult or confusion species taken and identified in the lab.

The method followed for data collection is outlined in detail in Chapter 2. All data collected in August were excluded from the main analysis due to equipment failures at several sites.

3.3.2 Moth diversity metrics

Moth species richness and abundance were defined by the accumulative total of species caught during sampling in June and July. All observed moth diversity measures followed a Gaussian error structure except the abundance data, which were transformed using log (x + 1). In order for the diversity indices to be calculated, a species-abundance matrix was constructed using the total abundance for the species caught at each site. Simpson's index (1-D) and Shannon-Weiner diversity indices were calculated, as was the expected moth species richness based on samples, rarefied moth species richness using the "diversity" function in the *vegan* package (Oksanen *et al.,* 2020) in R version 4.1.0 (R Core Team, 2021).

Moth species were classified based on their conservation status in the UK following Waring & Townsend (2017) for the macro-moths and Davies (2012) for the micro-moths. Moth species with an assigned national status of RBD, Nationally Scarce and Local status were combined as "rare" and all those with the assigned national status of common remained as such. The richness of common and rare moth species were calculated from the accumulative species list for June and July for each of the 40 sites.

3.3.3 Data analysis

All statistical analyses were carried out in R version 4.1.0 (R Core Team, 2021).

To assess the effect of habitat type and condition on moth community attributes, linear mixed-effects models (LMMs) were constructed for seven different response variables: 1) observed moth species richness, 2) rarefied moth species richness, 3) abundance of moth species, 4) number of common moth species, 5) number of rare moth species, 6) Simpson's index, and 7) Shannon-Weiner index. All observed response variables followed a Gaussian error structure except abundance, which followed a Gamma distribution. The measured response variables of Simpson and Shannon diversity followed negative binomial and log-normal distributions respectively. The fixed explanatory variables were habitat type (two levels) and habitat condition (three levels) and SSSI unit was assigned as the random effect. The statistical significance of each LMM was tested with type II analysis of variance (anova) and degrees of freedom were estimated via Satterthwaite's method using the *lmerTest* package (Kuznetsova *et al*., 2017). The distribution of residuals were checked for each model.

LMMs were also used to test the effect of habitat type and condition on the vegetation variables. The response variables of positive, negative and other plant species followed a Gaussian distribution, whilst all others were non-normal. Many of the vegetation variables were proportions of cover (%) containing zeros and so were transformed using the "logit" function in the *car* package (Fox & Weisberg, 2019). The fixed explanatory variables were habitat type and habitat condition, with SSSI unit being the random effect. The statistical significance of each LMM was tested with type II anova and degrees of freedom were estimated via Satterthwaite's method as described previously. The distribution of residuals were checked for each model.

The eleven vegetation variables (Table 2.4) were then introduced as explanatory variables in place of habitat and condition to account for the vegetation structure of each SSSI unit. As several vegetation variables were correlated, the variance inflation factor (vif) was calculated for each using the "vif" function in the *car* package (Fox & Weisberg, 2019). Variables with a vif >10 were removed from the main model and tested individually, selecting the variable with the lowest Akaike's Information Criterion (AIC) and highest r-squared values to remain in the model. R-squared values were obtained using the "tab_model" function in the *sjPlot* package (Lüdecke, 2021). SSSI unit was again assigned as the random effect. Type II anova was used to test the statistical significance of the fixed factors and degrees of freedom were estimated via

Satterthwaite's method using the *lmerTest* package (Kuznetsova *et al.,* 2017). Where habitat:condition interactions were identified, Tukey post hoc comparisons were made between the explanatory variables habitat type and condition using the *lsmeans* package (Lenth, 2016). The distribution of residuals was checked for each model. Effects and interactions were visualised with *ggplot2* (Wickham, 2016) using untransformed data. All LMMs were fitted using the "lmer" function in the *lme4* package (Bates *et al.*, 2015).

To assess differences in the moth community composition between habitat type and condition, moth species abundance data were visualised using the ordination method Non-metric Multidimensional Scaling (NMDS) which is based on Bray-Curtis pairwise distance. Species were first grouped by habitat type (Gra: Grassland, Pav: Pavement) and condition (Dec: Declining, Rec: Recovering, Fav: Favourable), then by unit (CHA: Crag House Allotment, FF: Farleton Fell, HRCP: Hutton Roof Commons Pavement, LCBF: Lancelot Clark Storth & Burton Fell, P: Ploverlands, DC: Dalton Crags, HPF: Holme Park Fell, HSP: Holme Stinted Pasture, N: Newbiggin, UP: Uberash Plain) and reserve (Hutton Roof and Farleton Knott) to assess community similarities. The eleven vegetation variables were then tested to see if they explained the moth community composition. This was done using the "metaMDS" and "envfit" function, respectively, in the *vegan* package (Oksanen *et al.* 2020). Any statistically significant vegetation variables identified were then overlaid to the original NMDS plot using *ggplot2* (Wickham, 2016).

Lastly, Indicator Species Analysis was performed to identify moth species that were indicators of habitat type (calcareous grassland and limestone pavement), condition (declining, recovering, and favourable), as well as habitat and condition groups (Gra: Grassland, Pav: Pavement, Dec: Declining, Rec: Recovering, Fav: Favourable) using the "multipatt" function in the *indispecies* package (Cáceres & Legendre*,* 2009), specifying the associated function "r.g" to account for uneven group sizes (Tichy & Chytry, 2006).

3.4 Results

A total of 3196 individuals of 174 moth species were recorded from 40 sites within 10 SSSI units (Appendix 1): 697 individuals of 72 species were sampled in round one (June), and 2499 of 140 species in round two (July). A total of 1600 individuals of 131 species were sampled within the grassland habitat and 1596 individuals of 140 species from the pavement habitat (see appendix for full species list for each habitat). Of the 174 species, 97 were macro-moths and 77 were micro-moth species. The moth species accumulation curve showed the sampling intensity to be adequate (Appendix 2). Geographically, the two sites fall within two biological recording areas: VC60 (West Lancashire) and VC69 (South Lakeland). One moth species was found in Lancashire for the first time: *Aproaerema sangiella*, and three species were recorded in Cumbria for the first time: *Clepsis rurinana*, *Elachista triseriatella* and *Aproaerema sangiella*. Additionally, *Coleophora striatipennella* was noted as new for VC69. A total of 45 species were recorded with a national status of either RDB3 (1), pRDB1 (1), Nationally Scarce B (7), Nationally Scarce A (3) or Local (32) (see Chapter 2 for category details).

3.4.1 Effects of habitat and condition on vegetation

Results of LMMs assessing differences between habitat types and habitat conditions, and their interaction on eleven vegetation variables measured at each of the sampled sites are presented in Table 3.1.

Of the vegetation variables that did not show a significant interaction between habitat and condition, habitat type was found to have a significant main effect on six of the vegetation variables (Table 3.1). Vegetation height (Fig. 3.2a), cover of woody plants (Fig. 3.2c), and the cover of ferns (Fig. 3.2e) were greater at the pavement habitats compared to the grassland. Conversely, the cover of grass (Fig. 3.2b) and also the total number of non-indicator plant species (any species of forb or grass that is not a positive or negative indicator of condition based on NE assessment) recorded at grassland sites were significantly higher than at the pavement sites (Fig. 3.2d). No significant differences were found for bryophyte cover, fern cover, the number of positive or negative indicator plant species (Table 3.1).

A Habitat:Condition interaction was found for the number of forbs in flower, whereby significantly more species of forbs were found to be in flower at recovering grassland than declining ($t_{30.8}$ = -3.18, p = 0.036), recovering ($t_{37.4}$ = 3.47, p = 0.015) and favourable pavement ($t_{30.8}$ = -4.23, p = 0.003). Favourable grassland also contained more species of forb in flower than favourable pavement ($t_{37.4}$ = 3.72, p = 0.008) (Figure 3.3b). The limestone pavements contained significantly more bare ground than the grassland in all conditions. In addition, pavements in favourable condition contained significantly more bare ground compared with those in recovering ($t_{30.8}$= 1.12, p = <0.001), but not those in declining condition ($t_{30.8}$ = 1.42, p = 0.739) (Figure 3.3c).

Table 3.1. LMM output testing the effect of habitat type and habitat condition and their interaction on each of the eleven vegetation variables. Unit was included as the random effect for each model and df was estimated by Satterthwaite's method. Significant values are highlighted in bold.

Response variable	**Fixed Effect**	**df**	**F-value**	**p-value**
Vegetation height	Habitat	1, 30	28.95	**<0.001*****
	Condition	2, 10	1.21	0.338
	Habitat:Condition	2, 30	2.6	0.090
Forb cover	Habitat	1, 30	28.17	**<0.001*****
	Condition	2, 10	1.06	0.381
	Habitat:Condition	2, 30	5.75	**0.007****
Woody plant cover	Habitat	1, 30	18.38	**<0.002*****
	Condition	2, 10	0.29	0.757
	Habitat:Condition	2, 30	0.65	0.528
Bryophyte cover	Condition	2, 10	0.26	0.778
	Habitat	1, 30	0.02	0.894
	Habitat:Condition	2, 30	0.50	0.611
Grass cover	Habitat	1, 30	162.86	**<0.001*****
	Condition	2, 10	1.25	0.328
	Habitat:Condition	2, 30	0.96	0.396
Fern cover	Habitat	1, 30	9.62	**0.004****
	Condition	2, 10	2.95	0.098
	Habitat:Condition	2, 30	1.609	0.217
Bare ground	Habitat	1, 40	246.69	**<0.001*****
	Condition	2, 40	0.29	0.753
	Habitat:Condition	2, 40	3.69	**0.034***
Number of forbs in flower	Habitat	1, 40	23.43	**<0.001*****
	Condition	2, 40	1.85	0.171
	Habitat:Condition	2, 40	3.58	**0.037***
Positive indicator plant species	Habitat	1, 30	0.14	0.715
	Condition	1, 10	0.41	0.673
	Habitat:Condition	1, 30	0.55	0.582
Negative indicator plant species	Habitat	1, 40	0.92	0.344
	Condition	2, 40	1.51	0.233
	Habitat:Condition	2, 40	0.03	0.970
Non-indicator plant species	Habitat	1, 30	4.86	**0.035***
	Condition	2, 10	0.94	0.424
	Habitat:Condition	2, 30	3.12	0.059

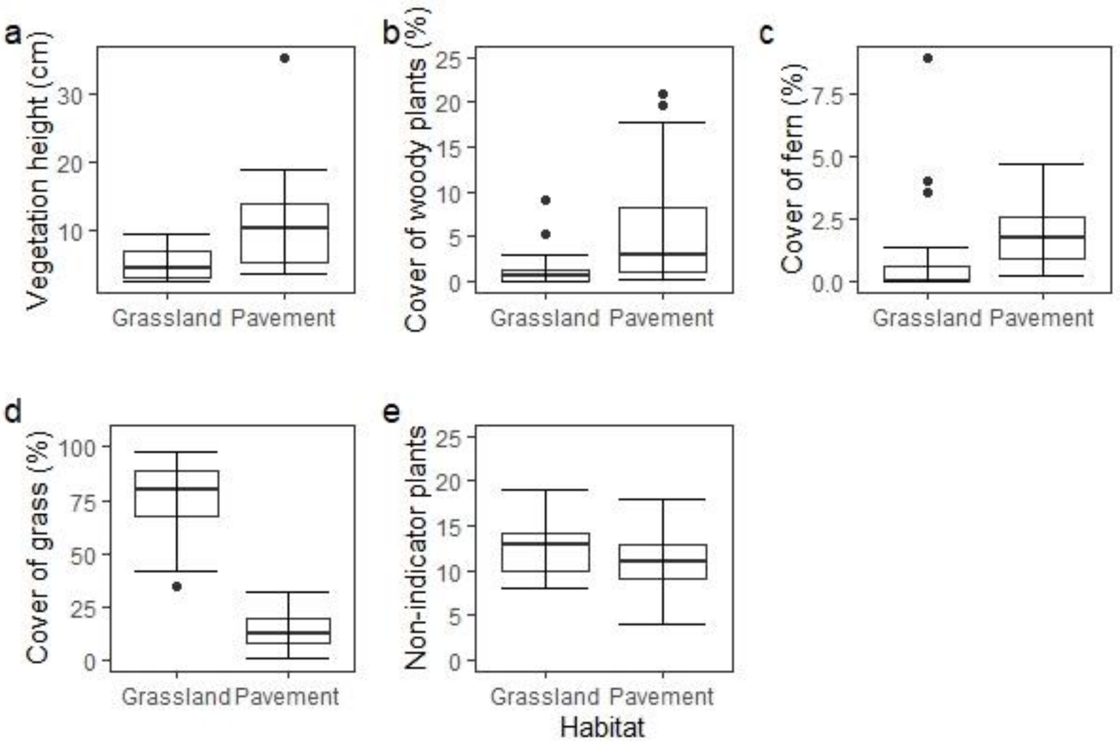


Figure 3.2. The effect of habitat type on vegetation variables. Displayed are the a) vegetation height, b) cover of grass, c) cover of woody plants, d) the number of non-indicator plant species, and e) the cover of fern for the calcareous grassland and limestone pavement habitats. The boxplot displays the median, first and third quartile and minimum and maximum values. Scales on the y-axis differ between variables.

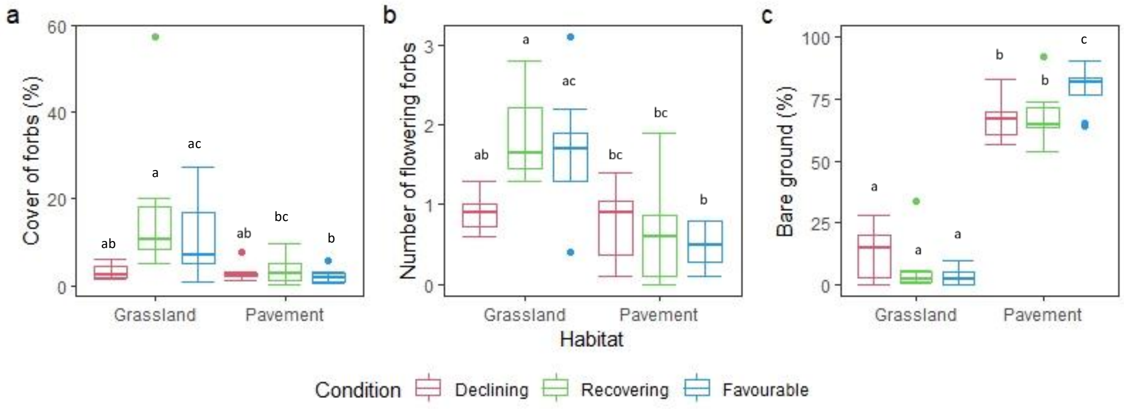


Figure 3.3. The effect of habitat type and habitat condition on vegetation variables. The percentage a) cover of forbs, b) the number of forbs in flower, and c) the percentage of bare ground grouped by condition for the grassland and pavement habitats. The boxplots display the median, first and third quartile and minimum and maximum values. Different letters above the bars represent significant differences between the habitat types and conditions as identified by post hoc analysis. Red bars = declining condition, green bars = recovering condition, and blue bars = favourable condition. Scales on the y-axis differ between variables.

3.4.2 Effects of habitat type and condition on moth diversity

The LMMs revealed little influence of habitat type or condition on moth community attributes (Table 3.2). Habitat type and condition did not have a significant effect on moth species richness (Fig. 3.4a), rarefied moth species richness (Fig. 3.4b), Simpson index (Figure 3.4c), Shannon index (Fig. 3.3d) or moth abundance (Fig. 3.4e), nor did it affect the number of common (Fig. 3.4f) or rare (Fig. 3.4g) moth species sampled. In addition, there were no significant interactions between habitat type and condition (Table 3.2).

Table 3.2. LMM output for each of the moth community attributes in relation to habitat type and habitat condition. Df estimated by Satterthwaite's method. SSSI unit was the random effect for each model.

Response variable	Fixed Effect	df	F-value	p-value
Species richness	Habitat	1, 30	0.28	0.604
	Condition	2, 10	0.76	0.494
	Habitat:Condition	2, 30	0.65	0.527
Log abundance	Habitat	1, 30	0.20	0.655
	Condition	2, 10	1.06	0.382
	Habitat:Condition	2, 30	2.60	0.091
Common species	Habitat	1, 30	0.13	0.723
	Condition	2, 10	1.03	0.394
	Habitat:Condition	2, 30	0.17	0.849
Rare species	Habitat	1, 30	0.43	0.516
	Condition	2, 10	0.73	0.508
	Habitat:Condition	2, 30	1.59	0.221
Simpson Index (1-D)	Habitat	1, 40	0.99	0.326
	Condition	2, 40	0.90	0.413
	Habitat:Condition	2, 40	2.81	0.072
Shannon Index	Habitat	1, 40	0.92	0.345
	Condition	2, 40	1.11	0.339
	Habitat:Condition	2, 40	1.18	0.319
Rarefied richness	Habitat	1, 30	0.00	0.959
	Condition	2, 10	0.27	0.773
	Habitat:Condition	2, 30	2.08	0.143

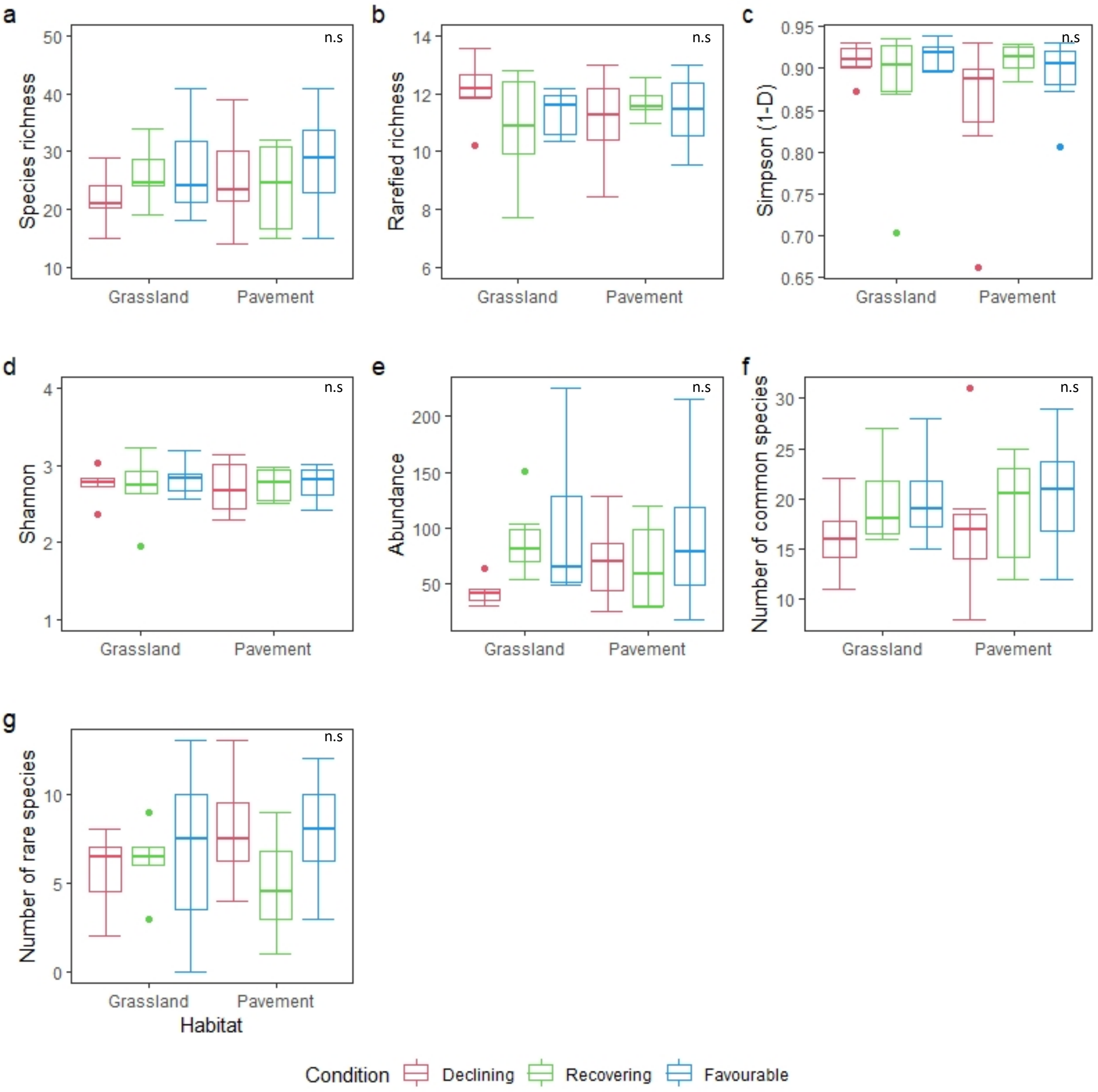


Figure 3.4. The effect of habitat type and habitat condition on observed and estimated measures of moth species diversity. Mean a) species richness, b) rarefied species richness, c) Simpson index, d) Shannon index, e) Abundance, f) number of common species and g) number of rare species for moth communities of the grassland and pavement habitats. Non-significant effects are denoted by “n.s”. Red bars = declining condition, green bars = recovering condition, and blue bars = favourable condition. The boxplot displays the median, first and third quartile and minimum and maximum values. Scales on the y-axis differ between diversity measure.

3.4.3 Effects of habitat, condition and vegetation on moth community composition

Habitat type and condition categories were combined to generate six habitat and condition combinations. Differences between habitat type and condition categories did not explain a significant component of variation in the NMDS (Fig. 3.5a & Table 3.3). However, moth community composition was significantly different between the SSSI units and the reserves (Fig. 3.5b & Table 3.3). The community composition of Crag House Allotment, Holme Park Fell, Holme Stinted Pasture and Newbiggin were all distinct from one another, but not from the other six units. Differences in moth community composition between reserves was primarily driven by the cover of forbs, with all other vegetation variables having a non-significant effect (Table 3.3).

Table 3.3. The effect of vegetation variables on moth species in sites of different habitat type (grassland vs. pavement) and condition (declining, favourable, recovering), unit and reserve based on species abundances.

Vector	r-squared	p-value
Cover of forbs	0.188	**0.015***
Number of positive indicator plant species	0.096	0.148
Number of negative indicator plant species	0.072	0.265
Total number of plant species	0.055	0.348
Cover of woody plants	0.049	0.389
Vegetation height	0.029	0.587
Number of forbs in flower	0.028	0.568
Number of non-indicator plant species	0.022	0.663
Cover of bryophytes	0.009	0.886
Cover of grasses	0.008	0.864
Cover of ferns	0.005	0.919
Bare ground	0.001	0.979
Factor		
Unit	0.809	**0.001*****
Reserve	0.337	**0.001*****
Habitat/Condition	0.116	0.531

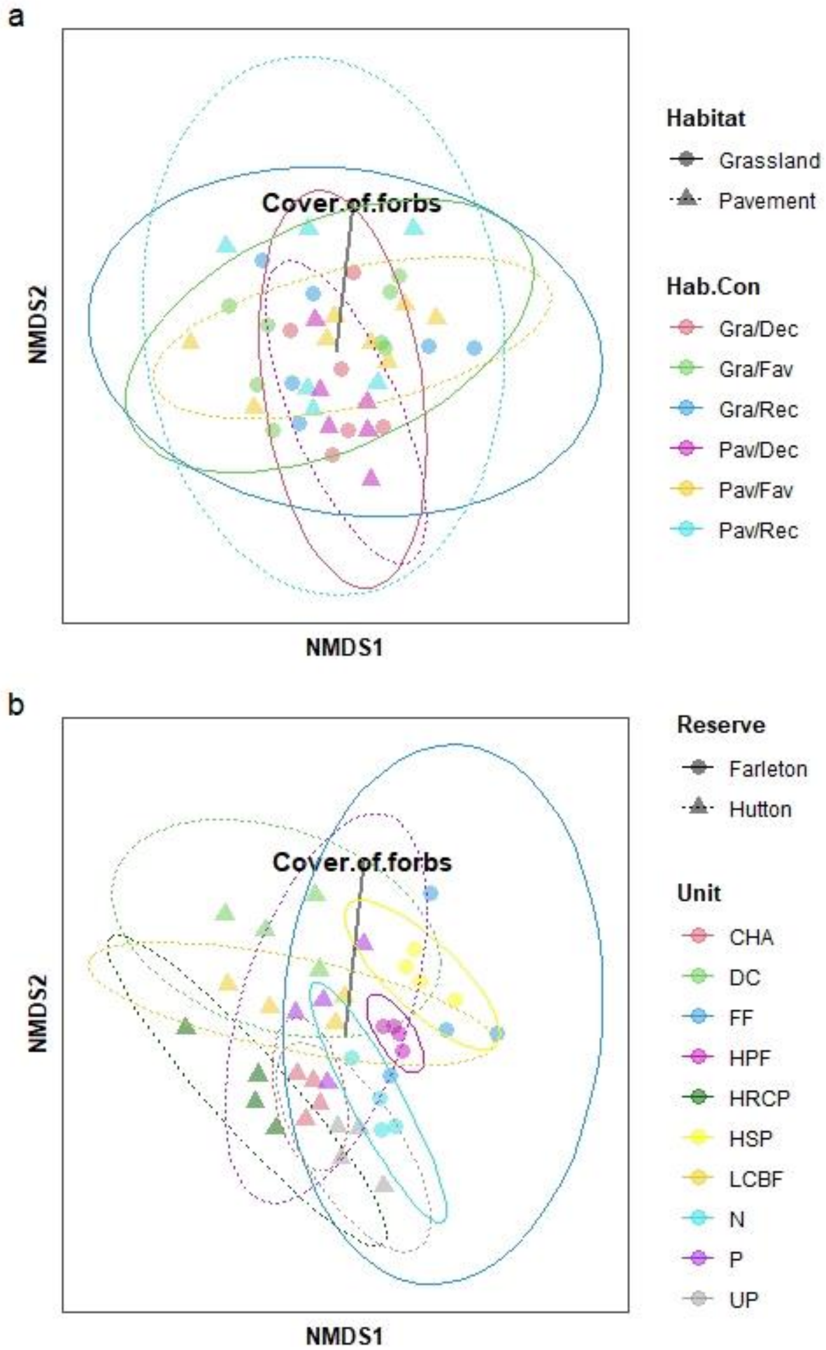


Figure 3.5. NMDS plot of the community composition of all moth species caught in June and July 2021 (stress = 0.25), grouped by a) habitat type (Gra: Grassland, Pav: Pavement) and condition (Dec: Declining, Rec: Recovering, Fav: Favourable) and b) SSSI unit (CHA: Crag House Allotment, FF: Farleton Fell, HRCP: Hutton Roof Commons Pavement, LCBF: Lancelot Clark Storth & Burton Fell, P: Ploverlands, DC: Dalton Crags, HPF: Holme Park Fell, HSP: Holme Stinted Pasture, N: Newbiggin, UP: Uberash Plain). Shapes represent a) the grassland (circle) and pavement (triangle) habitats and b) sites Farleton Knott (circle) and Hutton Roof (triangle). Significant environmental variables are represented as arrows (% cover of forbs). Each point represents a sample site and ellipses represent the 95% CI around the group centroid and are displayed for each of the six habitat/condition categories and ten units, with dashed and solid lines representing the habitats and reserves.

3.4.4 Effects of vegetation on moth diversity

There were only a few instances where moth community attributes were significantly related to vegetation variables (Table 3.4). The cover of grass had a significant negative effect on species richness, albeit slight (Fig. 3.6a). Bryophyte cover was found to have a positive effect on Simpson index (Fig. 3.6b) and Rarefied moth species richness (Fig. 3.6c). All other vegetation variables did not have a significant effect on the five measures of diversity (Table 3.4).

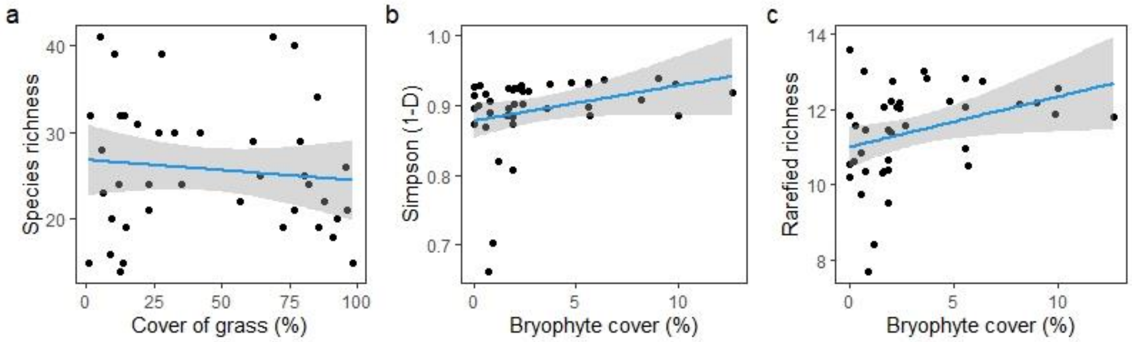


Figure 3.6. The effect of components of vegetation on estimated measures of moth species richness. The predicted effects of a) cover of grass on moth species richness, b) bryophyte cover on the Simpson index, and c) bryophyte cover on rarefied moth species richness with 95% confidence intervals. Scales on the y-axis differ between variables.

Table 3.4. LMM output for the effect of nine vegetation variables on five measures of diversity, with unit being the random effect for each model. Df estimated by Satterthwaite's method. Significant values are in bold.

Response variable	Fixed Effect	df	F-value	p-value
Species richness	Negative indicator plants	1, 39.669	0.05	0.825
	Positive indicator plants	1, 36.808	1.41	0.243
	Non-indicator plants	1, 38.090	1.49	0.230
	Number of forbs in flower	1, 39.096	1.17	0.286
	Vegetation height	1, 39.888	0.15	0.699
	Cover of woody plants	1, 38.368	0.05	0.832
	Cover of bryophytes	1, 32.086	0.28	0.600
	Cover of ferns	1, 39.366	0.04	0.844
	Cover of grass	1, 31.277	5.68	**0.023***
Log abundance	Negative indicator plants	1, 39.417	2.00	0.165
	Positive indicator plants	1, 36.178	0.21	0.649
	Non-indicator plants	1, 37.541	0.84	0.366
	Number of forbs in flower	1, 38.755	1.55	0.221
	Vegetation height	1, 39.707	0.01	0.908
	Cover of woody plants	1, 37.853	1.50	0.228
	Cover of bryophytes	1, 31.301	1.21	0.280
	Cover of ferns	1, 39.004	0.03	0.868

	Cover of grass	1, 30.551	1.58	0.219
Rarefied richness	Negative indicator plants	1, 40	0.15	0.704
	Positive indicator plants	1, 40	1.09	0.302
	Non-indicator plants	1, 40	0.12	0.732
	Number of forbs in flower	1, 40	1.37	0.248
	Vegetation height	1, 40	0.48	0.493
	Cover of woody plants	1, 40	2.22	0.144
	Cover of bryophytes	1, 40	5.02	**0.031***
	Cover of ferns	1, 40	0.01	0.929
	Cover of forbs	1, 40	1.19	0.282
Simpson index (1-D)	Negative indicator plants	1, 40	0.09	0.771
	Positive indicator plants	1, 40	0.47	0.498
	Non-indicator plants	1, 40	0.60	0.444
	Number of forbs in flower	1, 40	0.15	0.700
	Vegetation height	1, 40	1.49	0.229
	Cover of woody plants	1, 40	1.17	0.286
	Cover of bryophytes	1, 40	4.54	**0.039***
	Cover of ferns	1, 40	0.17	0.684
	Cover of grass	1, 40	0.28	0.601
Shannon index	Negative indicator plants	1, 40	1.24	0.271
	Positive indicator plants	1, 40	0.95	0.335
	Non-indicator plants	1, 40	0.08	0.775
	Number of forbs in flower	1, 40	0.58	0.450
	Vegetation height	1, 40	0.14	0.708
	Cover of woody plants	1, 40	0.35	0.560
	Cover of bryophytes	1, 40	3.29	0.077
	Cover of ferns	1, 40	0.07	0.787
	Cover of forbs	1, 40	1.56	0.219

3.4.5 Indicators of habitat type and condition

The indicator species analysis identified moth species that were differentially abundant in the two habitats of interest (grassland or pavement). Of the 174 species sampled, four species had a statistically significant association with the grassland and two species were identified as being associated with pavement (Table 3.5).

Table 3.5. Moth species identified as having a statistically significant association with the grassland and pavement habitats, including the total abundance, relative abundance (N), the percentage (%) of individuals sampled at each habitat, which habitat the moth species is an indicator for, the test statistic (IndVal), and the significance.

Moth species	N	Grassland (%)	Pavement (%)	Indicator for	IndVal	p-value
Elachista triseriatella	72	81.9	18.1	Grassland	0.368	0.006
Pyrausta despicata	158	94.3	5.7	Grassland	0.333	0.005
Scotopteryx luridata	24	83.3	16.7	Grassland	0.322	0.046

Agriphila straminella	45	91.1	8.9	Grassland	0.292	0.020
Charissa obscurata	92	12	88	Pavement	0.428	0.004
Coenotephria salicata	172	20.9	79.1	Pavement	0.302	0.016

When the three habitat condition categories were analysed, a number of species were identified as having a greater abundance for each of the conditions. Three species were found to have a significant association with habitats in decling condition, another two species with the recovering habitats, and seven species were found to be significantly associated with sites in favourable condition (Table 3.6).

Finally, a small number of species were statistically significantly associated with some of the habitat/condition categories. The recovering grassland and declining pavement had just one indicator species each, whilst pavement in favourable condition had three indicator species (Table 3.7). Each of the species identified during this analysis are also indicators within other factors: *Eulithis populata* an indicator of declining, *Scoparia ambigualis* an indicator of recovering, and *Coleophora albicosta* an indicator of favourable sites (Table 3.6), whilst *Charissa obscurata* and *Coenotephria salicata* are indicators of both the pavement habitat and sites in favourable condition (Tables 3.5 & 3.6).

Table 3.6. Moth species identified as having a significant association with declining, recovering, and favourable conditions, including the total abundance (N), the percentage of individuals sampled at each condition category (%), the condition the moth species is an indicator for, the test statistic (IndVal) and the significance.

Moth species	**N**	**Dec (%)**	**Rec (%)**	**Fav (%)**	**Indicator for**	**IndVal**	**p-value**
Eulithis populata	16	81.25	6.25	12.5	Declining	0.516	0.003
Apamea monoglypha	79	58.2	26.6	15.2	Declining	0.381	0.037
Xestia baja	9	88.9	11.1	0	Declining	0.342	0.041
Monochroa cytisella	7	14.3	85.7	0	Recovering	0.418	0.034
Crambus pascuella	5	0	100	0	Recovering	0.409	0.044
Scoparia ambigualis	168	20.2	60.1	19.7	Recovering	0.364	0.014
Charissa obscurata	92	7.6	12	80.4	Favourable	0.477	0.006
Coleophora albicosta	8	0	0	100	Favourable	0.442	0.008
Thalophila matura	80	2.5	21.25	76.25	Favourable	0.395	0.031

Crambus lathoniellus	62	11.3	22.6	66.1	Favourable	0.389	0.038
Coenotephria salicata	172	20.3	14.5	65.2	Favourable	0.379	0.010
Aplocera plagiata	12	0	0	100	Favourable	0.336	0.036
Eana osseana	29	3.4	0	96.6	Favourable	0.279	0.045

Table 3.7. Moth species identified as having a significant association with the habitat ((Gra: Grassland, Pav: Pavement) and condition (Dec: Declining, Rec: Recovering, Fav: Favourable) categories, including the total abundance (N), the percentage (%) of individuals sampled at each of the habitat/condition categories, the category the moth species is an indicator for, the test statistic (IndVal) and the significance.

Moth species	**N**	**Dec/ Gra (%)**	**Rec/ Gra (%)**	**Fav/ Gra (%)**	**Dec/ Pav (%)**	**Rec/ Pav (%)**	**Fav/ Pav (%)**	**Indicator for**	**IndVal**	**p-value**
Scoparia ambigualis	168	8.9	45.9	13.1	11.3	14.3	6.5	Rec/Gra	0.484	0.015
Eulithis populata	16	25	6.25	6.25	56.25	0	6.25	Dec/Pav	0.534	0.021
Charissa obscurata	92	3.3	0	8.7	4.3	12	71.7	Fav/Pav	0.725	<0.001
Coleophora albicosta	8	0	0	12.5	0	0	87.5	Fav/Pav	0.605	0.008
Coenotephria salicata	172	2.9	2.3	15.7	14.5	5.8	58.8	Fav/Pav	0.509	0.010

3.5 Discussion

One of the central aims of this study was to investigate the differences in moth communities between the limestone pavement and calcareous grassland habitats and their condition. The results showed that none of the observed and estimated moth diversity measures significantly differed between the habitat type or condition categories, suggesting that both habitats support similar levels of moth diversity. Why their propensities are similar is not fully known, but cross-habitat spill over may account for some of the similarity observed here as the two habitat types do co-occur as a matrix (Boesing *et al*., 2018). However, the sampling strategy sufficiently covered enough of the heterogeneity at both the grassland and pavement habitat types at the landscape level and so cannot be explained by spill over alone. It has been demonstrated that insect diversity significantly correlates with plant species richness (Hertzog *et al.,* 2016; Miller *et al.,* 2017) and it is known that both habitats support high levels of plant diversity (Ward & Evans, 1976; Willems *et al*., 1993). However, this study found that grasslands support significantly more plant species than pavements, so moth and plant diversity are likely to not be correlated in this instance. Moth diversity has also been found to differ between habitat types associated with different successional stages of farmland abandonment (open grassland, scrub, and forest), with moth diversity progressively increasing through each stage (Dantas de Miranda *et al*., 2019). Butterflies of Swedish grasslands followed a similar pattern of species richness, with forest cover also having a positive effect (Bergman *et al*., 2018). However, it may be that both habitat types support similar vegetation types and are therefore able to support similar levels of species richness due to shared resource provision (Dennis *et al*., 2006). Despite the similarities in moth diversity between habitat type and condition categories, a marginally significant habitat:condition interaction was found for moth abundance, whereby abundance was markedly lower at the grassland habitat in declining condition compared to all other categories. Whilst the finding is not statistically significant, it raises concerns regarding the potential trend for the future if the habitat is not brought out of declining condition. The reduction in habitat quality of open grasslands under intensive use have been associated with a significant decrease in the relative abundance of butterflies and burnet moth species in the southwest of Germany (Habel *et al*., 2019). However, species richness and abundance has been found to be significantly higher in abandoned semi-natural grasslands in some cases (Pöyry *et al*., 2004), which contradicts the findings of this study. Analysis of the species national statuses also found similar levels of common and rare moth species across the habitat types and condition, which has been observed with butterflies in Sweden across multiple habitat types (Berg *et al*., 2011).

In addition to a lack of habitat and condition effects on species diversity, moth community composition was also found to be similar across the habitat type and condition categories. Instead, significant differences lay between the SSSI units, with group differences being driven by the cover of forbs. The units Crag House Allotment (CHA), Holme Park Fell (HPF), Holme Stinted Pasture (HSP) and Newbiggin (N) all differed from one another, but still shared commonalities in composition with the remaining units. Uberash Plain (UP) also showed some distinctiveness in comparison to HPF and HSP but to a lesser extent. Interestingly, three of those four units were found at Farleton Knott, with just CHA being situated on Hutton Roof. This suggested that differences lay between Hutton Roof and Farleton Knott, which is supported by a significant difference in moth community composition between the two reserves, and that CHA shares more characteristics with Farleton Knott than it does with the rest of Hutton Roof. This is likely to reflect differences in environmental conditions; open, south-facing aspect with little scrub with livestock management. Hutton Roof has a higher cover of woodland, both natural (50.5 ha) and planted (11.7 ha at last assessment with extraction in recent years), than Farleton Knott (4.4 ha) and is becoming heavily scrubbed over mostly by Hawthorn and Blackthorn in the grassland and larger tree species predominated by Ash, Sycamore and Buckthorn on the pavements (Craven, 2012; Craven, 2013). Observations made during sampling suggest this regeneration has been left unmanaged for somewhere in the region of 10 – 20-years, which is likely to be highly influential to the variation observed. Abandonment results from a lack of strategic, structured management with the cessation of grazing, altering the composition of the vegetation and ultimately the moth community composition over time. Temporarily abandoned grasslands can support specialist macro and micro-moth species, but a diverse range of management is required to support the requirements of as many species as possible (Šumpich & Konvička, 2012). At what point abandonment will become detrimental here and whether or not that point has already been reached is unknown, but clear variances in moth community composition have been identified. Analyses of butterfly species associated with the species-rich grasslands of western Siberia found that community composition does indeed shift in response to succession during abandonment, with decreases in specialists noted (Trappe *et al*., 2017). There are plans by some landowners to increase the management effort with coppicing and the possibility of re-introducing cattle to Hutton Roof Commons Pavement (HRCP), Ploverlands (P), and UP (Friends of Hutton Roof and Martin Wain pers. comm.). This will reduce the development of rank grasses through biomass removal, slow successional processes, provide open, sunny rides favoured by a number of butterfly and moth species, and connect isolated and fragmented habitat patches (Ellis *et al*., 2019). The reversal of local population declines in recent years for some priority Lepidoptera (namely High Brown Fritillary and *Anania funebris*) in the Morecambe Bay area have been linked to an increase in conservation management efforts (Willott, 2017; Ellis *et al*., 2019).

In order to determine whether moth communities responded to differences in vegetation, despite there being few significant effects of habitat type or habitat condition, the effect of individual components of vegetation structure were analysed. It was found that the cover of grass had a statistically significant, albeit slight, negative effect on the observed species richness of moths. In a study assessing the drivers of decline in High Brown Fritillary, Ellis *et al.* (2019) found that “grassiness” had significantly increased throughout the Morecambe Bay area. With this increase in grass comes a decrease in herbaceous forbs and concomitant reductions in moth species richness as the plant community shifts. Interestingly, the cover of bryophytes (any mosses and/or lichens) made a significant positive contribution to the estimated diversity measures of rarefied moth species richness and Simpson’s diversity index. Bryophytes have been found to play a crucial role in this extreme environment and form the foundations upon which other species are able to exist. Limestone pavements and calcareous grasslands are nutrient, and water limited habitats, but bryophytes ameliorate these constraints. Lichens access nutrients for their own needs through the air but unlock nutrients in the rock through biological deterioration (Piervittori *et al*., 2004), with mosses enabling the storage of water that would otherwise drain instantly, thus facilitating the existence of higher plants by increasing the availability of limiting resources (Sand-Jensen & Hammer, 2012). It is also possible that moss provides a habitat in which many moth species may choose to pupate. Ellis *et al.* (2019) reported that High Brown butterflies that utilise the exposed rock outcrops such as those of the Morecambe Bay limestones, lay their eggs amongst mosses (Warren, 1995), which supports this idea.

The results from the vegetation surveys showed that a number of variables differed by habitat type and in some instances, by the condition of that habitat. It was found that not only vegetation height, but the cover of woody plants, was significantly greater on the pavements, with a marginally significant habitat:condition interaction, whereby vegetation height at pavements in recovering condition was taller than all other categories. This is likely primarily due to the inaccessibility to livestock and a lack of management intervention. Cattle are unable to access the majority of the pavement, even where it is broken and less blocky. Sheep on the other hand, utilise all but the steeply inclined features and were observed on the pavement whilst sampling the Newbiggin unit. Therefore, scrub development is likely being suppressed at the grassland habitats due to browsing and/or grazing. Despite being phased out across many of the sites due to overgrazing, sheep are still grazed at three of the units: Crag House Allotment on Hutton Roof and Newbiggin and Farleton Fell on Farleton Knott. These sites fall in to the unfavourable recovering and unfavourable declining categories. Elsewhere, cattle are now grazed in a number of units, some year-round, others cyclically, to replace traditional sheep grazing. These units are HPF and HSP on Farleton Knott, and Lancelot Clark Storth and Burton Fell (LC/BF) and Dalton Crags (DC) on Hutton Roof. All but DC (recovering) are in favourable condition. The remaining sites: HRCP, UP and P are not currently being grazed at all. In-fact, this has been the case at least since the last condition assessment was carried out in 2014. Only Hutton Roof Commons pavement is currently in favourable condition of this group, whilst the other two are declining. For these units, undergrazing is indeed the main justification for them being found to be in unfavourable or declining condition and puts them at high risk of further decline with an increase in the development of rank grasses already being noted (Natural England, 2014).

On the surface, limestone pavements are a somewhat homogenous feature, with distances between patches of vegetation often great (Vincent, 1995). The large and exposed slabs of carboniferous rock provide limited opportunities for vegetation to establish with most of the floristic interest being concentrated within the grikes (Ward & Evans, 1976). Therefore, it is no wonder that more bare ground was recorded at the pavement sites, however, there was significantly more at those in favourable condition. This finding fits well with the condition assessment criteria set out by NE, whereby pavement that is not in favourable condition tend to possess a higher percentage of scrub than those in favourable condition. The criteria set out by NE states that ideal scrub levels should be in the range of 5 - 25% (Natural England, 1988). When assessed, units that contain pavement that repeatedly exceed this, will fail one of the key criteria required for that feature to be classified as being in favourable condition. Like grasslands, pavements that develop a higher percentage of scrub through succession may be able to support higher levels of species richness and abundances through the increases in structural heterogeneity provided by the vegetation (Dantas de Miranda *et al.*, 2019), or it may act to fragment the habitat, disrupting dispersal ability (Hanski & Gilpin, 1997). Grikes on some pavements can be several feet deep (Goldie, 1996), each of which supports its own microclimate, hosting many shade-loving ferns and other woodland floor plant species in what is a much less hostile environment. In fact, fern cover was found to be significantly greater at pavements than grassland.

As to be expected, the grassland habitats contained a significantly greater cover of grass than the pavements and that they also supported a significantly greater number of plant species, other than the positive and negative indicator plant species, which did not significantly differ between the two habitat types. This was likely due to the fact that grasslands had a significantly greater cover of forbs, in particular those that were in recovering or favourable condition and that pavements can be largely void of any vegetation cover (Vincent, 1995). A similar habitat:condition interaction was found, whereby significantly more species of forbs were seen to be in flower during surveys at recovering and favourable grassland habitats than those in declining condition and pavement in all conditions, suggesting that insufficient management is in place for those said to be in decline. The grassland habitats in decline are indeed those that have either been temporarily abandoned or are being excessively sheep grazed, both of which contribute to reductions in plant diversity (Wehn *et al.,* 2017). Therefore, the possibilities of reintroducing a management regime of grazing should be a high priority for land owners with grasslands in declining condition.

The habitat assessments carried out by NE incorporate both biological (plant species) and geological features (rock formations) that are indicative of good quality for the SSSIs. The heavy focus on vegetation characteristics and plant species dismisses the wealth of literature that provides evidence that insects make excellent bioindicators (for example see: McGeogh, 1998; Anderson *et al*., 2011; Pizzolotto *et al*., 2018; Legal *et al*., 2020). Despite moths being well represented in the UK, very few are recognised as indicator species in conservation assessments (Lintott *et al*., 2014). The indicator species concept is commonly used as a conservation tool when considering how best to manage reserves. Species with a strong association to a particular site in comparison to others can be considered as indicators (Cáceres *et al*., 2010) and are determined using analyses of the observed presence and absence between sites (Dufrêne & Legendre, 1997). The species richness of moths and the number of morphologically similar species coupled with the fact that the majority are crepuscular or nocturnal in habit, have presented difficulties in the past which have resulted, generally, in them not being used in the assessment and notification of SSSIs. However, this should not continue in the future as moths are now a well-studied taxa in the UK, with a substantial proportion of that knowledge collected by an army of experts and amateur recorders. Whilst it is not appropriate to consider all moth species, a small number that represent habitat type and condition could be usefully incorporated into future assessments. Currently, just three butterfly species are recognised in the NE citation because of their important association with the limestone habitats of Hutton Roof. All three species are Biodiversity Action Plan (BAP) species of high conservation priority: High Brown Fritillary *Fabriciana adippe* ([Denis & Schiffermüller], 1775), Pearl-bordered Fritillary *Boloria euphrosyne* (Linnaeus, 1758), and Duke of Burgundy *Hamearis Lucina* (Linnaeus, 1758). Three species of moth are given mention in the citation but do not form part of the notification: Least Minor *Photedes captiuncula* (Treitschke, 1825) (RDB3), Chestnut-coloured Carpet *Thera cognata* (Thunberg, 1792) (Nationally Scarce B) and Thyme Pug *Eupithecia distinctaria* Herrich-Schäffer, 1848 (Nationally Scarce B). These six species of Lepidoptera are not included in the NE citation for Farleton Knott, which is perhaps in part due to having an incomplete understanding of the distribution for some of the species, however, it is known that there are extant populations of *F. adippe* at Holme Stinted Pasture and Holme Park Fell (Ellis *et al*., 2019). Whilst not identified as indicator species in this study, the three moth species given mention in the SSSI citation for Hutton Roof were caught at both Hutton Roof and Farleton Knott during sampling. *T. cognata* was recorded from the small patch of Juniper at Holme Stinted Pasture, the first records for the SSSI, *P. captiuncula* which is known primarily as a diurnal species, came to light at Newbiggin and over 100 *E. distinctaria* were sampled at 22 sites across the two reserves, which is undoubtedly due to the extensive presence of Thyme *Thymus drucei* in both habitats, the sole larval foodplant for this moth species.

Indicator species analysis was used to identify any differentially abundant moth species associated with the categories for the habitat type, condition, and habitat/condition factors. There were a number of significant associations, however, the results should be used as a tool to focus investigations on a species-by-species basis. *Elachista triseriatella* (Stainton, 1854) is a Nationally Scarce (A) species with little known about its life-history other than the larvae feed internally on *Festuca* species in association with calcareous grassland. Indeed, it was found to be significantly associated with the grassland habitat. The discovery of a significant and extensive population during sampling covering both the Lancashire and Cumbria biological recording areas provided the first known records for Cumbria and only the second for Lancashire, the first being noted nearby at Gait Barrows in 2000 (from MapMate: Langmaid & Palmer). Two species were identified as being indicators for all three factors. Annulet *Charissa obscurata* ([Denis & Schiffermüller], 1775) and Striped Twin-spot Carpet *Coenotephria salicata* (Curtis, 1830) were significant for the pavement habitat, favourable condition, and the favourable pavement (Fav/Pav) category, suggesting they have a strong association with the latter. *C. obscurata* is a species whose forewing colouration reflects its habitat preferences of rocky limestone around the coast and in the uplands (Fig. 3.7). It is widespread, but local with larvae feeding on a range of low-growing herbaceous plants (Waring & Townsend, 2017). *C. salicata* is a common species of exposed rocky and grassy habitats in the north west, predominating in the uplands which is reflected in the mottled grey forewing colouration (Fig. 3.7). The larvae feed on a number of *Galium* species which were found to grow in profusion during sampling (Crafter, 2005).

Figure 3.7. The macro-moth species *Coenotephria salicata* (left) and *Charissa obscurata* (right).

3.6 Conclusion

This study shows that levels of moth diversity are similar at both calcareous grasslands and limestone pavements and that the condition, as judged by NE, has little effect on moth communities. Whilst habitat in declining and unfavourable condition has little influence on moth diversity at present, the thresholds outlined in the vegetation assessments by NE that dictate condition may currently be at a level that does not allow it to be detrimental to moth diversity. However, it serves as a firm warning that habitat condition should not decline further. Ultimately, it is not just the condition of the individual unit that is at risk of poor condition, but the wider landscape that surrounds them as these are merely imaginary borders. However, what we do see is a marginally significant reduction in moth abundance in the grassland habitat in declining condition and that a higher cover of grass has a negative effect on moth species richness. Independent findings from other studies of the Morecambe Bay limestone have shown that the cover of grass has increased in the last decade. As the moth community composition at Hutton Roof and Farleton Knott appear to be driven by the cover of forbs, this increase in grasses in relation to condition is of concern. Moth communities sampled at each of the SSSI units were more unique at Farleton Knott than at Hutton Roof, suggesting differences are influenced at the landscape level. Moth species indicative of habitat type and condition were identified and could be useful for inclusion in future assessments. At the very least, *P. captiuncula*, *T. cognata*, and *E. distinctaria* could be considered for inclusion in the SSSI citation and notification as indicator species at both Hutton Roof and Farleton Knott, with the introduction of regular monitoring to ensure populations remain stable. Many aspects of the vegetation composition were found to concur with the expectations of NE for the different condition categories and vegetation structure varies between the habitats: the pavement supports a taller, woody plant community whilst the grassland can be floristically diverse if it is in favourable condition. It should be remembered that these habitats were born from human activities, therefore, adequate levels of management through a combination of grazing mixed livestock and scrub clearance/clear-felling will be essential if the desired habitat heterogeneity and favourable condition status are to be achieved across the board in the coming years.

Chapter 4

The Effect of Habitat Condition and Vegetation on the Functional Diversity and Trait Composition of the Macro-moth Community of Limestone Habitats

4.1 Abstract

Calcareous grasslands and limestone pavements are some of the rarest habitats found in the UK, where a number of unique plant and insect communities can be found. Gaining an understanding of the relationships between habitat type, habitat condition, vegetation structure and the trait composition and functional diversity of the macro-moth community will help inform land managers and conservation agencies about moth responses to habitat change and may allow prediction of how those communities will respond to future land use and environmental change. Here, the effects of habitat type (grassland vs pavement), condition (declining, recovering, favourable) and vegetation on the traits and functional diversity of the macro-moths at Hutton Roof and Farleton Knott SSSIs in NW England are assessed. Moth and vegetation data were collected from the field and analysed alongside species traits (morphological, habitat/hostplant selection and life history traits) obtained from the literature. The macro-moth communities were found to be comprised of a mix of ubiquitous species, with the trait composition of the macro-moth community significantly driven by the cover of forbs and marginally by woody plants. Trait composition did not significantly differ between the six habitat and condition categories, but significant differences were observed between the reserves and SSSI units with distinctive trait profiles identified at a small number of units at Farleton Knott and Hutton Roof. Unsurprisingly, significantly more macro-moth species associated with grasslands were sampled at the grassland habitat than the pavement, however, the presence of woodland moth species was also significantly greater in grassland than pavement samples. Analysis also found that woodland moth species significantly increased with a decrease in the cover of grass. This may be in response to the encroachment of woody plant species as successional processes are left undermanaged. This study has detected significant differences between habitat types for a number of macro-moth traits, but analysis also showed that the measures of functional diversity did not significantly differ between habitat type or condition, which has been shown to be a normal response in heterogenous landscapes. However, analysis of the vegetation variables in relation to functional diversity found that grass cover was positively related to moth functional richness and plant species richness (non-indicator species) reduced moth functional

dissimilarity, which suggests that there may be an underlying influence of habitat condition. Appropriate management levels will be essential to reverse succession and promote traits associated with the grassland macro-moth species.

4.2 Introduction

Anthropogenic activities are significantly altering biodiversity on a global scale with habitat loss and destruction being a significant contributor (Maxwell *et al.,* 2016). Nowhere is this more evident than in the UK, with *The State of Nature Report* (Hayhow *et al*., 2019) showing that the trend since the 1970s continues to be one of loss, with post-war agricultural intensification thought to be a significant driver (Robinson & Sutherland, 2002; Reidsma *et al*., 2006). Intensive land use reduces biodiversity and homogenises habitats, with the mechanisms of decline often multifaceted. They include over fertilisation, the application of pesticide, herbicide, fungicide, increases in stocking densities, changes in crop rotation, and land drainage (Robinson & Sutherland, 2002). In addition, climate change is affecting species' phenologies and geographical distributions, disrupting finely balanced interspecific interactions, resulting in population declines and loss of species richness (Wilson & Fox, 2021). Limestone pavements and calcareous grasslands are vulnerable to the synergistic effects of land use change and climatic change (Ward & Evans, 1976; Goldie, 1996; Poschlod & WallisDeVries, 2002 and references within).

Over 70% of the total land area available in the UK is dedicated to agricultural practices (DEFRA, 2020) and with a significant part of its biodiversity associated with agricultural land, the pressures faced by species found here are immensurable. Just 10% of the total land area in the UK is protected (JNCC, 2021). Even within protected areas, ecological communities are not immune from the deleterious effects of human activity and often form isolated oases within a green desert. In addition to loss of taxonomic diversity, it is also clear that human activity may drive changes in the functional composition of communities, which may disrupt ecosystem functioning (Mooney, 2010). Halting losses have become a key aim of conservation (Balvanera *et al.,* 2006). Understanding the functional traits of those species with the ability to persist in the face of environmental change is key to determining the fate of the ecosystems they inhabit as reduced diversity has been well documented across multiple taxa not just in the UK, but across Europe (Donald *et al*., 2006; Brooks *et al*., 2012; Hallman *et al*., 2017; Habel *et al*., 2019).

Sites of Special Scientific interest form a major part of the protected area network in the UK (Gaston *et al*., 2006). Condition assessments of such sites are principally based on resident plant communities, though it is not clear that these condition assessments reflect the health of other taxonomic groups. There are over 2500 species of moth in the UK and the high levels of variation in the traits they possess and their response to environmental conditions (McGill *et al*., 2006), makes them excellent indicators of environmental change (Thomas, 2005). Moths perform a diverse range of functional roles as herbivores, pollinators and form an important part of the diets of many higher taxa (Fox *et al.,* 2013). Functional traits can be defined as those characteristics that affect a species reproductive potential, survival, and growth (Violle *et al*., 2007). Just as butterfly communities are influenced by landscape heterogeneity (Perović *et al*., 2015), the moth communities too will be a product of the habitat configuration and land use intensity. Functional traits weighted by their abundances are an important tool for identifying changes in individual or combinations of traits in response to environmental change such habitat type or condition (Tscharntke *et al*., 2012; Aguirre-Gutiérrez *et al*., 2017). The moth species present as a result of these environmental filters have a wider effect on ecosystem functioning (Lavorel & Garnier, 2002). Functional diversity is defined as *“the value and range of the functional traits of the organisms in a given ecosystem*” (Tilman, 2001) and explains the distribution of functional traits that contribute to the structure of an ecosystem, going beyond merely identifying species. Species richness has traditionally been the standard for assessing diversity at protected sites, but this measure alone does not tell us how many species occupy any given niche (Lewis *et al*., 2014). Assessing functional diversity of trait assemblages along environmental gradients can be used to identify patterns in moth community composition alongside measures of species richness to provide a more complete picture of the nature and functionality of a community (Guariento *et al*., 2020).

There is a long history of moths being studied in the UK, with extensive data available from the network of fixed-point light traps from the Rothamsted Insect Survey (RIS) and the network of amateur recorders from across the country whose records are submitted to the National Moth Recording Scheme (NMRS) (Shortall *et al.,* 2009). Despite this, there are still huge knowledge gaps for the life histories of many species, in particular, the micro-moths (Sterling & Parsons, 2012). However, more is known about the macro-moth species that occur here, which is in part, due to their conspicuous size. Moreover, detailed information is now available for almost every species with the exception of a small number of species where larvae are yet to be found in the wild (Waring & Townsend, 2017). As an easy to sample group of species, moths have been suggested to make an ideal warning system in the wake of ecosystem disruption and change with the establishment of regular monitoring (Merckx & Slade, 2014).

For a habitat to be suitable, not only should it provide the right larval hostplants for adults to lay their eggs, but be able to provide shelter from adverse weather, protection from predation and energy in the form of pollen and nectar for those that feed. These provisions may occur in different parts of a habitat and so the area required will be greater than the area offered by the hostplant (Hanski & Ovaskainen, 2000). As specialist habitats such as calcareous grassland and limestone pavement scrub over and become fragmented, the risks associated with isolation increase when compared to those areas that are larger and better connected (MacArthur & Wilson, 1967). Habitat loss, fragmentation and the deterioration in quality does have a negative impact on Lepidoptera and has been identified as the principal driver of decline in butterfly species in Europe (Öckinger *et al*., 2010). Furthermore, moth species associated with exposed, nitrogen depleted habitats such as those being assessed here, are experiencing the greatest declines (Fox *et al.,* 2014). Moreover, species with a narrower larval feeding niche and low dispersal abilities have been found to be more sensitive to reduced heterogeneity (Franzén *et al*., 2012). For example, threatened butterfly species such as The Duke of Burgundy *Hamearis lucina* (Linnaeus, 1758) are characterised as having a low dispersal ability (Kotiaho *et al.,* 2005; Hayes *et al.,* 2018) and have experienced a reduction in site occupancy and abundance in recent years despite an abundance of larval foodplant availability (Asher *et al.,* 2010). Specialist species may also be at greater risk from climate related pressures, habitat loss and fragmentation and biological enemies such as parasites (Thomas, 2005). Therefore, a resource-based view of habitats based on species requirements at the landscape level across a network of patches will be vital for identifying their conservation needs and may build a more resilient network of resources going forward (Dennis *et al*., 2006; Dennis *et al*., 2013).

Over time, species trait composition responds to succession. The functional richness of ground beetles was found to decline over time in grasslands being restored (Barber *et al*., 2017). Trait composition also shifted from smaller, phytophagous species in younger habitat (0-years old) to the restored grassland (28-years old) beetle community comprising of large, carnivorous species, which suggests species are quick to re-assemble to where the habitat is most-suitable (Barber *et al*., 2017). There is a wealth of literature available on the trait composition and functional diversity of many insect groups found at grasslands, woodlands and along gradients between the two, with land use intensities often considered (e.g., Forrest *et al*., 2015; Aguirre-Gutiérrez *et al*., 2017; Ubach *et al*., 2020; Mora *et al*., 2021). Unfortunately, the same does not exist for limestone pavements, with little interest shown beyond the flora being extensively studied (Ward & Evans, 1976). The lack of comparative studies is of concern as this is a rare habitat which remains threatened.

The aim of this chapter was to explore the effects of habitat type (limestone pavement vs calcareous grassland), habitat condition (declining, recovering, favourable) and vegetation on the trait composition and functional diversity of the macro-moth community at Hutton Roof and Farleton Knott SSSIs, NW England. The research questions to be addressed were as follows:

1. Does the composition of traits in the macro-moth community differ between habitat type and habitat condition?
2. Can the variation in trait composition and functional diversity of macro-moth communities be explained by plant community attributes?
3. Does habitat type, habitat condition, and/or the vegetation affect functional diversity?

4.3 Study site and experimental design

Sampling was carried out at Hutton Roof and Farleton Knott, north west England, UK (Figure 2.1), which lie to the east of the Arnside and Silverdale AONB, forming part of the Morecambe Bay limestone series. The two reserves cover approximately 687 ha and are of a mid-altitudinal position ranging from 140 – 270 m ASL.

Two habitat types were sampled at each of the ten SSSI units (calcareous grassland and limestone pavement), within which two sites were sampled, totalling 40 sites (Figure 2.2). The habitat condition of each unit, as classified by NE, fell into three categories: declining (3 units), recovering (3 units), and favourable (4 units).

Nine vegetation variables (Table 2.4) were measured within nine 1 m^2 quadrats at 5-metre intervals along two 30-metre transects in each site (Figure 2.4), with measurements being averaged for the site. A further three vegetation variables (Table 2.5) were recorded by walking each transect, recording the presence/absence of plant species listed by NE as positive and negative indicators of habitat quality, noting any other species not on the list (non-indicator species) within a 1-metre boundary straddling the transect. Indicator species lists differed for Hutton Roof and Farleton Knott to account for the variations in floral assemblages.

Nocturnal moths were sampled in June and July 2021 with each of the 40 sites being sampled once per month, covering one SSSI unit per night when weather conditions permitted. A single UV LED light trap (Figure 2.3) was placed in the centre of the vegetation sampling transect and checked at dawn the following morning. Moths were identified on site with any difficult or confusion species removed and identified in the lab.

The method followed for data collection is outlined in detail in Chapter 2. All data collected in August were excluded due to equipment failures at several sites.

4.3.1 Macro-moth trait data

Only macro-moth species were used in the analysis of traits due to limited trait information available for micro-moth species. After removing moth species with incompletely known life histories, 96 macro-moth species were considered for analysis.

Trait information was extracted from the Butterfly and Moth Traits Database compiled by Cook *et al.* (2021), with additional supporting foodplant information obtained from Waring and Townsend (2017). Six species traits were selected including morphological traits, life history traits, diet, and habitat specialisation. Each trait was represented by several categories resulting in a total of nineteen trait categories to be analysed (Table 4.1).

Table 4.1. Moth species traits selected for analysis, the levels within each and the trait description.

Trait	**Category**	**Details**
Forewing length		The mean of the minimum and maximum (mm)
Voltinism	Univoltine Multivoltine	Species with one generation per year are univoltine, two or more are multivoltine
Overwintering stage	Larva Pupa	
Hostplant specificity	Monophagous	Feeds on one hostplant
	Oligophagous	Feeds on a narrow range of hostplants within the same family
	Polyphagous	Feeds on multiple plant families
Hostplant type	Grasses	Feeds on any species of grass, rush, or sedge
	Forbs	Feeds on non-graminaceous herbaceous plants including ferns
	Trees and shrubs	Feeds on any broadleaf or coniferous trees and/or shrubs
	Lichen/algae	Feeds exclusively on lichen and/or algae
Habitat specificity	Woodland Heathland Moorland Grassland Wetland Coastal Montane/ upland	Species may occur in one or a combination the habitats listed

Forewing length

Forewing length is strongly correlated with body size and relates to the ability of an individual to disperse (García-Barros, 2000; García-Barros, 2005). Therefore, forewing length is important in understanding gene flow, population dynamics, resource accessibility and the impact of succession through the creation of barriers to moth species reaching these (Olden *et al*., 2004; Habel *et al*., 2018). The mean forewing length (mm) was calculated from the minimum and maximum measurements for each species. Forewing length is measured from the base of the forewing at the thorax to the apex.

Voltinism

Voltinism, the number of generations a species has in a year, is related to development speed and forms two categories; 1) univoltine species have a single generation each year and 2) multivoltine species produce two or more generations of imago in a year (WallisDeVries, 2014). For species reported to have one generation but with potential for a second generation in different years/regions a value of 0.5 was giving for each category as set out in the FD package (Laliberté *et al*., 2014).

Overwintering stage

The stage at which a species overwinters can influence survival from land uses such as grazing and mowing and may confer susceptibility to seasonal climate change (Börschig *et al.,* 2013). Overwintering stage fell into two categories: larva and pupa. None of the species included in the analysis overwintered as imago and only 6 of the 96 species overwintered as ova so not included as a stage. Those that overwinter as larvae may do so at varying stages of development, either hiding out in shallow soil or vegetation continuing to feed on milder days during early instars or as final instar, awakening in spring to pupate. Pupae may spend the winter in leaf litter, in the top layers of soil or under bark to name a few examples.

Larval hostplant specificity

Larval feeding niche breadth was determined by the hostplant specificity and classified as being dependant on a single plant species (monophagous), a narrow range of plant species within the same family (oligophagous) or as having a broad diet (polyphagous).

Larval hostplant type

As moths are well represented in many habitats, the dietary requirements of a community can be broad. Four broad hostplant types were used to describe the type of foodplants utilised by each species. All species that feed on graminaceous plants (grass, rush, and sedge) were grouped together, those that feed on herbaceous forbs (including ferns) were combined in the same group, species feeding on broadleaf and coniferous trees and shrubs were also combined, and species feeding on lichen and algae formed the final category. None of the species recorded fed on moss or fungi. If a species fed on more than one hostplant type, one divided by the number of types was giving for each category in which the species feed on and zero for all other categories. For example, a species reported to feed on both grasses and forbs was assigned a value of 0.5 for each of those hostplant types and a zero for the other two hostplant types as set out in the *FD* package (Laliberté *et al.,* 2014).

Habitat preference

Species can occur in a number of habitats, but many also display preferences, for example for calcareous or chalk grassland. Seven broad habitat categories were used: woodland, heathland, wetland, moorland, grassland, coastal, and montane/upland. Because a high proportion of recorded species show little preference for a particular habitat category, the number assigned to a species for each habitat category was as described for the previous trait. For example, a species reported to occur in woodland and heathland, was assigned a value of 0.5 for each of those two habitat categories and zero was given to the other four habitat categories as set out in the *FD* package (Laliberté *et al*., 2014).

4.3.2 Trait metrics

The community weighted mean (CWM) for a particular trait is the average value of the trait for all the species present in a community weighted by their abundance. To calculate the CWM for each trait at each site, a species abundance matrix using the moth sampling data and a species trait matrix of the six selected traits (19 categories within) was used. The forewing length of moths is strongly correlated with body size (García-Barros, 2015). Forewing length was a continuous trait with a Poisson distribution so was log-transformed to improve normality. Larval hostplant specificity was a categorical trait with three mutually exclusive levels. The other four traits were categorical traits with several non-exclusive levels: voltinism (two levels), overwintering stage (two levels), larval feeding guild (four levels), and habitat (seven levels) as species may not be exclusively allocated to one level of each trait. For example, *Acronicta rumicis* occurs in woodland, grassland, wetland, and montane habitats and so proportions were assigned to each habitat to equal to 1 (e.g., occurs in four habitats, each are assigned a value of 0.25). CWMs were calculated using a species matrix containing the functional traits in the "functcomp" function in the *FD* package, computing community-level weighted means of the trait values for each site (Laliberté *et al.,* 2014), in R version 4.1.0 (R Core Team, 2021).

4.3.3 Functional diversity metrics

Functional diversity (FD) is the variation in the value of functional traits amongst species. Using the "dbFD" function in the *FD* package (Laliberté & Legendre, 2010), five measures of functional diversity were computed using a trait x species matrix from the trait database compiled by Cook *et al*. (2021) for each of the macro-moth species sampled. Functional richness (FRic) is the amount of functional space a community fills, functional evenness (FEve) describes the distribution of abundance of the functional trait space, and functional divergence (FDiv), in a multivariance context, is the distribution of abundance within the space of the functional trait occupied by the species (Villéger *et al.,* 2008). Functional dissimilarity (FDis) is the mean distance in trait space of individual species to the centroid of all species, accounting for variations in species abundances by shifting the centroid position toward abundant species (Laliberté & Legendre, 2010), and Rao's quadratic entropy is the dissimilarity between the proportion of the abundance of species within a community (Botta-Dukát, 2005). All FD indices were calculated in R version 4.1.0 (R Core Team, 2021).

4.3.4 Data analysis

All statistical analyses were carried out in R 4.1.0 (R Core Team, 2021).

Linear mixed-effects models (LMMs) were used to assess if habitat type and condition have a significant effect on the CWM for each trait as well as on functional diversity metrics. Models were first constructed to test the effects of habitat type, condition, and their interaction on the nineteen CWM trait categories (Table 4.1) and the five functional diversity metrics FRic, FEve, FDiv, FDis and Rao. All trait CWMs followed a Gaussian distribution with the exception of forewing length (Poisson) and the larval hostplant specificities of monophagous (Poisson) and polyphagous (bimodal). Additionally, the explanatory variables FRic and FEve had Poisson and bimodal distributions respectively, with FDiv, FDis and Rao all having Gaussian distributions. The fixed explanatory variables were habitat type (grassland vs pavement) and condition (declining, recovering, and favourable), with unit being the random effect. The statistical significance of each LMM was tested with type II anova and degrees of freedom were estimated via Satterthwaite's method using the *lmerTest* package (Kuznetsova *et al*., 2017). The distribution of residuals were checked for each model.

Similar models were then run including the vegetation variables as the explanatory variables for both the traits and measures of functional diversity. To reduce multicollinearity effects, the variance inflation factor (vif) was calculated for correlated variables using the "vif" function in the *car* package (Fox & Weisberg, 2019) and variables with a vif > 10 were removed from the main model and tested individually, selecting the most parsimonious model based on the Akaike's Information Criterion (AIC) and r-squared values. Type II anova was used to test the statistical significance of the fixed factors and degrees of freedom were estimated via Satterthwaite's method using the lmerTest package (Kuznetsova *et al*., 2017). Where habitat:condition interactions were identified, Tukey post hoc comparisons were made between the explanatory variables habitat type and condition using the lsmeans package (Lenth, 2016). The distribution of residuals were checked for each model. Effects and interactions were visualised with *ggplot2* (Wickham, 2016) using untransformed data. All LMMs were fitted using the "lmer" function in the *lme4* package (Bates *et al*., 2015).

To assess variation in the composition of moth traits, data were visualised with two NMDS plots based on Bray-Curtis pairwise distance, one grouped by habitat type (Gra: Grassland, Pav: Pavement) and condition (Dec: Declining, Rec: Recovering, Fav: Favourable), and the other by SSSI unit (CHA: Crag House Allotment, FF: Farleton Fell, HRCP: Hutton Roof Commons Pavement, LCBF: Lancelot Clark Storth & Burton Fell, P: Ploverlands, DC: Dalton Crags, HPF: Holme Park Fell, HSP: Holme Stinted Pasture, N: Newbiggin, UP: Uberash Plain) and reserve (Farleton Knott and Hutton Roof). Habitat type, condition, SSSI unit, and reserve as well as vegetation variables were then tested to see if they significantly influenced the composition of traits. This was done using the "metaMDS" and the "envfit" functions in *vegan* (Oksanen *et al.,* 2020). NMDS plots, with 95% confident intervals for each factor and significant vegetation variables (as vectors) were plotted using *ggplot2* (Wickham, 2016).

4.4 Results

A total of 1992 individuals of 96 species of macro-moth were included in the analysis, with 1189 individuals of 82 species sampled in the pavement habitat and 841 individuals of 87 species sampled in the grassland habitat. Seven species were monophagous, 28 were oligophagous and 61 were polyphagous. 72 of the macro-moth species had strictly one generation per year (univoltine), eight species had two or more generations (multivoltine) and 16 species were noted as being both uni - and multivoltine. 16 macro-moth species fed on grasses, 48 on forbs, 55 on trees and shrubs, and five on lichens and algae. The macro-moth species were similarly ubiquitous throughout the habitat types with 87 occurring in woodland, 20 in heathland, 34 in moorland, 44 in grassland, 29 in wetland, 20 in coastal, and 70 in montane/upland habitats.

A list of moth species and their associated traits can be found in Appendix 4.

4.4.1 Effect of habitat and condition on trait CMWs

There were significant effects of habitat type on the CWM for five out the 19 trait categories analysed, and a significant interaction between habitat type and condition was found for only one trait (Table 4.2).

Table 4.2. LMM output from assessing the effect of habitat type and condition status on each category for the six trait CWMs. Df were estimated by Satterthwaite's method. Significant values are in bold.

Response variable	Fixed Effect	df	F-value	p-value
Forewing length	Habitat	1, 30	4.26	**0.048***
	Condition	2, 10	0.03	0.974
	Habitat:Condition	2, 30	2.10	0.140
Monophagy	Habitat	1, 30	0.10	0.749
	Condition	2, 10	0.12	0.890
	Habitat:Condition	2, 30	0.95	0.399
Oligophagy	Habitat	1, 30	0.09	0.763
	Condition	2, 10	0.14	0.868
	Habitat:Condition	2, 30	1.71	0.198
Polyphagy	Habitat	1, 30	0.02	0.889
	Condition	2, 10	0.30	0.750
	Habitat:Condition	2, 30	2.75	0.080
Univoltine	Habitat	1, 30	0.37	0.549
	Condition	2, 10	0.63	0.553
	Habitat:Condition	2, 30	0.05	0.954
Multivoltine	Habitat	1, 30	0.37	0.549
	Condition	2, 10	0.63	0.553
	Habitat:Condition	2, 30	0.05	0.954

Overwintering as larvae	Habitat	1, 30	0.35	0.561
	Condition	2, 10	0.82	0.468
	Habitat:Condition	2, 30	0.74	0.484
Overwintering as pupae	Habitat	1, 30	0.02	0.900
	Condition	2, 10	0.30	0.749
	Habitat:Condition	2, 30	0.06	0.941
Hostplant: grasses	Habitat	1, 30	4.40	**0.044***
	Condition	2, 10	0.31	0.743
	Habitat:Condition	2, 30	0.32	0.731
Hostplant: forbs	Habitat	1, 30	2.37	0.135
	Condition	2, 10	0.19	0.827
	Habitat:Condition	2, 30	0.70	0.504
Hostplant: trees and/or shrubs	Habitat	1, 30	0.25	0.622
	Condition	2, 10	0.08	0.929
	Habitat:Condition	2, 30	0.72	0.495
Hostplant: lichen and algae	Habitat	1, 30	0.71	0.407
	Condition	2, 10	0.32	0.731
	Habitat:Condition	2, 30	3.43	**0.046***
Habitat: woodland	Habitat	1, 30	18.35	**<0.001*****
	Condition	2, 10	0.58	0.579
	Habitat:Condition	2, 30	0.17	0.846
Habitat: heathland	Habitat	1, 30	4.73	**0.038***
	Condition	2, 10	2.31	0.150
	Habitat:Condition	2, 30	3.11	0.060
Habitat: moorland	Habitat	1, 30	3.61	0.067
	Condition	2, 10	0.86	0.452
	Habitat:Condition	2, 30	2.33	0.114
Habitat: grassland	Habitat	1, 30	0.01	0.905
	Condition	2, 10	0.01	0.991
	Habitat:Condition	2, 30	0.13	0.878
Habitat: wetland	Habitat	1, 30	3.14	0.087
	Condition	2, 10	1.06	0.383
	Habitat:Condition	2, 30	1.59	0.221
Habitat: coastal	Habitat	1, 30	11.02	**0.002****
	Condition	2, 10	0.24	0.792
	Habitat:Condition	2, 30	0.02	0.984
Habitat: upland and montane	Habitat	1, 30	0.04	0.843
	Condition	2, 10	0.16	0.859
	Habitat:Condition	2, 30	0.20	0.822

Macro-moth species in the grasslands had, on average, significantly larger forewings than those species found in the pavements (Figure 4.1a). Perhaps it was to be expected that a greater number of individuals of species whose larvae feed on grasses were indeed sampled at the grassland sites (Figure 4.1c), but interestingly, the grassland habitat also supported significantly more individuals of species typically associated with woodland habitats compared to pavements (Figure 4.1b). Limestone pavements contained more individuals of coastal (Figure 4.1d) and heathland (Figure 4.1e) macro-moth species.

A habitat:condition interaction was found for macro-moth species feeding on lichen and algae, where the CWM for that trait was slightly greater at limestone pavement sites in recovering condition than all other habitat and condition categories (Fig. 4.2). However, as the p-value was close to the significance limit (p = 0.046), none of the post hoc pairwise comparisons were significant.

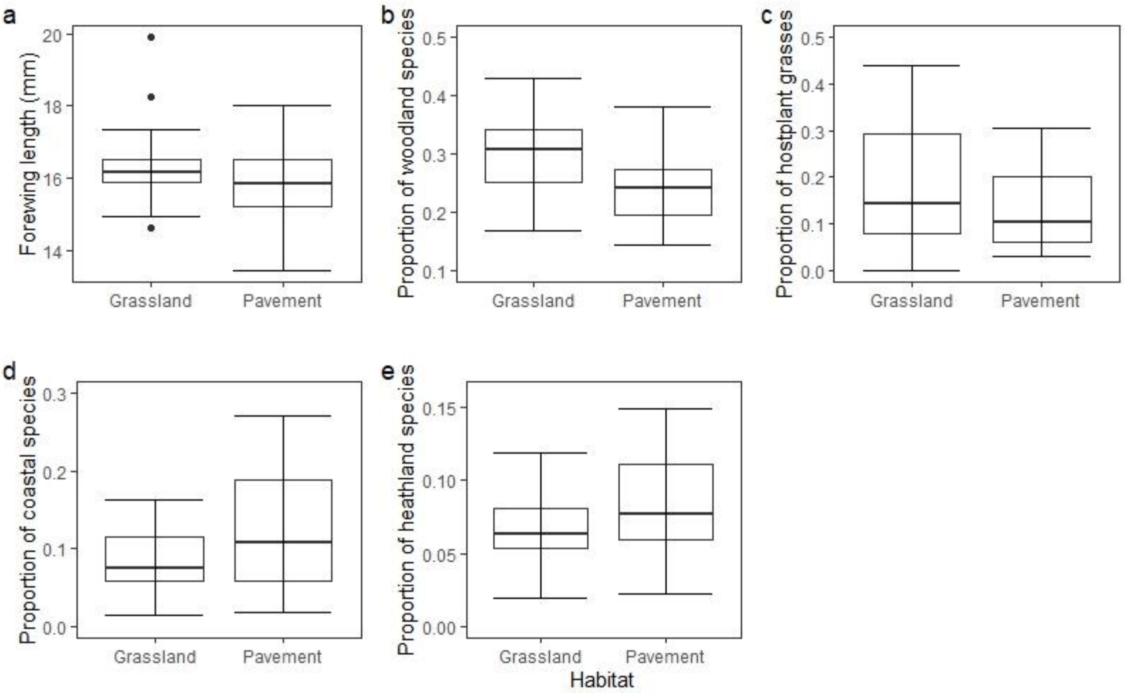


Figure 4.1. The effect of habitat type on trait CWMs. The trait CWMs of a) forewing length (mm), b) species associated with woodland, c) species whose larval hostplants are grasses, d) species associated with coastal habitats grouped by habitat type, and e) species associated with heathland. Boxplots display the median, first and third quartile and minimum and maximum values. Scales on the y-axis differ for each trait.

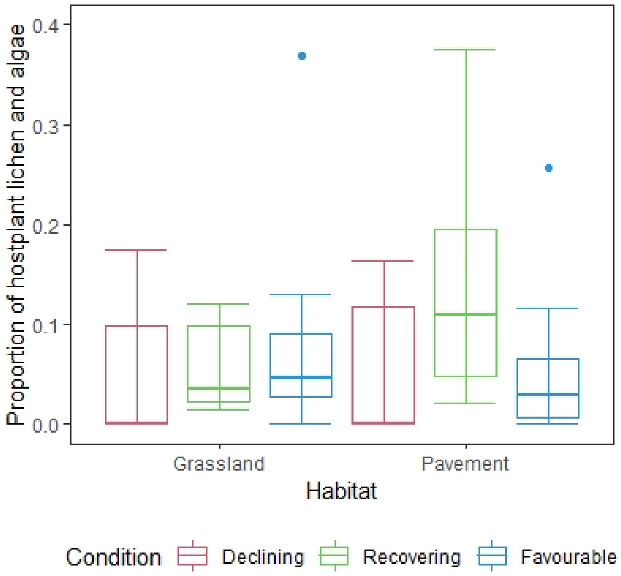


Figure 4.2. The effect of habitat type and habitat condition on the trait CWM for macro-moth species whose larval hostplant is lichen and algae. Red bars = declining condition, green bars = recovering condition, and blue bars = favourable condition. The boxplot displays the median, first and third quartile and minimum and maximum values.

The NMDS of the trait CWMs found that the composition of each of the six habitat/condition categories were not significantly different from one another (Fig. 4.3a), however, significant differences were found between the reserves and SSSI units (Table 4.3). The trait CWMs of the macro-moth community at Farleton Knott are narrowly dispersed in comparison to those at Hutton Roof, with an almost clear segregation between the two reserves. In addition, distinctive trait compositions are seen between Holme Park Fell (HPF) and Newbiggin (N) and also between Hutton Roof Commons Pavement (HRCP) and Ploverlands (P), however, extensive overlap occurs between all the SSSI units (Fig. 4.3b).

Table 4.3. The contribution of habitat and condition, unit, and reserve to the composition of trait CWMs. Significant values are in bold.

Vector	r2	p-value
Larval hostplant specificity		
Monophagous	0.65	**0.001*****
Polyphagous	0.15	0.051
Oligophagous	0.07	0.248
Motility		
Forewing length	0.96	**0.001*****
Voltinism		
Univoltine species	0.52	**0.001*****

Multivoltine species	0.52	**0.001*****
Overwintering stage		
Pupae	0.87	**0.001*****
Larvae	0.8	**0.001*****
Larval hostplant type		
Forbs	0.82	**0.001*****
Lichens and algae	0.62	**0.001*****
Trees and shrubs	0.46	**0.001*****
Grasses	0.25	**0.011***
Habitat preference		
Wetland	0.41	**0.001*****
Moorland	0.37	**0.001*****
Coastal	0.35	**0.001*****
Grassland	0.33	**0.001*****
Woodland	0.28	**0.003****
Montane/upland	0.05	0.398
Heathland	0.04	0.479
Factor		
Unit	0.65	**0.001*****
Reserve	0.23	**0.001*****
Habitat/Condition	0.02	0.539

Table 4.4. The effect of vegetation variables on the composition of trait CWMs. Significant values are in bold.

Vector	r-squared	p-value
Cover of forbs	0.25	**0.016** *
Cover of woody plants	0.15	0.066
Number of forbs in flower	0.11	0.126
Number of positive indicator plant species	0.08	0.189
Cover of grasses	0.05	0.363
Cover of bryophytes	0.04	0.477
Cover of ferns	0.04	0.466
Cover of bare ground	0.04	0.471
Total number of plant species	0.02	0.746
Number of non-indicator plant species	0.01	0.852
Number of negative indicator plant species	0.01	0.886
Vegetation height	0.01	0.876

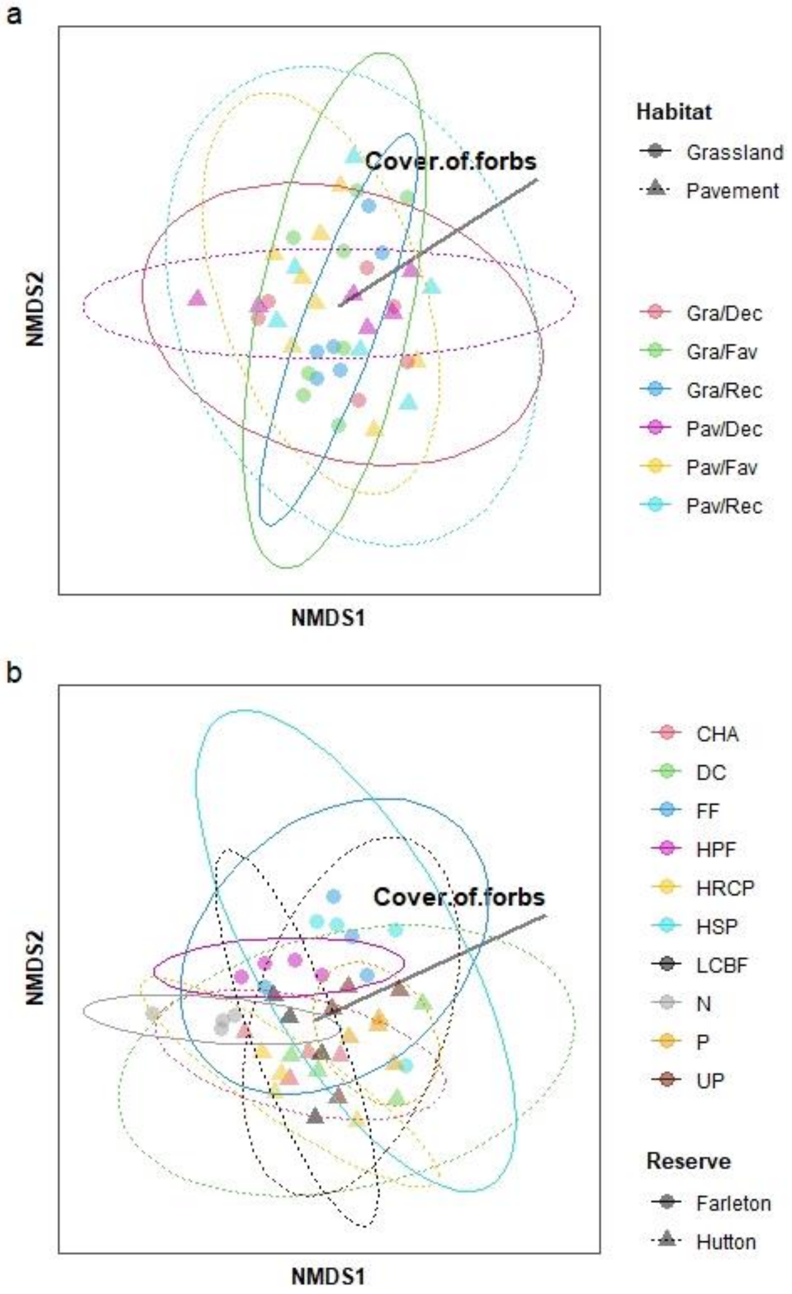


Figure 4.3. NMDS plots of the macro-moth trait CWMs (stress = 0.13) grouped by a) habitat type (Gra: Grassland, Pav: Pavement) and condition (Dec: Declining, Rec: Recovering, Fav: Favourable) and b) reserve (Farleton Knott vs. Hutton Roof) and SSSI unit (CHA: Crag House Allotment, FF: Farleton Fell, HRCP: Hutton Roof Commons Pavement, LCBF: Lancelot Clark Storth & Burton Fell, P: Ploverlands, DC: Dalton Crags, HPF: Holme Park Fell, HSP: Holme Stinted Pasture, N: Newbiggin, UP: Uberash Plain). Shapes represent a) grassland (circle) and pavement (triangle) habitat, and b) Farleton Knott (circle) and Hutton Roof (triangle) reserves. Significant environmental variables are represented as arrows (% cover of herbaceous plants). Each point represents a sample site and ellipses represent the 95% CI around the group centroid and are displayed for each of the six habitat/condition categories and ten units, with dashed and solid lines representing the habitats and reserves.

Differences in the composition of the trait CWMs were driven by the cover of forbs, with all other extrinsic variables having a non-significant effect (Table 4.4). A number of intrinsic variables were found to be statistically significant. Of the three larval hostplant specificity categories, only monophagous species made a significant contribution to the similarity on composition of trait CWMs among sampled sites. Forewing length, all levels of voltinism, both overwintering stages, and all larval hostplant categories were also statistically significant. Moth species whose larval foodplants are grasses contributed least to the trait composition similarity of the moth community with forb feeders explaining the greatest proportion of the observed predicted variation. The habitat preference categories were also significant in explaining differences in trait composition, except for species associated with of montane/upland and heathland habitats, which were the only non-significant trait CWMs for the habitat preference categories (Table 4.3).

4.4.2 Effects of vegetation variables on trait CWMs

A number of macro-moth trait CWMs were significantly related to vegetation variables (Appendix 5). The number of monophagous moth species saw a slight significant increase in response to negative indicator plant species ($F_{1, 33.068} = 4.68$, $p = 0.038$) and the cover of woody plants ($F_{1, 37.176} = 10.43$, $p = 0.003$), but significantly decreased when more non-indicator plant species were present ($F_{1, 36.289} = 7.24$, $p = 0.011$) (Fig. 4.4a, b, & c). Moreover, oligophagous moth species significantly increased in response to positive indicator plant species ($F_{1, 35.634} = 5.36$, $p = 0.026$) and the height of vegetation ($F_{1, 38.514} = 6.40$, $p = 0.016$), and negatively to non-indicator plant species ($F_{1, 38.453} = 5.21$, $p = 0.028$), however, the latter was driven by a single site (Fig. 4.4d, e & f). Conversely, positive indicator plant species ($F_{1, 37.309} = 4.86$, $p = 0.034$) and vegetation height ($F_{1, 39.422} = 4.34$, $p = 0.043$) were found to be significantly negatively correlated with polyphagous moth species. However, polyphagous species showed a positive response to the non-indicator plant species ($F_{1, 39.571} = 10.11$, $p = 0.003$) which was influenced by one particular site (Fig. 4.4g, h & i). The forewing length of the macro-moths significantly increased, albeit only slightly, in response to higher numbers of non-indicator plant species ($F_{1, 38.516} = 4.74$, $p = 0.036$) (Fig. 4.4j) and voltinism was found to be negatively affected by negative indicator plant species, whereby, they were found to negtively influence univoltine moth species ($F_{1, 33.130} = 11.62$, $p = 0.002$) (Fig. 4.4k) and a positively affect multivoltine species ($F_{1, 33.130} = 11.62$, $p = 0.002$) (Fig. 4.4l).

Additionally, moths that overwintered as larvae were found to be significantly negatively affected by higher numbers of non-indicator plant species ($F_{1, 38.227} = 4.42$, $p = 0.042$)

(Fig. 4.5a) and those that use grasses as their larval foodplants were negatively affected by a higher cover of bryophytes ($F_{1, 32.067}$ = 4.96, p = 0.003) (Fig. 4.5b). Converserly, as bryophyte cover increased, the abundance of upland and montane moth species also significantly increased ($F_{1, 36.518}$ = 5.01, p =0.031) (Fig. 4.5k). Species that feed on trees and shrubs were significantly negatively affected by higher numbers of non-indicator plant species ($F_{1, 36.015}$ = 5.65, p = 0.023) (Fig. 4.5c) and lichen and algae feeders were positively affected by the number of forbs in flower ($F_{1, 33.668}$ = 7.38, p = 0.010) (Fig. 4.5d). Both macro-moth species whose larval foodplants are lichen and algae and species associated with woodland habitats were significantly negatively affect by the cover of grass ($F_{1, 31.767}$ = 4.32, p = 0.046 and $F_{1, 31.650}$ = 7.37, p = 0.012 respectively) (Fig. 4.5e & Figure 4.5f). Conversely, the cover of grass was found to positively correlate with macro-moth species associated with coastal habitats ($F_{1, 30.960}$ = 7.32, p = 0.011) (Fig. 4.5j). Heathland macro-moth species were found to be significantly affected by the height of vegetation ($F_{1, 39.967}$ = 7.21, p = 0.010), but positively affected by the cover of woody plants ($F_{1, 38.737}$ = 8.75, p = 0.005) and grass ($F_{1, 36.002}$ = 6.94, p = 0.012) (Fig. 4.5g, h & i).

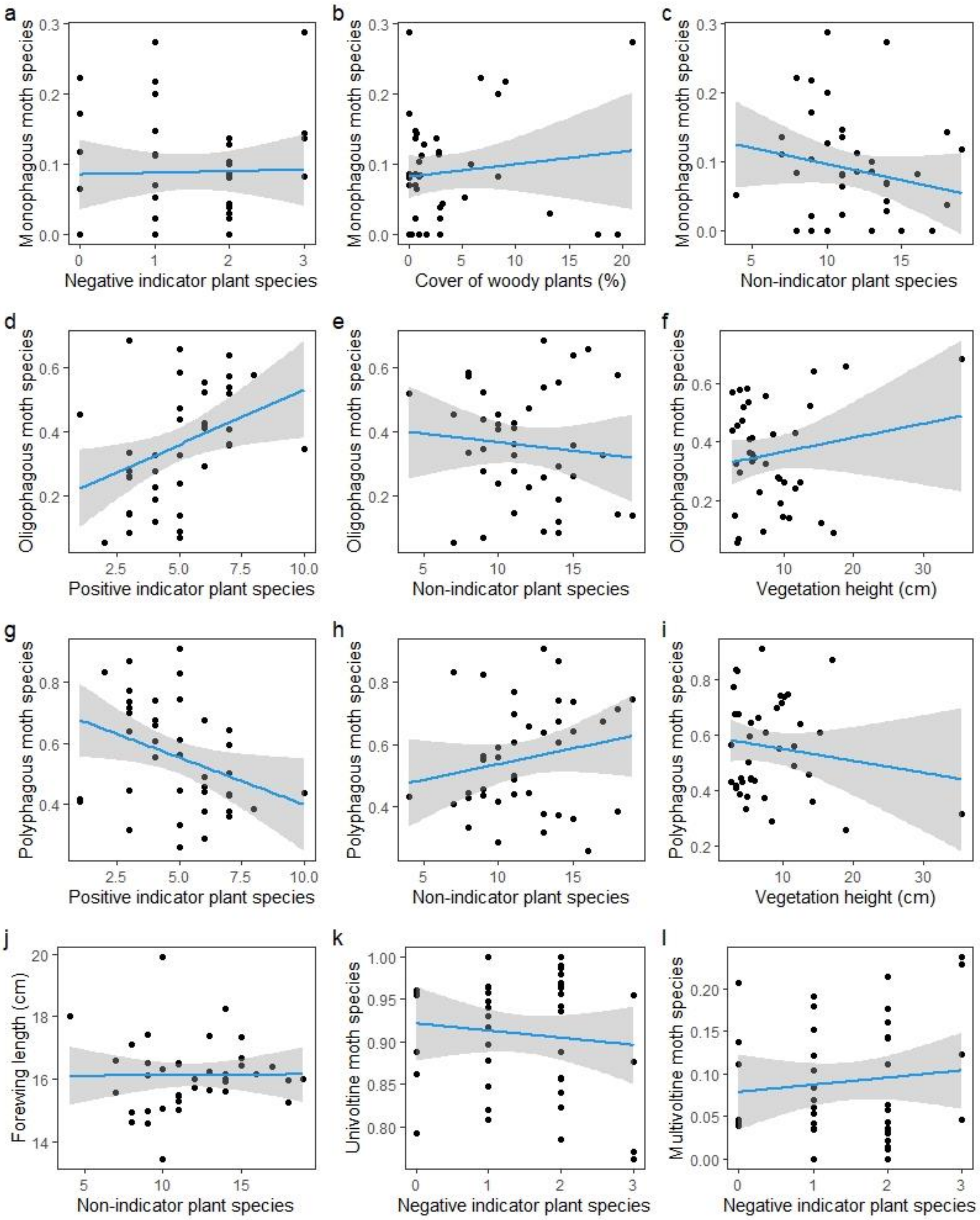


Figure 4.4. The effect of components of vegetation on macro-moth trait CWMs. The predicted effects of a) negative indicator plant species, b) the cover of woody plants, and c) non-indicator plant species on monophagous moth species, d) positive indicator plant species, e) non-indicator plant species, and f) vegetation height on oligophagous moth species, g) positive indicator plant species, h) non-indicator plant species, and i) vegetation height on polyphagous moth species, j) non-indicator plant species on forewing length, k) negative indicator plant species on univoltine moth species and l) negative indicator plant species on multivoltine moth species with 95% confidence intervals. Scales on the y-axis differ between variables.

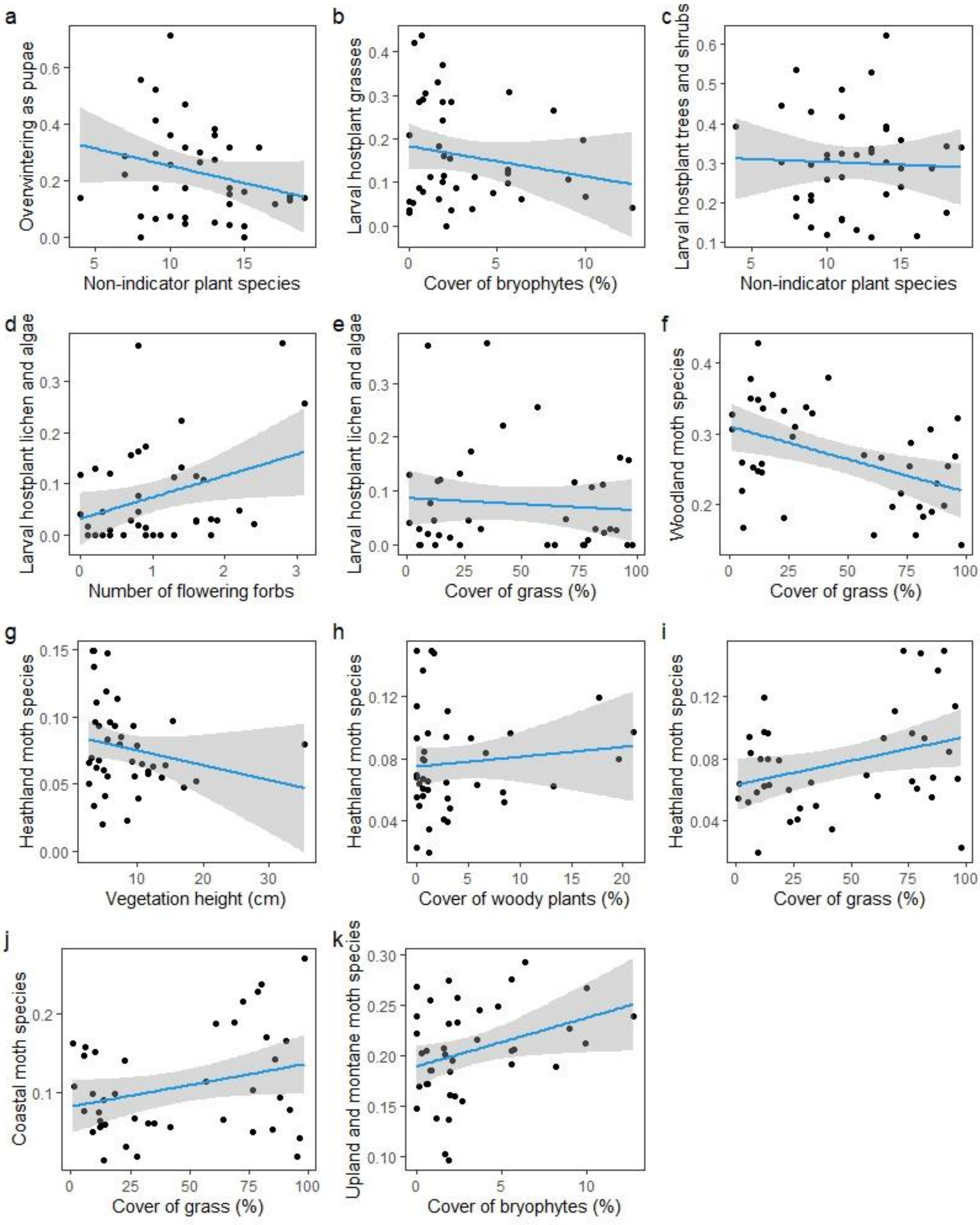


Figure 4.5. The effect of components of vegetation on macro-moth trait CWMs. The predicted effects of a) non-indicator plant species on moths that overwinter as pupae, b) the cover of bryophytes on moth species whose larval hostplants are grasses, c) non-indicator plant species, d) the number of flowering forbs, and e) the cover of grass on moth species whose larval hostplants are lichen and algae, f) cover of grass on woodland moth species, g) vegetation height, and h) the cover of woody plants on heathland moth species, i) the cover of grass on woodland moth species, j) cover of grass on coastal moth species and k) the cover of bryophytes on upland and montane moth species with 95% confidence intervals. Scales on the y-axis differ between variables.

4.4.3 Effects of habitat, condition, and vegetation variables on functional diversity

As with the trait analyses, habitat and condition also had little influence on functional diversity metrics (Table 4.4), with non-significant effects of habitat type, condition or their interaction observed for any of the five FD indices (Fig. 4.6).

Additionally, functional diversity was found to be explained by a small number of vegetation variables (Table 4.5). The cover of grass had a significant positive effect on functional richness (Fig. 4.7a), whilst non-indicator plant species had a significant negative effect on the functional dissimilarity of the macro-moth community (Fig. 4.7b). All other vegetation variables did not have a significant effect on any of the five measures of functional diversity.

Table 4.5. LMM output for the effect of habitat type and habitat condition on each of the functional diversity measures. Unit was the random effect for each model. Df estimated by Satterthwaite's method.

Response variable	Fixed Effect	df	F-value	p-value
FRic	Habitat	1, 40	1.54	0.221
	Condition	2, 40	1.56	0.223
	Habitat:Condition	2, 40	0.21	0.810
FEve	Habitat	1, 40	1.95	0.170
	Condition	2, 40	2.88	0.068
	Habitat:Condition	2, 40	0.50	0.613
FDiv	Habitat	1, 30	1.31	0.262
	Condition	2, 10	0.42	0.670
	Habitat:Condition	2, 30	1.51	0.238
FDis	Habitat	1, 30	0.01	0.932
	Condition	2, 10	0.14	0.875
	Habitat:Condition	2, 30	0.32	0.730
RaoQ	Habitat	1, 30	0.00	0.993
	Condition	2, 10	0.05	0.954
	Habitat:Condition	2, 30	0.96	0.908

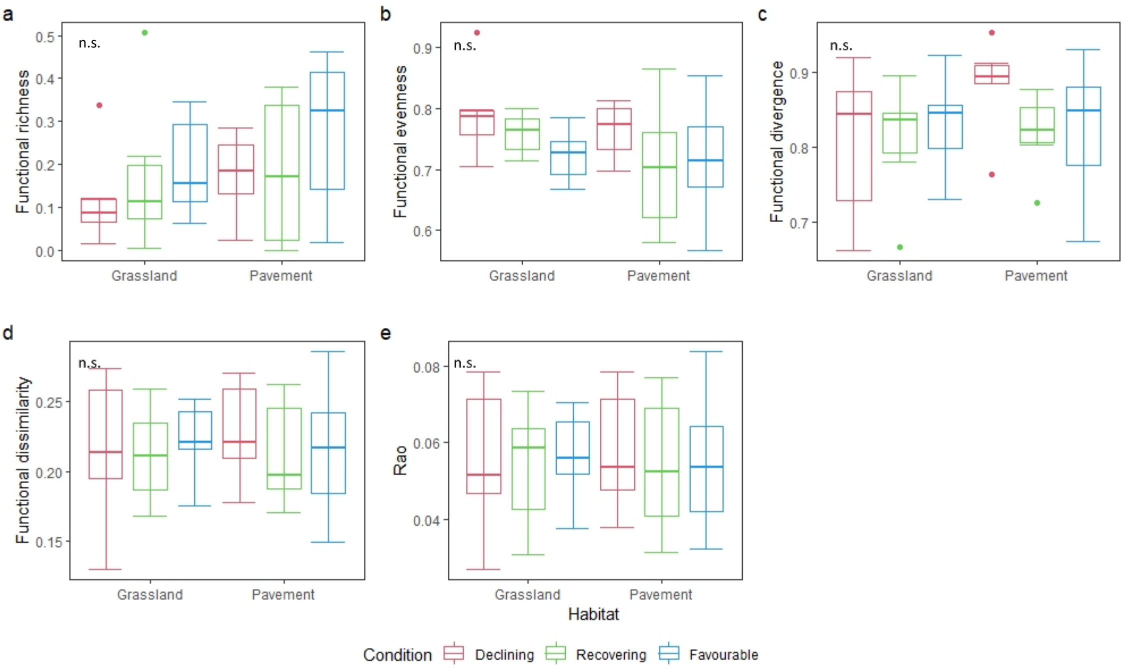


Figure 4.6 The effect of habitat type and habitat condition on five functional diversity metrics: a) functional richness, b) functional evenness, c) functional divergence, d) functional dissimilarity, and e) Rao for the grassland and pavement habitats. Red bars = declining condition, green bars = recovering condition, and blue bars = favourable condition and the non-significant effects are denoted by “n.s”. Red bars = declining condition, green bars = recovering condition, and blue bars = favourable condition. Boxplots display the median, first and third quartile and minimum and maximum values. Scales on the y-axis differ between the FD indices.

Table 4.6. LMM output for the effect of vegetation variables on moth functional diversity measures with unit as the random effect and df were estimated by Satterthwaite’s method. Significant values are in bold.

Vector	Fixed Effect	df	F-value	p-value
FRic	Negative indicator plant species	1, 38.615	1.73	0.196
	Positive indicator plant species	1, 39.165	0.01	0.932
	Non-indicator plant species	1, 39.988	1.18	0.284
	Flowering herbaceous plant species	1, 35.603	0.15	0.701
	Vegetation height	1, 39.865	0.00	0.994
	Cover of woody plants	1, 39.283	0.77	0.387
	Cover of bryophytes	1, 33.342	3.46	0.072
	Cover of ferns	1, 32.553	0.73	0.398
	Cover of grass	1, 32.455	4.74	**0.037***
FEve	Negative indicator plant species	1, 40	0.63	0.431
	Positive indicator plant species	1, 40	0.38	0.540
	Non-indicator plant species	1, 40	1.75	0.193
	Flowering herbaceous plant species	1, 40	0.33	0.571
	Vegetation height	1, 40	1.55	0.220
	Cover of woody plants	1, 40	0.49	0.488

	Cover of bryophytes	1, 40	0.97	0.331
	Cover of ferns	1, 40	2.93	0.095
	Cover of forbs	1, 40	2.34	0.134
FDiv	Negative indicator plant species	1, 39.888	2.35	0.133
	Positive indicator plant species	1, 39.977	4.00	0.052
	Non-indicator plant species	1, 39.826	3.92	0.055
	Flowering herbaceous plant species	1, 38.516	0.01	0.924
	Vegetation height	1, 39.968	1.56	0.219
	Cover of woody plants	1, 38.981	0.12	0.733
	Cover of bryophytes	1, 37.068	0.69	0.413
	Cover of ferns	1, 36.231	0.56	0.460
	Cover of grass	1. 36.147	0.51	0.482
FDis	Negative indicator plant species	1, 37.378	1.90	0.177
	Positive indicator plant species	1, 37.573	0.58	0.452
	Non-indicator plant species	1, 39.799	4.41	**0.042***
	Flowering herbaceous plant species	1, 33.789	0.74	0.395
	Vegetation height	1, 39.516	0.23	0.637
	Cover of woody plants	1, 39.982	2.38	0.130
	Cover of bryophytes	1, 33.971	0.01	0.927
	Cover of ferns	1, 33.895	0.66	0.421
	Cover of forbs	1, 37.078	3.67	0.063
RaoQ	Negative indicator plant species	1, 36.266	2.55	0.112
	Positive indicator plant species	1, 36.687	0.11	0.747
	Non-indicator plant species	1, 39.247	3.56	0.067
	Flowering herbaceous plant species	1, 34.321	0.19	0.663
	Vegetation height	1, 39.154	0.33	0.568
	Cover of woody plants	1, 39.821	3.57	0.066
	Cover of bryophytes	1, 32.767	0.12	0.734
	Cover of ferns	1, 32.623	0.02	0.903
	Cover of grass	1, 32.514	0.53	0.471

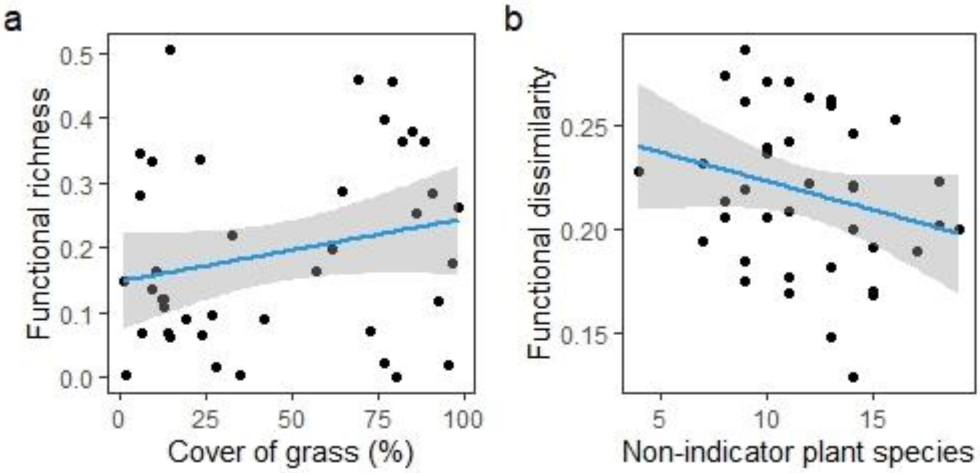


Figure 4.7. The effect of components of vegetation on the macro-moth trait CWMs. The predicted effects a) functional diversity and b) functional dissimilarity with 95% confidence intervals are displayed. Scales on the y-axis differ between variables.

4.5 Discussion

The aim of this study was to assess how the trait composition and functional diversity of the macro-moth community differed between limestone pavement and calcareous grassland habitats and their condition. Trait composition was found to be similar between the habitat and condition categories, whereas significant differences lay between the SSSI units and reserves. Traits displayed an even spread between the SSSI units, however, greater distinctiveness was observed between the units Holme Park Fell and Newbiggin and also between Hutton Roof Commons Pavement and Ploverlands. The overall composition of the habitats at these units, as observed on the ground, do show dissimilarities and therefore, may go some way to explain the differences found in the analysis. The functional composition of plants changes in response to habitat management and grazing, promoting higher levels of species richness (Garrido *et al*., 2019), which could explain some of these observed differences. In fact, analysis found that the composition of traits was driven by the cover of forbs. When considered alongside the significant difference in trait composition between the two reserves, it may be that the differences in vegetation in response to condition are influencing species occupancy at the two reserves. It is clear that between Hutton Roof and Farleton Knott, the composition of the vegetation differs at the landscape level. Observations made during sampling showed Farleton Knott to be more open in nature and overall, more floristically diverse than Hutton Roof and this is supported in the SSSI citations for both reserves (Natural England, 1988; Natural England, 1988). This difference is recognised by Natural England and it is clearly stated within the guidance on the definitions of favourable condition that the sum of designated features is much less than the extent of the SSSI of Hutton Roof (Craven, 2013). Assessments are detailed and plant community assemblages well defined, but they do not consider habitat surrounding the designated feature, and it is these areas that may be contributing to the differences in moth trait composition observed between the reserves. Furthermore, despite the stringency, not all aspects of the vegetation influential to the composition of moth traits are covered in the assessments.

Surprisingly, little weight is given to lichens, algae, and bryophytes as part of the vegetation assemblages for the designated features of calcareous grassland and limestone pavement. As already explored in Chapter 3, bryophytes have been found to play a crucial role in the development of higher plants in limestone habitats (Sand-Jensen & Hammer, 2012), are known to be favoured by the butterfly *F. adippe* for egg laying in this habitat (Warren, 1995), and are susceptible to the negative effects of climatic perturbations (Nelson *et al*., 2022). Analysis also found the cover of bryophytes to favour upland and montane macro-moth species. Lichen and algae feeders were also influenced by a number of components of the vegetation structure. A habitat:condition interaction was found, with significantly more lichen and algae feeders being sampled at the limestone pavement habitat in recovering condition compared to all other categories. Why more lichen and algae feeding species would be found at pavement sites in recovering condition compared to pavements in declining or favourable condition is unknown, but it is likely to be due to chance as the differences in vegetation structure between condition categories for this habitat type are negligible. It is possible that sampling at a recovering unit coincided with the mass emergence of footmen moth species, all of which utilise lichens and algae as larvae. However, this study provides evidence that supports the important role lichens, algae and bryophytes play within the macro-moth community here.

Even if a SSSI unit met the criteria for favourable condition, it does not necessarily mean the surrounding area will be favourable also. The advancing stages of succession at Hutton Roof has likely contributed to the shift in trait composition of the macro-moth community identified here. There is evidence to support the theory that moth community composition shifts mirror succession. Allowing the transition from grassland to intermediate successional stages results in a significant loss of grassland habitat specialists (Habel *et al*., 2019). This also supports the findings of the present study, whereby, variation in the abundance of species that feed on trees and shrubs accounted for a much larger component of the trait variation in the moth community than the species that feed on grasses. A marginal significance for woody plants contributing to the trait composition of the moth community was also found, supporting the idea that woody encroachment is an important driver of the trait composition of macro-moths. Perhaps it was therefore unsurprising that non-indicator plant species (a measure of herbaceous plant diversity here) was negatively related to the presence of species that utilise trees and shrubs as larval foodplants. Any macro-moth species that persist in the pockets of grassland either side of the barrier of scrub on the plateau of Hutton Roof, may be at risk of the negative effects of isolation from habitat fragmentation and reduced patch size, particularly for highly specialised species (Öckinger *et al*., 2011; Slancarova *et al*., 2016; Habel *et al.,* 2018). The matrix between semi-natural habitats is key in sustaining Lepidoptera populations (Warren & Bourn., 2010).

As to be expected, significantly more macro-moth species whose larval foodplant included grasses were sampled at the grassland habitat. However, the unexpected finding was that significantly more woodland species were sampled in the grassland habitat than in the pavement. This is consistent with findings of land abandonment studies where the encroachment of woodland into grassland is driving this shift toward species with a preference for woodland habitats (Ubach *et al*., 2020; Mora *et al*., 2021). The development of vegetation on pavements is slower and may explain the difference found between the two habitat types. The detection of a significant number of woodland macro-moth species in what should be open grassland highlights the threat of encroachment and succession to grassland habitats. Vegetation encroachment only occurs as a result of insufficient levels of management intervention and is a major threat to the Lepidopteran diversity of grasslands (Balmer & Erhardt, 2000). Analysis also found that the abundance of species typically associated with woodland habitats decreased significantly as grass cover increased at a site, which further supports the suggestion that the trait composition of the moth community present in the studied grassland habitat may have shifted in response to the encroachment of woody species. The traits of moth species in Europe have been found to be strongly differentiated by habitat type, particularly species that feed on trees and shrubs and forbs (Potocký *et al*., 2018). Furthermore, the study noted that moth traits did not follow the same response as butterflies, suggesting that the traits of the two groups respond differently to their environment, highlighting the problems for using butterflies as indicators of habitat quality for other Lepidopterans. Additionally, a significant habitat effect for coastal and heathland species was found, whereby, more species associated with these habitats were sampled at the pavement. Heathland species showed a mixed response to the composition of the vegetation, with significantly lower abundance being sampled where the vegetation was taller, but the presence of woody plant species and grasses favoured them. Therefore, a matrix of woody vegetation of intermediate height, along with grasses, are favoured by heathland macro-moth species, which highlights the complexities in provisioning for as many species as possible. The cover of grass was also found to be important for coastal species, but significantly more coastal species were sampled at the pavement habitat. Little grass grows across much of the limestone pavement and it is often restricted to within the grikes. However, grass does occur extensively in areas of broken pavement within the matrix. Some areas of limestone pavement are extremely weathered, allowing much more grass to become established within the pavement, which may be contributing to the habitat preference seen for this group.

Several of the traits significantly contributed to the structure of the macro-moth community. The macro-moth community is predominantly comprised of species that show preference for wetland, moorland, coastal, woodland and grassland habitats. Hutton Roof and Farleton Knott are limestone outcrops of an intermediate altitudinal position, thus extremely water deficient, and yet wetland habitat species made a significant contribution to the composition of traits. Whilst a surprising outcome, many of the macro-moth species can occur in a wide range of habitats, with very few showing fidelity to one particular habitat type, coupled with the fact that habitat categories have been grouped together by similarity to simplify analyses and interpretation. However, NMDS does not account for differences in abundance between habitat types and in fact, a marginal significance was found whereby, wetland macro-moth species were more abundant at the limestone pavement than at the grassland habitat. Why the pavement habitat would support more wetland macro-moth species than the grassland habitat is unclear, but it may be that transiently wet areas occur within the habitat, particularly within the deeper grikes. Additionally, macro-moth species associated with wet woodland may utilise emergent woodland at the two reserves, as a wide range of polyphagous macro-moth species feed on trees and shrubs (Crafter, 2005). The rank grasses noted at some of the SSSI units in declining condition may also be a suitable surrogate for macro-moth species that feed on grass species associated with wetlands in the face of the preferred habitat being unavailable. Grassland moth species have been found to have significantly increased in abundance and distribution in the UK which is suggested to be driven by climate change favouring an extended growth season for grasses in autumn/winter (Fox *et al*., 2021). Similar trends have also been observed for other grassland Lepidoptera species. Butterflies such as Ringlet have significantly expanded their range and abundance, particularly since the early 2000s (Fox *et al*., 2015). *The State of Britain's Larger Moths Report* (Fox *et al*., 2021) found that the distribution of grassland and woodland species had significantly increased (12% and 8% respectively), whilst moorland species had experienced a significant decrease (13%) in range over the same period. Species associated with all other broad habitat types had either seen increases or no change during the same period.

The macro-moth community has been identified as being dominated by ubiquitous species, but it is also extremely polyphagous. 64% of species were polyphagous compared to just 7% of macro-moths sampled being monophagous. Species with broad habitat and larval hostplant requirements are able to utilise a greater proportion of available resources, whereas habitat specialists generally have a narrower foodplant breadth. Polyphagous moth species showed a significant positive response to higher numbers of non-indicator plant species, whilst those species with the narrowest feeding specificity were significantly negatively affected. Conversely, positive indicator plant species had a significant positive effect on oligophagous moth species and a negative effect on polyphagous moth species. Many of the oligophagous species were particularly abundant and included species such as *Epirrhoe galiata* and *Coenotephria salicata*, both of which feed on *Galium* species, accounting for 16% of all moths sampled. *Galium sterneri* and *Asperula cynanchica*, both species on the list of positive indicators for both reserves, grow in profusion throughout much of the grassland and pavement. However, they were much less abundant at grasslands where the vegetation was taller.

Despite the small proportion of monophagous moth species compared to polyphagous species, monophagy was the only feeding specificity trait to make a significant contribution to the macro-moth community composition variation. Whilst the number of macro-moth species with restricted feeding requirements was relatively low, one species, *Eupithecia distinctaria,* whose larvae feed solely on *Thymus drucei*, was particularly abundant at both reserves, occurring at over half of the sampling sites and accounted for 5% of all moths sampled. However, not all monophagous species are habitat specialists just as not all polyphagous species are habitat generalists, but the majority do fall within these generalisations. Monophagous and oligophagous butterfly species have been found to be associated with stable environments and undisturbed habitats (Börschig *et al*., 2013), whilst moth communities of degraded, highly fragmented, and high land use intensity habitats show a shift toward polyphagy and generalist traits typical of reduced specialisation (Mangles *et al*., 2017; Merckx *et al*., 2019). Dependence on a single plant species imposes restrictions to well-connected habitat patches that can support larger quantities of the food source and so these species are less likely to use the surrounding matrix than habitat generalists (Brotons *et al*., 2003).

Forewing length was found to be significantly longer at the grassland habitat, which may favour the more mobile species of Lepidoptera due to the distance between resources (Merckx *et al*., 2019). However, forewing length did not differ between the habitat condition categories with similar results being found for moths in response to varying land use intensities of grasslands in Europe (Mangles *et al*., 2017). What is of concern here is that macro-moths with a longer forewing length are more likely to be in decline than those with a smaller forewing length. This was found to be consistent across habitats, which is contradictory to the findings in this study (Coulthard *et al*., 2019; Blumgart, 2021). Why this is the case is not fully understood, but it may be that the macro-moth species associated with the limestone pavement habitat will be less susceptible to decline, potentially as a result of greater resource stability through slower successional processes. Moth species with longer forewings have higher migration and colonisation abilities, which is associated with the ability to exploit a wider range of resources, and as a result may be better able to disperse (Dennis *et al*., 2012; Merckx *et al*., 2019).

It is well known that smaller, more sedentary species of butterfly such as Duke of Burgundy are more vulnerable to decline than those that are larger (Asher *et al*., 2010; Hayes *et al.,* 2018), thus providing additional evidence that butterflies do not make suitable surrogates for moth species as indicators of habitat quality. In addition, forewing length reflects dispersal ability which is important for gene flow, the colonisation of new sites and population dynamics (Olden *et al*., 2004).

Results from the analyses show that the estimated measures of functional diversity do not significantly differ between the grassland and pavement habitat types and habitat condition categories. It is not unusual for functional diversity to be similar across heterogenous landscapes (Perović *et al*., 2015), however, it has been found to differ between habitat types and land use intensities for moths (Uhl *et al*., 2021) and other taxonomic groups (Forrest *et al*., 2015). Moreover, vegetation structure and land use has been shown to define the functional diversity of butterflies (Aguirre-Gutiérrez *et al*., 2017). In fact, this study identified a similar response to vegetation structure, whereby the cover of grass significantly increased functional richness. Condition was found to have a marginally significant effect on functional evenness with higher values at limestone pavements in recovering and favourable condition compared with other habitats and conditions, suggesting that the abundance of traits may be more evenly distributed on pavement than in grassland, which may be a positive signal of greater ecosystem stability at this habitat (Mason *et al.,* 2005; Mason *et al*., 2013).

4.6 Conclusion

The trait composition and functional diversity of the macro-moth community of Farleton Knott and Hutton Roof SSSIs do not follow the condition status determined by NE, nor do they differ between habitat type. Vegetation was found to have a greater influence on traits than habitat type or habitat condition. However, there was variation in trait composition at the landscape level, between the SSSI units and reserves. Identifying areas with significant deviances in trait composition will be useful in providing a focus for future conservation efforts. Differences in the macro-moth trait profiles between the two reserves mirror successional stages, with woodland moth species forming a significant component of the grassland habitat. Similar findings from grassland abandonment studies in Europe highlights a serious threat to this specialised moth community (Ubach *et al*., 2020; Mora *et al*., 2021), suggesting that a focus on vegetation and plant species presence/absence during condition assessments by NE are not sufficient at detecting shifts in community composition within higher taxonomic groups. The macro-moth community is comprised of mostly ubiquitous, polyphagous species, but habitat specialists can also be abundant and make a significant contribution to the trait composition of the macro-moth community. As high levels of plant diversity are essential for maintaining the trait composition of the macro-moth community, an increase in management will be essential to maintain and potentially increase openness at both sites. This study further highlights the knowledge gaps around the insect communities of limestone pavements and the findings should prompt the assessment of additional vegetation components such as bryophytes.

Chapter 5

General Discussion

5.1 Thesis overview

This is the first multi-species study of nocturnal Lepidoptera of an area of limestone pavement and grassland in NW England, and the first known sampling effort of the limestone pavement habitat in the UK, despite limestone pavements being one of the rarest habitats globally (JNCC, 2021). Lack of study, in part, is due to inaccessibility of these remote locations, which can make it challenging to carry out sampling, but with advances in the equipment used to survey nocturnal moths, these challenges can be surmounted. Although the vegetation of SSSIs is comprehensively assessed, this is restricted to the designated features only. Despite the extensive and detailed nature of condition assessments that incorporate vegetation, the findings of this study highlight the limitations this approach has in detecting changes in moth communities.

The main focus of this study was to assess how the moth communities of Hutton Roof and Farleton Knott responded to habitat type and habitat condition. The findings presented in this thesis provide evidence that limestone pavements have the propensity to support similar levels of moth diversity as calcareous grasslands, and that the condition of these habitats, as currently assessed, does not adversely affect moth species richness or composition. Similarly, there was little association between habitat type and habitat condition for functional diversity measures, a finding which contrasts with evidence from previous studies (Aguirre-Gutiérrez *et al*., 2017). A key finding of this study is that there were significant differences in the community composition and trait composition between SSSI units and at the landscape level, between the reserves, which are being driven by the cover of forbs. Woody plants were also influential to the trait composition of the macro-moth community. There were clear differences in vegetation structure between the habitats – the grassland can be rich in forbs if it is in good condition and the pavements support a range of flora but favour taller, woody vegetation potentially due to the inaccessibility to livestock. As significant differences were found in the vegetation structure between the two habitat types, but no difference in species richness, functional richness, or trait composition, then it is likely that factors outside these areas, that have not been measured in this study, are influencing the observed segregation between the two reserves, which is most likely to be due to the homogenisation of the habitats. When considering these results in the context of observations made on the ground, it is likely that the habitat surrounding the grassland at Hutton Roof is influencing the differences in species and trait compositions at the two reserves as vegetation sampling identified clear differences in the plant community composition between the two habitats. In support of the idea that the moth communities are being influenced by the habitat surrounding the designated features, significantly more woodland moth species were sampled at the grassland habitat despite pavements hosting the taller, woody plant community. Moth community composition has been found to shift with succession from open grassland to woodland, with species richness oftentimes increasing during the short term, but reducing in the long term, with a loss of specialist species and an overall reduction in species richness with the homogenisation of habitats (Pöyry *et al*., 2004; Ubach *et al*., 2020; Mora *et al*., 2021). Monitoring the moth communities going forward will help with identifying shifts, allowing for mitigation and prevention of future loss.

Calcareous grasslands are florally diverse and have been found to support up to 40 plant species per m^2 (Willems *et al*., 1993). As forbs form an integral part of these grasslands, Natural England suggest the sward at Hutton Roof and Farleton Knott should contain between 30 – 90% forbs, with any areas falling outside of this target likely to be a product of eutrophication and insufficient biomass removal, both of which favour grasses (Craven, 2013). "Floweriness", or the percentage of sward that is likely to flower, is also taken into consideration during condition assessments. In this study, the number of forb species in flower were counted. Nectar and pollen are vital resources for many invertebrates, and whilst most plant and pollinator interactions are generalised, flower diversity and the number of visitors to flowers have been shown to be highly correlated (Fründ *et al*., 2010). Both the cover of forbs (herbaceous plants excluding graminoids) and the number of forbs in flower were significantly higher at grassland sites than at pavements. However, both were significantly higher at grasslands in recovering and favourable condition compared to those in decline. Forbs play a key role as the main driver of the moth community composition and trait composition of the macro-moths. As to be expected, the grassland habitat supported a significantly greater cover of grass than the pavement habitat, but species richness was also found to significantly decrease with the cover of grass. An increase in grass cover in semi-natural grasslands has been linked to decreased abundances of specialist species of Lepidoptera (Ellis *et al*., 2019). Whilst non-significant, the grasslands in declining condition were the ones with a greater cover of grass than forbs and so the findings presented here may be suggestive of negative change.

The fact that the condition has also been found to have a limited influence on these habitats supports the idea that another factor, not directly measured in the study, is significantly influencing the observed differences in moth communities. Hutton Roof hosts a higher percentage of woodland and scrub than Farleton Knott and it is this that is likely to be the main factor involved in what we see. This study has inadvertently identified that current conservation management plans are likely not to be going far enough to conserve the designated features at some of the SSSI units. Conservation is expensive, particularly so for priority habitats, often requiring a highly skilled and experienced workforce to lead the work (Armsworth *et al*., 2011), but funding priorities need to be directed toward biodiversity hotspots (Warren & Bourne, 2010).

This study also has identified that bryophytes play a role in moth community composition, being found to have a significant positive effect on the number of upland and montane species, rarefied moth species richness and Simpson diversity. Similarly, lichens and algae are an important larval hostplant group for a number of macro-moth species and the limestone pavement has been identified as supporting significantly more of both than the grassland habitat. However, neither group are considered in the assessment of SSSI condition, despite the potentially crucial ecosystem role they are playing, particularly at the limestone pavement habitat. Their potential as a medium for moths to pupate in could be highly important in the limestone pavement habitat. Pupae can desiccate if moisture levels are not maintained during this life-history stage and bryophytes have the propensity to cater for this need in water-limited environments (Sand-Jenson & Hammer, 2012). In addition, lichen, algae, and bryophytes form the foundations for higher plants to develop.

It was found that the levels of moth diversity to be similar between the pavement and grassland, but it should be remembered that sampling provided only a snapshot of the moth community during peak flight period for the majority of species. How the dynamics between the two habitats would change either side of the period of peak productivity is unknown and would be worthwhile investigating. Larval foodplant availability will likely influence this. We can hypothesise, based on the plant assemblages of either habitat, that grassland moth species will be restricted in line with the availability of forbs and grasses outside of the main growing period during spring and summer. Pavements on the other hand support more woody plant species, even at Farleton Knott where the pavements are much more open, and so it may be able to support more imago that are on the wing either side of this peak period. Spring is an extremely productive time of year in woodlands. Whilst this is only speculation it is entirely feasible that pavements may indeed have the propensity to support more moth species overall.

The value of limestone pavement for invertebrates is purported by Natural England to be higher where the scrub and woody vegetation on the limestone pavement are greater as they are said to improve the structural variety of the pavement and increases vegetation edge (Craven, 2013). However, the only record of systematic sampling of the invertebrate communities is provided by a study conducted by Liverpool Museum (Knight, 2003) across a restricted area at Hutton Roof over a short timeframe and so the evidence base underlying this assertation is limited. This study found that the pavement habitat supported taller, woody vegetation, but neither the species richness or functional diversity of moths differed in response to this, nor did they differ in response to condition. However, the macro-moth trait composition suggests that succession has advanced and is influencing the moth species composition, despite vegetation assessments not detecting a change. Barriers to achieving favourable condition do exist and must be identified and acted on, which includes the appropriate consideration and management of areas surrounding the grassland and pavement features. Natural England need to work with landowners, the local parish council, and other local groups in order to bring the reserves more-widely into favourable condition. Prevention is better than cure as is evident across the neighbouring Arnside and Silverdale AONB, whereby, sharp declines of some species of butterfly have prompted large-scale management interventions after inadequate levels were maintained during the 1990s and early 2000s, with succession being left to take hold during this period.

Whilst the levels of moth species richness and functional diversity were found to be similar between the limestone pavement and calcareous grassland habitats, what is still unknown, is how diverse they are compared to contiguous habitats. The diversity of the plant communities of Hutton Roof and Farleton Knott have been extensively studied and are ranked by their floristic diversity at a national scale, with baseline expectations having been rigorously developed in order to assess them (Ward & Evans, 1976). This simply does not exist for moths or any other taxa. It could be argued that using groups such as moths would be impractical as most are nocturnal, look morphologically similar, or are too small. It is unquestionable that the immobility of plants make them easier subjects to study, but their identification to species level can be just as difficult, if not more so, than moths. Some plant families are also extremely difficult to identify (e.g., there are over 250 *Hieracium* agg. microspecies) (BSBI, 2022). Moreover, a site with high levels of plant diversity does not mean similarly high levels of moth species richness should be expected, just as high levels of species diversity does not always translate into concomitant levels of functional diversity (Aguirre-Gutiérrez *et al*., 2017). Strategic sampling of the moth communities across the Morecambe Bay limestone series and further afield to areas such as Great Asby and Ingleborough would be essential in forming that foundation upon which future monitoring and conservation efforts for the moths of limestone habitats will be built on. Whilst there is a wealth of moth data available in the UK with over 100 fixed RIS light traps and over 24 million records in the NMRS database alone (Fox *et al*., 2021), data collected from fixed RIS light traps and NMRS do not go far enough to target populations and communities of moth species in threatened habitats. Are these data representative of the habitats such as those of Hutton Roof and Farleton Knott? Whilst they do provide general trends at a national level, the data are not representative of sites at a finer scale. The number of new species found for two Counties in a short amount of time and the abundances of some very restricted moth species informs us of how little we still know.

Light traps are the traditional method used to sample nocturnal moth communities, however, alternative methods could provide complementary data on a different suit of moth species and life history stages. It is well known that moths are strongly attracted to ultraviolet light sources (Brehm *et al*., 2021), however, this varies between families (Somers-Yeates *et al*., 2013; Merckx *et al*., 2014). Additionally, many micro-moth species seldom come to light despite being more numerous than macro-moths and are more frequently day-fliers (Sterling & Parsons, 2012). It is purported that day flying moth species tend to have a specialist diet breadth as the concentration of volatile organic compounds (VOCs) produced by plants are greater during the day than at night, whilst nocturnal moth species are most often generalists as VOCs are much reduced due to lower temperatures (Lin *et al*., 2022). It would be beneficial to collect additional data to better assess resource use within the habitats; the sampling methods approached in this study are the most efficient at capturing community diversity as fewer than 10% of moth species in the UK are diurnal. In addition, finding the early life history stage in the field is a labour-intensive task and requires extensive larval foodplant knowledge.

Prior to this study, many of the existing moth records for the recording area that covers Hutton Roof and Farleton Knott come from the land surrounding the reserves, mostly from gardens. Many of Reverend Vine Hall's moth records originate from the vicarage in Hutton Roof village and yet they are incorporated into reports linked to the reserve. Much of these data are from the 1950s and 1960s, with many moth species having undergone considerable change in abundance and distribution in that time and so, whilst they still hold historic value, they do not represent the current state of the two reserves. Our understanding of moths has also changed since that time, and the identifications made then may not be accurate. This study provides an additional and up to date record of the moth communities at the reserves.

It is unfortunate that data collected throughout August could not be included in the analyses. Five traps failed during the third round of sampling from the 40 in total due to a number of issues including battery failure and corrosion of the trap wiring. Despite multiple repairs and replacements, the poor weather that dominated a large proportion of the month meant there was no time to revisit during the period permission was allowed. Whilst the addition of new species began to tail off in August, a number of grassland specialists and second generations were just beginning to emerge. Species such as *Coenotephria saliciata*, the most dominant species from sampling, accounting for over 20% of all moths caught, was far more abundant during the second generation with over 100 individuals per trap in some cases. Local records suggest that there is usually a small second generation towards autumn and the literature supports this claim (Waring & Townsend, 2017; UK Moths, 2021). However, it does state that this small second generation is restricted to low altitudes. Whether or not this larger second generation is common for this species throughout its known range or if this reflects local conditions relating to climatic conditions and larval foodplant availability is unknown. Further systematic sampling in future years would help determine if this is a regular occurrence.

In addition to the indicator species identified in this study, a small number of other moths sampled were notable in the national context. *Elachista adscitella* Stainton, 1851 (Fig. 5.1a) were recorded across both reserves in both habitat types which is likely due to the presence of its main larval foodplant at both, *Sesleria caerulea*. Until now, it had not been recorded at either reserve, but has been recorded regularly at nearby Gait Barrows NNR since it was first found in the area in 1997 (from MapMate: Jones, R. P). Its habitat preference is said to be wooded habitats (UKMoths, 2021) and this may go some way toward explaining the even distribution of records between the two habitat types. However, it was recorded in higher numbers during both generations in open grasslands, so it is able to utilise areas with small, patchy areas of larval foodplant. *Clepsis rurinana* (Linnaeus, 1758) (Fig. 5.1b) is a pRDB1 species and was possibly the rarest moth species to have been caught during sampling. The larvae feed within a leaf roll from a wide range of trees and shrubs and are highly polyphagous, which supports the suggestion that not all rare species have a narrow feeding range (Flemish Entomological Society, 2022; Sterling & Parsons 2012). Three individuals came to light at one of the limestone pavement sites at Holme Park Fell, with one individual being retained. Examination of the hindwing confirmed it to be *C. rurinana* and was the first confirmed sighting in Cumbria.

The forewing colouration of some of the species are well-suited to the limestone (Fig. 5.2). Fewer than ten individuals of Galium carpet *Epirrhoe galiata* ([Denis &

Schiffermüller], 1775) (Fig.5.2a) have been recorded in Lancashire since 2000, many of which are from nearby Leck Fell and Gait Barrows (per MapMate). 141 individuals of this species were sampled across both reserves during June and July 2021, highlighting the importance of systematic sampling efforts for identifying local strongholds of what are thought to be extremely local species nationally.

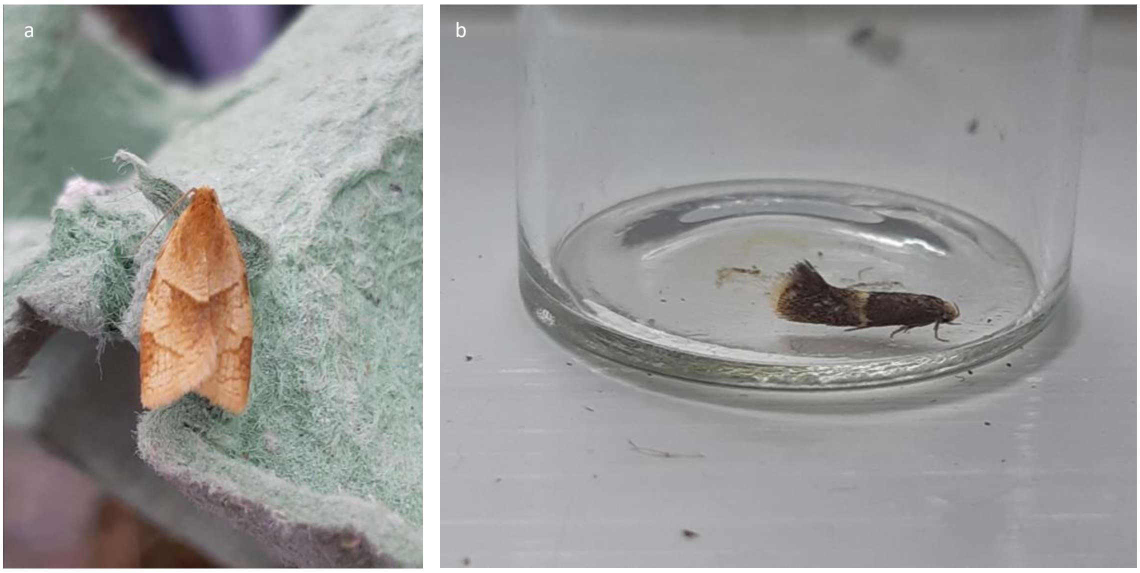


Figure 5.1 The micro-moths a) *Clepsis rurinana* and b) *Elachista adscitella*.

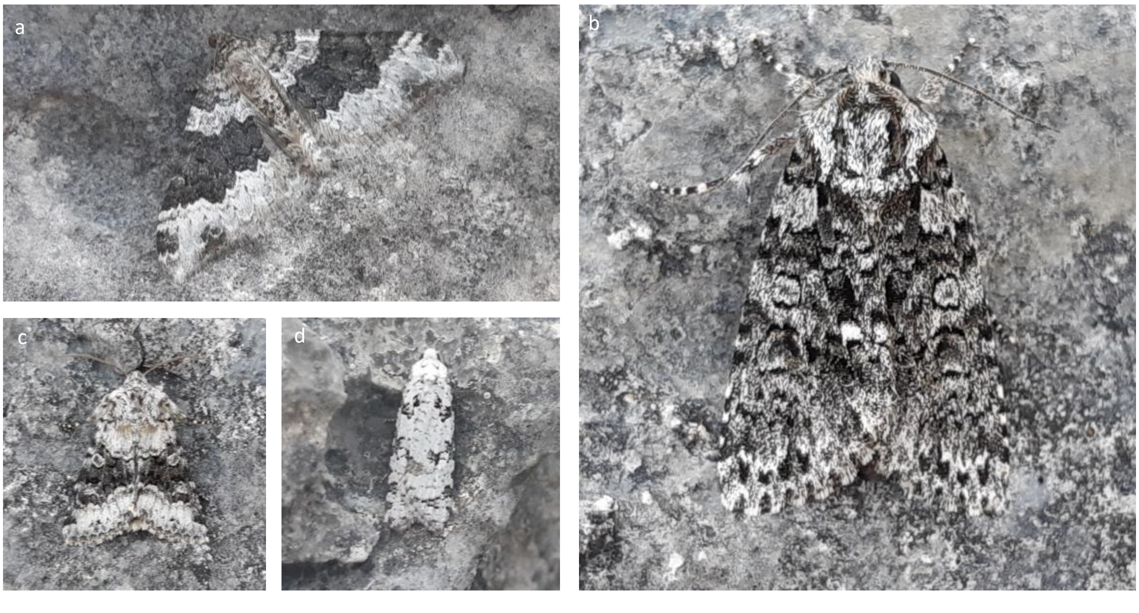


Figure 5.2 Demonstration of the camouflage of a) Galium Carpet, b) Knot-grass, c) Broad-barred White and d) *Eana penziana* ssp. *bellana* against the exposed limestone substrate.

5.2 Concluding remarks

The findings of this study should form a warning that condition assessments of SSSI units that focus on vegetation do not go far enough to protect moth communities. On the surface, the limestone pavement and grassland habitats of the Morecambe Bay area are quite different. Pavements support a tall, woody plant community that hosts a number of fern species amongst its fractured structure and the grasslands are floristically diverse and support an array of rare forbs and grasses. From assessments of moth species richness and functional diversity, both habitats are equally rich, and the assigned condition does little to detract from this. However, it remains to be seen if this stands true for other limestone pavements and grasslands in the area and we should seek to find out how they link together.

A number of moth species have been recorded in both the Lancashire and Cumbria biological recording areas for the first time, and extensive populations of relatively unknown species of national importance have been discovered using a simple, but extensive sampling strategy, with many more species being recorded once again after a long hiatus. Through using this sampling strategy, a profile of the moth community has been gained through analysis of their traits. It is apparent from these analyses that condition assessments based solely on vegetation and indicator plant species do not go far enough to identify changes to the trait composition of the macro-moth community. What has been identified is a silent shift in the composition of traits possessed by the macro-moth species in response to succession. In the interim, the formation of scrub from the cessation of grazing and other traditional methods of management can have a positive effect on biodiversity (Pöyry *et al*., 2004; Šumpich & Konvička, 2012). However, it has been widely found that the encroachment of vegetation has a negative effect on not just Lepidoptera, but a number of other insect groups (e.g., Kormann *et al*., 2015; Ernst *et al*., 2017; Mora *et al*., 2021). As with many studies on moths, baseline data are not available, and so we can only assume that the transition in traits identified between the two reserves is in line with a shift in the plant community from open grassland to scrub, and eventually woodland. Whilst the vegetation assessments detected little change from baseline expectations outlined by Natural England, the same cannot be said for the moth community and so regular monitoring of moths should be incorporated into future assessments.

Calcareous grasslands and limestone pavements are rare habitats in the UK and make a significant biodiversity contribution to what is considered one of the most nature-depleted countries globally. A lack of management being implemented within some of the units is resulting in the development of rank grasses and scrubbing over of internationally important habitats. Whilst allowing for structural heterogeneity in what is an extremely exposed landscape for the most part will be beneficial to some species, succession to woodland would be detrimental to a number of highly specialised and geographically restricted species. A dynamic and inclusive approach to management will be crucial going forward and moths need to come to the forefront when informing these decisions.

References

Agassiz, D., Beavan, S., & Heckford, R., 2013. *A Checklist of the Lepidopterist of the British Isles.* Royal Entomological Society, St Albans.

Aguirre-Gutiérrez, J., WallisDeVries, M., Marshall, L., Van't Zelfde, M., Villalobos-Arámbula, A., Boekelo, B., Bartholomeus, H ; Franzén, M., & Biesmeijer, J. 2017. Butterflies show different functional and species diversity in relationship to vegetation structure and land use. *Global Ecology and Biogeography*, 26(10), 1126-1137.

Allaby, M. 2015. *Site of special scientific interest*. A Dictionary of Ecology, A Dictionary of Ecology.

Anderson, A., McCormack, S., Helden, A., Sheridan, H., Kinsella, A., & Purvis, G. 2011. The potential of parasitoid Hymenoptera as bioindicators of arthropod diversity in agricultural grasslands. *Journal of Applied Ecology*, 48(2), 382–390.

Armsworth, P., Cantú-Salazar, L., Parnell, M., Davies, Z., & Stoneman, R. 2011. Management costs for small protected areas and economies of scale in habitat conservation. *Biological Conservation*, 144(1), 423-429.

Asher, J., Fox, R., & Warren, M., 2010. British butterfly distributions and the 2010 target. *Journal of Insect Conservation*, 15(1-2), 291–299.

Bainbridge, I., Brown, A., Burnett, N., Corbett, P., Cork, C., Ferris, R., Howe, M., Maddock, A., Mountford, E. & Pritchard, S. 2013. *Guidelines for the Selection of Biological SSSIs - Part 1: Rationale, Operational Approach and Criteria for Site Selection*. JNCC, Peterborough, ISBN 978-1-86107-625-0.

Balmer, O., & Erhardt, A. 2000. Consequences of Succession on Extensively Grazed Grasslands for Central European Butterfly Communities: Rethinking Conservation Practices. *Conservation Biology*, 14(3), 746-757.

Balvanera, P., Pfisterer, A., Buchmann, N., He, J., Nakashizuka, T., Raffaelli, D., & Schmid, B. 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters*, 9(10), 1146–1156.

Barber, N., Lamagdeleine-Dent, K., Willand, J., Jones, H., & McCravy, K. 2017. Species and functional trait re-assembly of ground beetle communities in restored grasslands. *Biodiversity and Conservation*, 26(14), 3481–3498.

Bates, D., Mächler, M., Bolker, B., & Walker, S. 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67(1), 1–48. doi: 10.18637/jss.v067.i01.

Baur, B. & Baur, A., 1995. Habitat-related dispersal in the rock-dwelling land snail *Chondrina clienta*. *Ecography*, 18(2), 123–130.

Berg, Å., Ahrné, K., Öckinger, E., Svensson, R., & Söderström, B. 2011. Butterfly distribution and abundance is affected by variation in the Swedish forest-farmland landscape. *Biological conservation*, 144(12), 2819–2831.

Bergman, K., Dániel-Ferreira, J., Milberg, P., Öckinger, E., & Westerberg, L. 2018. Butterflies in Swedish grasslands benefit from forest and respond to landscape composition at different spatial scales. *Landscape ecology*, 33(12), 2189–2204.

Blumgart, D., 2020. Theses. Lancaster Environment Centre. Investigating the Mechanisms behind Moth Declines : Plants, Land-use and Climate.

Boesing, A., Nichols, E., Metzger, J., & Maron, M. 2018. Land use type, forest cover and forest edges modulate avian cross-habitat spillover. *The Journal of Applied Ecology*, 55(3), 1252–1264.

Börschig, C., Klein, A., Von Wehrden, H., & Krauss, J. 2013. Traits of butterfly communities change from specialist to generalist characteristics with increasing land-use intensity. *Basic and Applied Ecology,* 14(7), 547-554.

Botta-Dukát, Z. 2005. Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *Journal of Vegetation Science*, 16(5):533–540. https://onlinelibrary.wiley.com/doi/pdf/10.1111/j.1654-1103.2005.tb02393.x.

Bowler, D., Eichenberg, D., Conze, K., Suhling, F., Baumann, K., Benken, T., Bönsel, A., Bittner, T., Drews, A., Günther, A., Isaac, N. J. B., Petzold, F., Seyring, M., Spengler, T., Trockur, B., Willigalla, C., Bruelheide, H., Jansen, F., Bonn, A., & Franzén, M. 2021. Winners and losers over 35 years of dragonfly and damselfly distributional change in Germany. *Diversity & Distributions*, 27(8), 1353–1366.

Boyes, D., Fox, R., Shortall, C., & Whittaker, R. 2019. Bucking the trend: the diversity of Anthropocene 'winners' among British moths. *Frontiers of Biogeography,* 11(3) e.43862

Boyes, D., Evans, D., Fox, R., Parsons, M., & Pocock, M., 2021. Is light pollution driving moth population declines? A review of causal mechanisms across the life cycle. *Insect Conservation and Diversity*, 14(2), 167-187.

Brehm, G., Niermann, J., Jaimes, N., Luisa, M., Enseling, D., Jüstel, T., Axmacher, J. C., Warrant, E., & Fiedler, K., 2021. Moths are strongly attracted to ultraviolet and blue radiation. *Insect Conservation and Diversity*, 14(2), 188-198.

Brooks, D. R., Bater, J. E., Clark, S. J., Monteith, D. T., Andrews, C., Corbett, S. J., Beaumont, D. A., Chapman, J. W., & Pocock, M. 2012. Large carabid beetle declines in a United Kingdom monitoring network increases evidence for a widespread loss in insect biodiversity. *The Journal of Applied Ecology*, 49(5), 1009–1019.

Brotons, L., Mönkkönen, M., & Martin, J. 2003. Are fragments islands? Landscape context and density-area relationships in boreal forest birds. *The American Naturalist*, 162(3), 343–357.

Brunbjerg, A., Bruun, H., Dalby, L., Fløjgaard, C., Frøslev, T., Høye, T., Goldberg, I., Læssøe, T., Hansen, D. D. M., Brøndum, L., Skipper, L., Fog, K., Ejrnæs, R., & Bacon, K. 2018. Vascular plant species richness and bioindication predict multi-taxon species richness. *Methods in Ecology and Evolution,* 9(12), 2372-2382.

BSBI., 2022. *Hieracium: Online Atlas of the British and Irish Flora.* [online] Available: https://www.brc.ac.uk/plantatlas/plant/hieracium [Accessed on 08/02/2022]

Burghardt, K., Tallamy, D., Philips, C., & Shropshire, K. 2010. Non-native plants reduce abundance, richness, and host specialization in lepidopteran communities. *Ecosphere,* 1(5), 1-22.

Butchart, S., Walpole, M., Carpenter, K., Carr., Geneviève, M., Chanson, J., Chenery, A., Csirke, J., Davidson, N., Dentener, F., Foster, M., Galli, A., Galloway, J., Collen, B., Genovesi, P., Gregory, R., Hockings, M., Kapos, V., Lamarque, J., Leverington, F., Loh, J., Mcgeoch, M., Mcrae, L., Minasyan, A., Van Strien, A., Morcillo, M., Oldfield, T., Pauly, D., Quader, S., Revenga, C., Sauer, J., Skolnik, B., Spear, D., Stanwell-Smith, D., Stuart, S., Scharlemann, J., Symes, A., Tierney, M., Tyrrell, T., Vie, J-C., Watson, R., Almond, R., Baillie, J., Bomhard, B., Brown, C., & Bruno, J. 2010. Global biodiversity: indicators of recent declines. *Science*, 328, 1164–1168.

Cáceres, M. & Legendre, P. 2009. Associations between species and groups of sites: indices and statistical inference. *Ecology,* 90(12): 3566-3574.

Cáceres, M., Legendre, P., & Moretti, M. 2010. Improving indicator species analysis by combining groups of sites. *Oikos*, 119(10), 1674-1684.

Clausnitzer, V., Kalkman, V., Ram, M., Collen, B., Baillie, J., Bedjanič, M., Darwall, W. R., Dijkstra, K.-D., Dow, R., Hawking, J., Karube, H., Malikova, E., Paulson, D., Schütte, K., Suhling, F., Villanueva, R., von Ellenrieder, N., & Wilson, K. 2009. Odonata enter the biodiversity crisis debate: The first global assessment of an insect group. *Biological Conservation,* 142(8), 1864-1869

Conrad, K., Warren, M., Fox, R., Parsons, M., & Woiwod, I. 2006. Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. *Biological Conservation*, 132, 279–291.

Cook, P., Tordoff, G., Davis, A., Parsons, M., Dennis, E., Fox, R., Botham, M., & Bourn, N. 2021. *Traits data for the butterflies and macro-moths of Great Britain and Ireland*, *2021*. NERC EDS Environmental Information Data Centre. (Dataset). https://doi.org/10.5285/5b5a13b6-2304-47e3-9c9d-35237d1232c6

Coulthard, E., Norrey, J., Shortall, C., & Harris, W. 2019. Ecological traits predict population changes in moths. *Biological Conservation*, 233, 213–219.

Crafter, T. 2005 *Foodplant List for the Caterpillars of Britain's Butterflies and Larger Moths.* Atropos, England.

Craven, A. 2012. *Definitions of Favourable Condition for Designated Features of Interest, Farleton Knott.* Natural England

Craven, A. 2013. *Definitions of Favourable Condition for Designated Features of Interest, Hutton Roof Crags.* Natural England

Cumbria Wildlife Trust., 2019. *Hutton Roof Crags.* [online] Available: https://www.cumbriawildlifetrust.org.uk/nature-reserves/hutton-roof-crags

Dantas de Miranda, M., Pereira, H., Corley, M., & Merckx, T. 2019. Beta diversity patterns reveal positive effects of farmland abandonment on moth communities. *Scientific reports*, 9(1), 1549.

Davis, A. 2012. *A Review of the Status of Microlepidoptera in Britain*. Butterfly Conservation, Wareham. (Butterfly Conservation Report No. S12-02)

Debinski, D., Moranz, R., Delaney, J., Miller, J., Engle, D., Winkler, L., McGranahan, D., Barney, R., Trager, J., Stephenson, A., & Gillespie, M. 2011. A cross-taxonomic comparison of insect responses to grassland management and land-use legacies. *Ecosphere*, 2(12), Art131-16.

DEFRA., 2019. *At a Glance: Summary of Targets in our 25-year Environment Plan.* [online] Available: https://www.gov.uk/government/publications/25-year-environment-plan/25-year-environment-plan-our-targets-at-a-glance [Accessed on 10/03/2020]

DEFRA., 2019. *Natural England’s Impact Risk Zones for Sites of Special Scientific Interest.* [online] Available: https://magic.defra.gov.uk/Metadata_for_magic/SSSI%20IRZ%20User%20Guidance%20MAGIC.pdf [Accessed on 22/01/2020]

DEFRA, 2020. *Farming Statistics – final crop areas, yields, livestock populations and agricultural workforce on 1 June 2020 United Kingdom.* [online] Available: Farming statistics - final crop areas, yields, livestock populations and agricultural workforce on 1 June 2020 - UK (publishing.service.gov.uk) [Accessed on 17/01/2021]

Dennis, E., Brereton, T., Morgan, B., Fox, R., Shortall, C., Prescott, T., & Foster, S. 2019. Trends and indicators for quantifying moth abundance and occupancy in Scotland. *Journal of Insect Conservation*, 23(2), pp.369–380.

Dennis, R., Dapporto, L., Dover, J., & Shreeve, T. 2013. Corridors and barriers in biodiversity conservation: A novel resource-based habitat perspective for butterflies. *Biodiversity and Conservation*, 22(12), 2709-2734.

Dennis, R., Hardy, P., & Dapporto, L. 2012. Nestedness in island faunas: Novel insights into island biogeography through butterfly community profiles of colonization ability and migration capacity. *Journal of Biogeography*, 39(8), 1412-1426.

Dennis, R., Shreeve, T., & Van Dyck, H. 2006. Habitats and Resources: The Need for a Resource-based Definition to Conserve Butterflies. *Biodiversity and Conservation*, 15(6), 1943-1966.

Diekmann, M., Jandt, U., Alard, D., Bleeker, A., Corcket, E., Gowing, D., Stevens, C., & Duprè, C. 2014. Long-term changes in calcareous grassland vegetation in North-western Germany – No decline in species richness, but a shift in species composition. *Biological Conservation, 172*, 170-179.

Donald, P., Sanderson, F., Burfield, I., & Van Bommel, F. 2006. Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990–2000. *Agriculture, Ecosystems & Environment*, 116(3), 189–196.

Duffy, J., Godwin, C., & Cardinale, B. 2017. Biodiversity effects in the wild are common and as strong as key drivers of productivity. *Nature*, 549(7671), 261-264.

Dufrêne, M. & Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, 67(3), 345-366.

Ellis, S., Bourne, N., & Bulman, C. 2012 Landscape-scale conservation for butterflies and moths: Lessons from the UK. [online] Available: file:///C:/Users/justi/OneDrive/Desktop/landscape-scale-conservation-for-butterflies-and-moths-low-resolution.pdf [Accessed on 24/02/22]

Ellis, S., Wainwright, D., Berney, F., Bulman, C., & Bourn, N. 2010. Landscape-scale conservation in practice: Lessons from northern England, UK. *Journal of Insect Conservation*, 15(1-2), 69-81.

Ellis, S., Wainwright, D., Dennis, E., Bourn, N., Bulman, C., Hobson, R., Jones, R., Middlebrook, I., Plackett, J., Smith, R. J., Wain, M., & Warren, M. 2019. Are habitat changes driving the decline of the UK's most threatened butterfly: The High Brown Fritillary Argynnis adippe (Lepidoptera: Nymphalidae)? *Journal of Insect Conservation,* 23(2), 351-367.

Enkhtur, K., Brehm, G., Boldgiv, B., & Pfeiffer, M. 2021. Effects of grazing on macro-moth assemblages in two different biomes in Mongolia. *Ecological indicators*, 133, 108421.

Ernst, L., Tscharntke, T., & Batáry, P. 2017. Grassland management in agricultural vs. forested landscapes drives butterfly and bird diversity. *Biological Conservation,* 216, 51-59.

Esri. 2020. Map of the sampling sites within the SSSI units. C;\\Users\justi\OneDrive\My Documents\ArcGIS\Projects\Species per site.aprx [Accessed on 28/06/2021]

Fahrig, L. 2001. How much habitat is enough? *Biological Conservation,* 100(1), 65-74.

Flemish Entomological Society, 2022. *Clepsis rurinana – Catalogue of the Lepidoptera of Belgium.* [online] Available: https://projects.biodiversity.be/lepidoptera/species/5824/ [Accessed on 10/02/2022]

Forrest, J., Thorp, R., Kremen, C., Williams, N., & Clough, Y. 2015. Contrasting patterns in species and functional-trait diversity of bees in an agricultural landscape. *The Journal of Applied Ecology,* 52(3), 706-715.

Fox, J., & Weisberg, S. 2019. *An R Companion to Applied Regression*. Third edition. [online] Sage, Thousand Oaks CA. [Available] https://socialsciences.mcmaster.ca/jfox/Books/Companion/.

Fox, R., 2013. The decline of moths in Great Britain: A review of possible causes. *Insect Conservation and Diversity*, 6(1), 5-19.

Fox, R., Brereton, T., Asher, J., August, T., Botham, M., Bourn, N., Cruickshanks, K., Bulman, C., Ellis, S., Harrower, C., Middlebrook, I., Noble, D., Powney, G., Randle, Z., Warren, M., & Roy, D. 2015. *The State of the UK's Butterflies 2015*. Butterfly Conservation and the Centre for Ecology & Hydrology, Wareham, Dorset.

Fox, R., Dennis, E., Harrower, C., Blumgart, D., Bell, J., Cook, P., Davies, A., Evans-Hill, L., Haynes, F., Hill, D., Issac, N., Parsons, M., Pocock, M., Prescot, T., Randle, Z., Shortall, C., Tordoff, G., Tuson, D. & Bourne, N. 2021. *The State of Britain's Larger Moths 2021.* Butterfly Conservation, Rothamsted Research and UK Centre for Ecology and Hydrology, Wareham, Dorset, UK.

Fox, R., Oliver, T., Harrower, C., Parsons, M., Thomas, C., Roy, D., & Pärt, T. 2014. Long-term changes to the frequency of occurrence of British moths are consistent with opposing and synergistic effects of climate and land-use changes. *Journal of Applied Ecology*, 51(4), pp.949–957.

Fox, R., Parsons, M., Chapman, J., Woiwod, I., Warren, M., & Brooks, D., 2013. *The State of Britain's Larger Moths*. Butterfly Conservation and Rothamsted Research, Wareham, Dorset, UK.

Fox, R., Parsons, M., & Harrower, C. 2019. *A Review of the Status of Macro-moths of Great Britain*. Butterfly Conservation report to Natural England.

Franzén, M., Schweiger, O., & Betzholtz, P. 2012. Species-area relationships are controlled by species traits. *PloS One*, 7(5), E37359.

Fröberg, L., Stoll, P., Baur, A., & Baur, B. 2011. Snail herbivory decreases cyanobacterial abundance and lichen diversity along cracks of limestone pavements. *Ecosphere*, 2(3), 38–43.

Fründ, J., Linsenmair, K., & Blüthgen, N. 2010. Pollinator diversity and specialization in relation to flower diversity. *Oikos*, 119(10), 1581-1590.

Fry, R., & Waring, P., 2001. *A Guide to Moth Traps and Their Use.* 2nd ed. Orpington, Kent: Amateur Entomologists' Society.

Gámez-Virués, S., Perović, D., Gossner, M., Börschig, C., Blüthgen, N., De Jong, H., Simons, N., Klein, A-M., Krauss, J., Maier, G., Scherber, C., Steckel, J., Rothenwöhrer, C., Steffan-Dewenter, I., Weiner, C., Weisser, W., Werner, M., Tscharntke, T., & Westphal, C. 2015. Landscape simplification filters species traits and drives biotic homogenization. *Nature Communications*, 6(1), 8568.

García-Barros, E., 2000. Body size, egg size, and their interspecific relationships with ecological and life history traits in butterflies (Lepidoptera: Papilionoidea, Hesperioidea). *Biological Journal of the Linnean Society*, 70(2), 251-284.

García-Barros, E. 2015. Multivariate indices as estimates of dry body weight for comparative study of body size in Lepidoptera. *Nota Lepidopterologica*, 38(1), 59-74.

Garrido, P., Mårell, A., Öckinger, E., Skarin, A., Jansson, A., Thulin, C., & Root-Bernstein, M. 2019. Experimental rewilding enhances grassland functional composition and pollinator habitat use. *Journal of Applied Ecology*, 56(4), 946-955.

Gaston, K., Charman, K., Jackson, S., Armsworth, P., Bonn, A., Briers, R., Callaghan, C., Catchpole, R., Hopkins, J., Kunin, W., Latham, J., Opdam, P., Stoneman, R., Stroud, D., & Tratt, R. 2006. The ecological effectiveness of protected areas: The United Kingdom. *Biological Conservation*, 132(1), 76-87.

Gaston, K., Davies, T., Bennie, J., & Hopkins, J. 2012. Reducing the ecological consequences of night-time light pollution: Options and developments. *Journal of Applied Ecology*, 49(6), 1256-1266.

Gaston, K., & Hudson, J., 1994. Regional patterns of diversity and estimates of global insect species richness. *Biodiversity & Conservation,* 3(6), 493-500

Goldie, H. 1996. The limestone pavements of Great Asby Scar, Cumbria, UK. *Environmental Geology*, 28(3), 128-136.

Grass, I., Lehmann, K., Thies, C., & Tscharntke, T. 2017. Insectivorous birds disrupt biological control of cereal aphids. *Ecology, 98*(6), 1583-1590

Grimaldi, D., & Engel, M. S., 2005. *Evolution of the Insects.* Cambridge University Press.

Guariento, E., Strutzenberger, P., Truxa, C., & Fiedler, K. 2020. The trinity of ecological contrasts: A case study on rich insect assemblages by means of species, functional and phylogenetic diversity measures. *BMC Ecology*, 20(1), 29.

Habel, J., Segerer, A., Ulrich, W., & Schmitt, T. 2019. Succession matters: Community shifts in moths over three decades increases multifunctionality in intermediate successional stages. *Scientific Reports*, 9(1), 5586.

Habel, J., Teucher, M., & Rödder, D. 2018. Mark-release-recapture meets Species Distribution Models: Identifying micro-habitats of grassland butterflies in agricultural landscapes. *PloS One*, 13(11), E0207052.

Habel, J., Trusch, R., Schmitt, T., Ochse, M., & Ulrich, W., 2019. Long-term large-scale decline in relative abundances of butterfly and burnet moth species across south-western Germany. *Scientific Reports,* 9(1), 14921-9.

Habel, J., Ulrich, W., Biburger, N., Seibold, S., Schmitt, T., Didham, R., & Batary, P. 2019. Agricultural intensification drives butterfly decline. *Insect Conservation and Diversity*, 12(4), 289–295.

Hallmann, C., Zeegers, T., Klink, R., Vermeulen, R., Wielink, P., Spijkers, H., Steenis, W., & Jongejans, E. 2020. Declining abundance of beetles, moths, and caddisflies in the Netherlands. *Insect Conservation and Diversity*, 13(2), 127-139.

Hanski, I., & Gilpin, M. 1997. Metapopulation Biology: Ecology, Genetics, and Evolution. *Ecology*, 78(7), 2270–2271.

Hanski, I., & Ovaskainen, O. 2000. The metapopulation capacity of a fragmented landscape. *Nature*, 404(6779), 755-758.

Hayes, M., Rhodes, M., Turner, E., Hitchcock, G., Knock, R., Lucas, C., & Chaney, P. 2018. Determining the long-term habitat preferences of the Duke of Burgundy butterfly, *Hamearis lucina*, on a chalk grassland reserve in the UK. *Journal of Insect Conservation*, 22(2), 329-343.

Hayhow, D., Eaton, M., Stanbury, A., Burns, F., Kirby, W., Bailey, N., Beckmann, B., Bedford, J., Boersch-Supan, P. , Coomber, F., Dennis, E., Dolman, S., Dunn, E., Hall, J., Harrower, C., Hatfield, J., Hawley, J., Haysom, K., Hughes, J., Johns, D., Mathews, F., McQuatters-Gollop, A., Noble, D., Outhwaite, C., Pearce-Higgins, J., Pescott, O., Powney, G., & Symes, N. 2019. *The State of Nature 2019*. The State of Nature partnership. [online] Available: https://nbn.org.uk/wp-content/uploads/2019/09/State-of-Nature-2019-UK-full-report.pdf [Accessed on 19/01/2022]

Heath, J., 1965. *A genuinely portable MV light trap.* Entomologists' Record and Journal of Variation 77: 236–238.

Hertzog, L., Meyer, S., Weisser, W., & Ebeling, A. 2016. Experimental Manipulation of Grassland Plant Diversity Induces Complex Shifts in Aboveground Arthropod Diversity. *PloS ONE*, 11(2), 0148768.

Hilty, J., Lidicker, W., & Merenlender, A., 2006. *Corridor Ecology: The Science and Practice of Linking Landscapes for Biodiversity Conservation*. Washington, Island Press

Hosken, D., & Stockley, P., 2004. Sexual selection and genital evolution. *Trends in Ecology & Evolution*, 19(2), pp.87–93.

Infusino, M., Brehm, G., Di Marco, C., & Scalercio, S. 2017. Assessing the efficiency of UV LEDs as light sources for sampling the diversity of macro-moths (Lepidoptera). *European Journal of Entomology*, 114(1), 25-33.

Jonas, J., Whiles, M., & Charlton, R., 2002. Aboveground Invertebrate Responses to Land Management Differences in a Central Kansas Grassland. *Environmental Entomology*, 31(6), 1142–1152.

Jonason, D., Franzen, M., & Ranius, T., 2014. Surveying moths using light traps: effects of weather and time of year. *PLoS ONE*, 9(3), p.e92453.

JNCC., 2009. *Common Standards Monitoring for Upland Habitats.* [online] Available: file:///C:/Users/justi/OneDrive/Desktop/SSSI%20habitat%20assessment%20documents/CSMUplandHabitats2009.pdf [Accessed on 13/02/2020]

JNCC., 2020. *Limestone Pavements – Special Areas of Conservation.* [online] Available: https://sac.jncc.gov.uk/habitat/H8240/ [Accessed on 07/02/2020]

JNCC, 2021. C1. *Protected Areas*. [online] Available: UKBI - C1. Protected areas | JNCC - Adviser to Government on Nature Conservation. [Accessed on 17/01/2022]

JNCC., 1989. *Guidelines for the selection of biological SSSI’s Part 2: Detailed guidelines for habitats and species groups: Non-Montane Rock Habitats.* [online] Available: https://hub.jncc.gov.uk/assets/56b06487-3de0-4b47-aae5-461f208e5153 [Accessed on 04/05/2021]

Kamp, J., Frank, C., Trautmann, S., Busch, M., Dröschmeister, R., Flade, M., Gerlach, B., Karthäuser, J., Kunz, F., Mitschke, A., Schwarz, J., & Sudfeldt, C. 2020. Population trends of common breeding birds in Germany 1990–2018. *Journal of Ornithology*, 162(1), 1-15.

Kehoe, R., Frago, E., & Sanders, D. 2021. Cascading extinctions as a hidden driver of insect decline. *Ecological Entomology*, 46(4), 743-756.

Kimber, I., 2020. *Guide to the Moths of Great Britain and Ireland.* [online] Available: https://www.ukmoths.org.uk/ [Accessed on 05/03/2020]

Knight, G., 2003. Liverpool Museum Invertebrate Survey – Hutton Roof Crags National Nature Reserve, Cumbria 2001-2002; National Museums Liverpool; 156pp

Knuff, A., Staab, M., Frey, J., Dormann, C., Asbeck, T., & Klein, A. 2020. Insect abundance in managed forests benefits from multi-layered vegetation. *Basic and Applied Ecology*, 48, 124-135.

Kotiaho, J., Kaitala, V., Komonen, A., & Päivinen, J. 2005. Predicting the Risk of Extinction from Shared Ecological Characteristics. *Proceedings of the National Academy of Sciences*, 102(6), 1963-1967.

Kormann, U., Rösch, V., Batáry, P., Tscharntke, T., Orci, K., Samu, F., & Scherber, C. 2015. Local and landscape management drive trait-mediated biodiversity of nine taxa on small grassland fragments. *Diversity & Distributions,* 21(10), 1204-1217.

Kuznetsova, A., Brockhoff, P., & Christensen, R. 2017. lmerTest Package: Tests in Linear Mixed Effects Models. *Journal of Statistical Software*, 82(13), 1--26. doi:10.18637/jss.v082.i13

Lake, S., Liley, D., Still, R., & Swash, A. 2020. *Britain's Habitats: A field Guide to the Wildlife Habitats of Great Britain and Ireland*. 2nd Edition. Wild Guides Ltd, Hampshire, UK.

Laliberté, E., & Legendre, P. 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology,* 91:299-305.

Laliberté, E., Legendre, P., & Shipley, B. 2014. FD: measuring functional diversity from multiple traits, and other tools for functional ecology*. Ecology*, 91(1), 299-305.

Langmaid, J., Palmer, S., Parsons, M., & Young, M., 2016. *Micro-moth Verification Guidelines.* [online] Available: http://mothscount.org/uploads/Micro-moth%20verification%20guidance%20(final).pdf [Accessed on 03/03/2020]

Lavorel, S., & Garnier, E. 2002. Predicting Changes in Community Composition and Ecosystem Functioning from Plant Traits: Revisiting the Holy Grail. *Functional Ecology*, 16(5), 545-556.

Lawton, J. H., Brotherton, P. N. M., Brown, V. K., Elphick, C., Fitter, A. H., Forshaw, J., Haddow, R. W., Hilborne, S., Leafe, R. N., Mace, G. M., Southgate, M. P., Sutherland, W. J., Tew, T. E., Varley, J., & Wynne, G. R. 2010. Making Space for Nature: a review of England's wildlife sites and ecological network. Report to Defra.

Legal, L., Valet, M., Dorado, O., De Jesus-Almonte, J., Lopez, K., & Cereghino, R. 2020. Lepidoptera are Relevant Bioindicators of Passive Regeneration in Tropical Dry Forests*. Diversity*, 12(6), 231.

Lenth, R. V. 2016. Least-Squares Means: The R Package lsmeans. *Journal of Statistical Software*, 69(1), 1-33.

Levin, S. 2001. *Encyclopaedia of Biodiversity*. San Diego: Academic Press.

Lewis, R., Pakeman, R., Angus, S., & Marrs, R. 2014. Using compositional and functional indicators for biodiversity conservation monitoring of semi-natural grasslands in Scotland. *Biological Conservation*, 175, 82-93.

Lintott, P., Bunnefeld, N., Fuentes-Montemayor, E., Minderman, J., Blackmore, L., Goulson, D., & Park, K. 2014. Moth species richness, abundance, and diversity in fragmented urban woodlands: implications for conservation and management strategies. *Biodiversity and Conservation*, 23(11), pp.2875–2901.

Lister, B., & Garcia, A., 2018. Climate-driven declines in Arthropod abundance restructure rainforest food web. *Proceeding of the National Academy of Sciences in the United States of America,* 115(44), E10397-E10406

Lovett, G., & Ruesink, M., 1995. Carbon and nitrogen mineralisation from decomposing gypsy moth frass. *Oecologia 104*(2), 133-138

Lüdecke, D. 2021. *sjPlot: Data Visualization for Statistics in Social Science. R package version 2.8.9*, https://CRAN.R-project.org/package=sjPlot.

MacArthur, R., & Wilson, E. 1967. *The Theory of Island Biogeography*. New Jersey: Princeton University Press.

Macgregor, C., Pocock, M., Fox, R., & Evans, D. 2015. Pollination by nocturnal Lepidoptera, and the effects of light pollution: a review. *Ecological Entomology*, 40(3), pp.187–198.

Macgregor, C., Williams, J., Bell, J., & Thomas, C., 2019. Moth biomass increases and decreases over 50 years in Britain. *Nature Ecology & Evolution, 3*(12), 1645-1649.

Magic, 2021. Magic Map Application. [online] Available: https://magic.defra.gov.uk/

Mangels, J., Fiedler, K., Schneider, F., & Blüthgen, N. 2017. Diversity and trait composition of moths respond to land-use intensification in grasslands: generalists replace specialists. *Biodiversity and Conservation*, 26(14), pp.3385–3405.

Martin, E., Reineking, B., Seo, B., & Steffan-Derwenter, I. 2013. Natural enemy interactions constrain [pest control in complex agricultural landscapes. *Proceeding of the National Academy of Sciences of the United States of America,* 110(14), 5534-5539

Maskell, L., Smart, S., Bullock, J., Thompson, K., & Stevens, C. 2010. Nitrogen deposition causes widespread loss of species richness in British habitats. *Global Change Biology*, 16(2), 671–679.

Mason, N., Mouillot, D., Lee, W., & Wilson, J. 2005. Functional richness, functional evenness, and functional divergence: the primary components of functional diversity. *Oikos,* 111(1), 112–118.

Mason, N., De Bello, F., Mouillot, D., Pavoine, S., & Dray, S. 2013. A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients. *Journal of Vegetation Science,* 24(5), 794-806.

Mayhew, P., 2007. Why are there so many insect species? Perspectives from fossils and phylogenies. *Biological Reviews,* 82(3), 425-454

Maxwell, S., Fuller, R., Brooks, T., & Watson, J. 2016. Biodiversity: The ravages of guns, nets, and bulldozers. *Nature*, 536(7615), 143-145.

McGeogh, M., 1998. The selection, testing and application of terrestrial insects as bioindicators. *Biological reviews of the Cambridge Philosophical Society*, 73(2), 181–201.

McGill, B., Enquist, B., Weiher, E., & Westoby, M. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, 21(4), 178-185.

McKinney, M., & Lockwood, J. 1999. Biotic homogenization: A few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution*, 14(11), 450-453.

Merckx, T., Feber, R., Dulieu, R., Townsend, M., Parsons, M., Bourn, N., Riordan, P., & Macdonald, D. 2009. Effect of field margins on moths depends on species mobility: Field-based evidence for landscape-scale conservation. *Agriculture, Ecosystems and Environment*, 129(1), pp.302–309.

Merckx, T. & Slade, E., 2014. Macro-moth families differ in their attraction to light: implications for light-trap monitoring programmes. *Insect Conservation and Diversity*, 7(5), 453–461.

Merckx, T., Van Dyck, H., & Isaac, N. 2019. Urbanization-driven homogenization is more pronounced and happens at wider spatial scales in nocturnal and mobile flying insects. *Global Ecology and Biogeography*, 28(10), 1440-1455.

Miller, J., Hahn, P., Damschen, E., & Brennan, J. 2017. Functional dependence underlies a positive plant-grasshopper richness relationship. *Basic and Applied Ecology*, 21, 94–100.

Møller, A. 2019. Parallel declines in abundance of insects and insectivorous birds in Denmark over 22 years. *Ecology and Evolution*, 9(11), pp.6581–6587.

Mooney, H., 2010. The ecosystem-service chain and the biological diversity crisis. Philosophical transactions. *Biological Sciences*, 365(1537), 31–39.

Mora, A., Wilby, A., & Menéndez, R. 2021. Abandonment of cultural landscapes: butterfly communities track the advance of forest over grasslands. *Journal of Insect Conservation,* http://doi.org/10.1007/s10841-021-00365-0

Mora, C., Tittensor, D., Adl, S., Simpson, A., Worm, B., & Mace, G., 2011. How many species are there on Earth and in the Ocean? (On the number of species on Earth and in the Ocean). *PloS Biology,* 9(8), E1001127

Mori, A., Furukawa, T., & Sasaki, T. 2013. Response diversity determines the resilience of ecosystems to environmental change. *Biological Reviews of the Cambridge Philosophical Society*, 88(2), 349-364.

mothscount.org., 2019. National Moth Recording Scheme – Moths Count. [online] Available: http://mothscount.org/text/27/National_Moth_Recording_Scheme.html

Mortelliti, A., Amori, G., & Boitani, L. 2010. The role of habitat quality in fragmented landscapes: A conceptual view and prospectus for future research. *Oecologia,* 163(2), 535-547

Mouchet, M., Villéger, S., Mason, N., & Mouillot, D. 2010. Functional diversity measures: An overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology*, 24(4), 867-876.

National Moth Recording Scheme. 2020. *Online Moth Recording.* [online] Available: http://www.mothrecording.org/index.php?c=folder&m=fol&mm=fol [Accessed on 23/01/2020]

Natural England. 1988. Designated Sites: Hutton Roof Crags. [online] Available: https://designatedsites.naturalengland.org.uk/PDFsForWeb/Citation/1003388.pdf [Accessed on 24/05/2021

Natural England. 1988. Designated Sites: Farleton Knott. [online] Available: https://designatedsites.naturalengland.org.uk/PDFsForWeb/Citation/1003143.pdf [Accessed on 24/05/2021]

Natural England. 2014. Condition of the SSSI Units for the Site Hutton Roof Crags SSSI. [online] Available: https://designatedsites.naturalengland.org.uk/ReportUnitCondition.aspx?SiteCode=S1003388&ReportTitle=Hutton%20Roof%20Crags%20SSSI [Accessed 30/03/2021]

Natural England., 2020. Priority Habitat Inventory (North) (England). [online] Available: Priority Habitat Inventory (North) (England) | Natural England Open Data Geoportal (arcgis.com) [Accessed on 24/05/2021]

Natural England., 2020. *Sites of Special Scientific Interest – Managing Your Land.* [online] Available: https://www.gov.uk/guidance/protected-areas-sites-of-special-scientific-interest [Accessed on 22/01/2020]

Natural England., 2022. Sites of Special Scientific Interest Units (England). Available: https://naturalengland-defra.opendata.arcgis.com/datasets/Defra::sites-of-special-scientific-interest-units-england/about [Accessed on 05/07/2022]

Nelson, M., Leavitt, S., Heller, K., Muggia, L., & Lumbsch, H. 2022. Contrasting patterns of climatic niche divergence in *Trebouxia* – a clade of lichen-forming algae. *Frontiers in Microbiology*, 13, 791546.

New, T., 2004. Moths (Insecta: Lepidoptera) and conservation: background and perspective. *Journal Of Insect Conservation*, 8(2), pp.79–94.

New, T., 2014. Lepidoptera and conservation, Chichester, West Sussex: John Wiley & Sons, Inc.

Öckinger, E., Bergman, K.-O., Franzén, M., Kadlec, T., Krauss, J., Kuussaari, M., Pöyry, J., Smith, H., Steffan-Dewenter, I., & Bommarco, R. 2011. The landscape matrix modifies the effect of habitat fragmentation in grassland butterflies. *Landscape Ecology*, 27(1), 121–131.

Öckinger, E., Eriksson, A., & Smith, H. 2006. Effects of grassland abandonment, restoration and management on butterflies and vascular plants. *Biological Conservation,* 133(3), 291-300.

Öckinger, E., Schweiger, O., Crist, T., Debinski, D., Krauss, J., Kuussaari, M., & Bommarco, R. 2010. Life-history traits predict species responses to habitat area and isolation: A cross-continental synthesis. *Ecology Letters*, 13(8), 969-979.

Oksanen, J., Blanchet, F., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P., O'Hara, R., Simpson, G., Solymos, P., Stevens, M., Szoecs, E., & Wagner, E. 2020. Vegan Package: Community Ecology Package. https://cran.r-project.org, https://github.com/vegandevs/vegan

Olden, J., LeRoy, P., Douglas, M., Douglas, M., & Fausch, K. 2004. Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology & Evolution*, 19(1), 18-24.

Ollerton, J., Winfree, R., & Tarrant, S., 2011. How many flowering plants are pollinated by animals? *Oikos,* 120(3). 321-326

Opdam, P., & Wascher, D. 2004. Climate change meets habitat fragmentation: Linking landscape and biogeographical scale levels in research and conservation. *Biological Conservation*, 117(3), 285-297.

Owens, A., Cochard, P., Durrant, J., Farnworth, B., Perkin, E., & Seymoure, B. 2020. Light pollution is a driver of insect declines. *Biological Conservation*, 241, 108259.

Perović, D., Gámez-Virués, S., Börschig, C., Klein, A., Krauss, J., Steckel, J., Rothenwöhrer, J., Erasmi, C., Tscharntke, T., Westphal, C., &   Kleijn, D. 2015. Configurational landscape heterogeneity shapes functional community composition of grassland butterflies. *The Journal of Applied Ecology,* 52(2), 505-513.

Piervittori, R., Salvadori, O. & Isocrono, D., 2004. Literature on lichens and biodeterioration of stonework. IV. *The Lichenologist*, 36(2), 145–157.

Pizzolotto, R., Mazzei, A., Bonacci, T., Scalercio, S., Iannotta, N., & Brandmayr, P. 2018. Ground beetles in Mediterranean olive agroecosystems: Their significance and functional role as bioindicators (Coleoptera, Carabidae). *PloS ONE*, 13(3), 0194551.

Poschlod, P., & WallisDeVries, M. 2002. The historical and socioeconomic perspective of calcareous grasslands—lessons from the distant and recent past. *Biological Conservation*, 104(3), 361-376.

Potocký, P., Bartoňová, A., Beneš, J., Zapletal, M., Konvička, M., Didham, R., & Oliver, T. 2018. Life-history traits of Central European moths: gradients of variation and their association with rarity and threats. *Insect Conservation and Diversity*, 11(5), pp.493–505.

Potts, S., Biesmeijer, J., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. 2010. Global pollinator declines: Trends, impacts and drivers. *Trends in Ecology & Evolution*, 25(6), 345-353.

Pöyry, J., Lindgren, S., Salminen, J., & Kuussaari, M. 2004. Restoration of Butterfly and Moth Communities in Semi-Natural Grasslands by Cattle Grazing. *Ecological Applications*, 14(6), 1656–1670.

R Core Team. 2021*. R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Available: https://www.R-project.org/.

Randal, Z., 2013. *Moth Recorders Handbook.* [online] Available: file:///C:/Users/justi/OneDrive/Desktop/Moth%20Recorders%20Handbook%202013(1).pdf [Accessed on 03/03/2020]

Rayment, M., 2011. *Benefits of Sites of Special Scientific Interest.* [online] Available: file:///C:/Users/pattonj/OneDrive/Desktop/Papers%20for%20Masters%20research%20proposal/finalreportsssis-benefits%20(1).pdf [Accessed on 22/01/2020]

Reidsma, P., Tekelenburg, T., Van den Berg, M., & Alkemade, R. 2006. Impacts of land-use change on biodiversity: An assessment of agricultural biodiversity in the European Union. *Agriculture, Ecosystems & Environment*, 114(1), 86-102.

Robinson, R., & Sutherland, W. 2002. Post-War Changes in Arable Farming and Biodiversity in Great Britain. *Journal of Applied Ecology*, 39(1), 157–176.

Sánchez-Bayo, F., & Wyckhuys, K. 2019. Worldwide decline of the entomofauna: A review of its drivers. *Biological Conservation* 232, 8-27

Sand-Jensen, K., & Hammer, K. 2012. Moss cushions facilitate water and nutrient supply for plant species on bare limestone pavements. *Oecologia,* 170(2), 305-312.

Seibold, S., Gossner, M., Simons, N., Blüthgen, N., Müller, J., Ambarlı, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J., Linsenmair, K., Nauss, T., Penone, C., Prati, D., Schall, P., Schulze, E-D., Vogt, J., Wöllauer, S., & Weisser, W. 2019. Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature*, 574(7780), 671-674.

Shortall, C., Moore, A., Smith, E., Hall, M., Woiwod, I., & Harrington, R. 2009. Long-term changes in the abundance of flying insects. *Insect Conservation and Diversity*, 2(4), 251–260.

Slancarova, J., Bartonova, A., Zapletal, M., Kotilinek, M., Faltynek Fric, Z., Micevski, N., Kati, V., Konvicka, M., & Lötters, S. 2016. Life History Traits Reflect Changes in Mediterranean Butterfly Communities Due to Forest Encroachment. *PloS ONE*, 11(3), E0152026.

Smart, S., Dunbar, M., Emmett, B., Marks, S., Maskell, L., Norton, L., Rose, P., Simpson, I. 2010. An Integrated Assessment of Countryside Survey data to investigate Ecosystem Services in Great Britain. Technical Report No. 10/07 NERC/Centre for Ecology & Hydrology 230pp.

Soga, M., & Koike, S. 2012. Relative importance of quantity, quality, and isolation of patches for butterfly diversity in fragmented urban forests. *Ecological Research, 27*(2), 265-271

Somers-Yeates, R., Hodgson, D., McGregor, P., Spalding, A., & French-Constant, R. 2013. Shedding Light on Moths: Shorter Wavelengths Attract Noctuids More than Geometrids. *Biology Letters* 9, no. 4 (2013): 20130376.

Sterling, P., & Parsons, M. 2012. *Field guide to the micro moths of Great Britain and Ireland*. Dorset, England: British Wildlife Publishing.

Stevens, C., Dise, N., Gowing, D., & Mountford, J. 2006. Loss of forb diversity in relation to nitrogen deposition in the UK: Regional trends and potential controls. *Global Change Biology,* 12(10), 1823-1833.

Stork, N. 2018. How Many Species of Insects and Other Terrestrial Arthropods Are There on Earth? *Annual Review of Entomology*, 63(1), 31-45.

Suding, K., Lavorel, S., Chapin I., Cornelissen, J., Díaz, S., Garnier, E., Goldberg, D., Hooper, D., Jackson, S., & Navas, M. 2008. Scaling environmental change through the community-level: A trait-based response-and-effect framework for plants. *Global Change Biology*, 14(5), 1125-1140.

Summerville, K., & Crist, T. 2004. Contrasting effects of habitat quantity and quality on moth communities in fragmented landscapes. *Ecography*, 27(1), 3-12

Šumpich, J. & Konvička, M., 2012. Moths and management of a grassland reserve: regular mowing and temporary abandonment support different species. *Biológia*, 67(5), 973–987.

Swank, W., Waide, T., Crossley, J., & Todd, B. 1981. Insect defoliation enhances nitrate export from forest ecosystems. *Oecologia*, 51(3), 297-299

Thomas, J., 2005. Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. *Philosophical Transactions of the Royal Society*, 360: 339 - 357

Thomas, J., Telfer, M., Roy, D., Preston, C., Greenwood, J., Asher, J., Fox, R., Clarke, R., & Lawton, J. 2004. Comparative losses of British butterflies, birds, and plants and the global extinction crisis. *Science*, 303(5665), pp.1879–1881.

Tichy, L., & Chytry, M. 2006. Statistical determination of diagnostic species for site groups of unequal size. *Journal of Vegetation Science,* 17 (6):809, 2006.

Tilman, D. 2001*. Functional diversity*. In: Levin, S. A. Encyclopaedia of biodiversity. Academic Press, 109-120.

Tikoca, S., Hodge, S., Tuiwawa, M., Brodie, G., Pene, S., & Clayton, J. 2016. An appraisal of sampling methods and effort for investigating moth assemblages in a Fijian forest. *Austral Entomology*, 55(4), 455-462.

Trappe, J., Kunz, F., Weking, S., & Kamp, J. 2017. Grassland butterfly communities of the Western Siberian forest steppe in the light of post-Soviet land abandonment. *Journal of Insect Conservation*, 21(5-6), 813–826.

Tscharntke, T., Tylianakis, J., Rand, T., Didham, R., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T., Dormann, C., Ewers, R., Fründ, J., Holt, R., Holzschuh, A., Klein, A., Kleijn, D., Kremen, C., Landis, D., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W., & Westphal, C. 2012. Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biological Reviews of the Cambridge Philosophical Society*, 87(3), 661-685.

Ubach, A., Páramo, F., Gutiérrez, C., & Stefanescu, C. 2020. Vegetation encroachment drives changes in the composition of butterfly assemblages and species loss in Mediterranean ecosystems*. Insect Conservation and Diversity*, 13(2), 151-161.

Uhl, B., Wölfling, M., & Fiedler, K. 2021. Qualitative and Quantitative Loss of Habitat at Different Spatial Scales Affects Functional Moth Diversity. *Frontiers in Ecology and Evolution*, 9, 2021–04-01, Vol.9.

UK Moths, 2021. Striped Twin-spot Carpet. [online] available: Striped Twin-spot Carpet | UKMoths [Accessed on 07/12/2021]

Valkó, O., Zmihorski, M., Biurrun, I., Loos, J., Labadessa, R., & Venn, S. 2016. Ecology and Conservation of Steppes and Semi-Natural Grasslands. *Hacquetia*, 15(2), 5–14.

van Grunsven, R., Donners, M., Boekee, K., Tichelaar, I., van Geffen, K., Groenendijk, D., Berendse, F., & Veenendaal, E. 2014. Spectral composition of light sources and insect phototaxis, with an evaluation of existing spectral response models. *Journal of Insect Conservation*, 18(2), pp.225–

van Grunsven, R., Becker, J., Peter, S., Heller, S., & Hölker, F. 2019. Long-Term Comparison of Attraction of Flying Insects to Streetlights after the Transition from Traditional Light Sources to Light-Emitting Diodes in Urban and Peri-Urban Settings. *Sustainability*, 11(22), p.6198.

Van Noordwijk, C., Baeten, L, Turin, H., Heijerman, T., Alders, K., Boer, P., Mabelis, A. A., Aukema, B., Noordam, A., Remke, E., Siepel, H., Berg, M. P., Bonte, D. 2017. 17 years of grassland management leads to parallel local and regional biodiversity shifts among a wide range of taxonomic groups. *Biodiversity and Conservation*, 26(3), 717–734.

van Swaay, C. 2002. The importance of calcareous grasslands for butterflies in Europe. *Biological Conservation*, 104(3), 315–318.

Villéger, S., Mason, N., & Mouillot, D. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology,* 89:2290-2301.

Vincent, P. 1995. Limestone Pavements in the British Isles: A Review. *The Geographical Journal,* 161(3), 265-274.

Violle, C., Navas, M., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. 2007. Let the Concept of Trait Be Functional. *Oikos*, 116(5), 882-892.

Wagner, D. 2020. Insect Declines in the Anthropocene. *Annual Review of Entomology,* 65(1), 457-480.

WallisDeVries, M. 2014. Linking species assemblages to environmental change: Moving beyond the specialist-generalist dichotomy. *Basic and Applied Ecology*, 15(4), 279-287.

WallisDeVries, M., Poschlod, P. & Willems, J. 2002. Challenges for the conservation of calcareous grasslands in north-western Europe: integrating the requirements of flora and fauna. *Biological Conservation*, 104(3), 265–273.

Ward, S., & Evans, D. 1976. Conservation assessment of British limestone pavements based on floristic criteria. *Biological Conservation*, 9(3), 217-233.

Waring, P., & Townsend, M. 2017. *Field Guide to the Moths of Great Britain and Ireland.* Third edition. Bloomsbury Publishing Plc. London.

Warren, M. 1995. *Managing local microclimates for the high brown fritillary, Argynnis adippe. In Ecology and conservation of butterflies* (pp. 198-210). Springer, Dordrecht.

Warren, M., & Bourn, N. 2010. Ten challenges for 2010 and beyond to conserve Lepidoptera in Europe. *Journal of Insect Conservation*, 15(1-2), 321-326.

Wehn, S., Taugourdeau, S., Johansen, L., Hovstad, K., & Tanentzap, A. 2017. Effects of abandonment on plant diversity in semi-natural grasslands along soil and climate gradients. *Journal of Vegetation Science,* 28(4), 838-847.

Wenzel, M., Schmitt, T., Weitzel, M., & Seitz, A. 2006. The severe decline of butterflies on western German calcareous grasslands during the last 30 years: A conservation problem. *Biological Conservation*, 128(4), 542-552.

Whittaker, T. 2020. *Ingleborough Nature Reserves Monitoring: Ninth Report on the Moths Survey 2020.* [online] Available:

https://www.dropbox.com/s/q8t0cio087oy6a4/Ingleborough%20Moths%20Ninth%20Report%202020.pdf?dl=0 [Accessed on 07/01/2022]

Wickham, H. 2016. Ggplot2: Elegant graphics for data analysis (2nd ed.). [online] Springer International Publishing. [Available] https://ggplot2.tidyverse.org

Wildlife and Countryside Act, 1981. *Sites of Special Scientific Interest.* [online] Available: Wildlife and Countryside Act 1981 (legislation.gov.uk) [Accessed on 11/10/2021]

Willems, J., Peet, R., & Bik, L. 1993. Changes in chalk-grassland structure and species richness resulting from selective nutrient additions. *Journal of Vegetation Science*, 4(2), 203-212.

Willis, S., 2011. The classification and management of limestone pavements : an endangered habitat. Thesis. University of Liverpool.

Willott, E. 2017. The ecology of Anania funebris, a nationally scarce day-flying moth, in South Cumbria, UK. Thesis. Lancaster University.

Wilson, S. & Fernández, F. 2013. *National survey of limestone pavement and associated habitats in Ireland: Irish Wildlife Manuals, No. 73*. National Parks and Wildlife Service, Department of Arts, Heritage and the Gaeltacht, Ireland.

Wilson, R., & Fox, R., 2021. Insect responses to global change offer signposts for biodiversity and conservation*. Ecological Entomology*, 46(4), 699–717.

Woodcock, B. *et al.,* 2005. Grazing management of calcareous grasslands and its implications for the conservation of beetle communities. *Biological Conservation*, 125(2), 193–202.

Woodland Trust., 2019. *Dalton Crags.* [Online] Available : https://www.woodlandtrust.org.uk/visiting-woods/wood/12521/dalton-crags/ [Accessed on 20/04/2021]

Xu, J. & Wang, Q., 2010. Form and nature of precopulatory sexual selection in both sexes of a moth. *Naturwissenschaften*, 97(7), pp.617–625.

Yela, J., & Holyoak, M. 1997. Effects of moonlight and meteorological factors on light and bait trap catches of noctuid moths (Lepidoptera: Noctuidae). *Environmental Entomology,* 26(6), 1283-1290.

Appendices

Appendix 1. List of all species recorded during sampling in June, July and August 2021, ordered by the classification used in the British checklist devised by Agassiz, Bevan and Heckford (2013). Both the taxon and vernacular are provided for each species along with their family, the numner of individuals of each werwe sampled and their national status.

Code	Taxon	Vernacular	Family	Individuals	Status
3.003	*Korscheltellus fusconebulosa*	Map-winged Swift	Hepialidae	3	Local
5.001	*Opostega salaciella*	a moth	Opostegidae	2	Local
7.012	*Nematopogon schwarziellus*	a moth	Adelidae	1	Common
12.036	*Monopis laevigella*	Skin Moth	Tineidae	1	Common
15.014	*Gracillaria syringella*	a moth	Gracillariidae	1	Common
15.015	*Aspilapteryx tringipennella*	a moth	Gracillariidae	3	Common
15.029	*Parornix devoniella*	a moth	Gracillariidae	1	Common
15.056	*Phyllonorycter salicicolella*	a moth	Gracillariidae	1	Common
16.001	*Yponomeuta evonymella*	Bird-cherry Ermine	Yponomeutidae	2	Common
16.019	*Paraswammerdamia albicapitella*	a moth	Yponomeutidae	1	Common
16.02	*Paraswammerdamia nebulella*	a moth	Yponomeutidae	9	Common
17.012	*Ypsolopha sequella*	a moth	Ypsolophidae	1	Common
18.001	*Plutella xylostella*	Diamond-back Moth	Plutellaidae	3	Migrant
20.006	*Argyresthia dilectella*	a moth	Plutellaidae	2	Nationally Scarce B
20.022	*Argyresthia bonnetella*	a moth	Argyresthiidae	1	Common
32.038	*Depressaria badiella*	a moth	Depressariidae	9	Local
35.001	*Aproaerema sangiella*	a moth	Gelechiidae	12	Nationally Scarce A
35.017	*Neofaculta ericetella*	a moth	Gelechiidae	2	Common
35.022	*Dichomeris marginella*	Juniper Webber	Gelechiidae	3	Local
35.026	*Acompsia cinerella*	a moth	Gelechiidae	2	Local
35.04	*Bryotropha terrella*	a moth	Gelechiidae	3	Common
35.046	*Bryotropha senectella*	a moth	Gelechiidae	8	Local
35.049	*Bryotropha similis*	a moth	Gelechiidae	1	Local
35.065	*Monochroa cytisella*	a moth	Gelechiidae	7	Local
35.081	*Oxypteryx atrella*	a moth	Gelechiidae	1	Local
35.093	*Mirificarma mulinella*	a moth	Gelechiidae	1	Common
35.12	*Scrobipalpa artemisiella*	Thyme Moth	Gelechiidae	5	Nationally Scarce B
35.141	*Teleiodes vulgella*	a moth	Gelechiidae	2	Common
37.048	*Coleophora mayrella*	a moth	Coleophoridae	3	Common
37.063	*Coleophora albicosta*	a moth	Coleophoridae	9	Common

37.099	*Coleophora striatipennella*	a moth	Coleophoridae	2	Common
38.008	*Elachista triseriatella*	a moth	Elachistidae	73	Nationally Scarce A
38.017	*Elachista adscitella*	a moth	Elachistidae	219	Nationally Scarce B
38.023	*Elachista biatomella*	a moth	Elachistidae	1	Nationally Scarce B
38.025	*Elachista atricomella*	a moth	Elachistidae	1	Common
38.037	*Elachista canapennella*	a moth	Elachistidae	2	Common
39.001	*Blastodacna hellerella*	a moth	Parametriotidae	1	Common
41.002	*Blastobasis adustella*	a moth	Blastobasidae	19	Common
41.003	*Blastobasis lacticolella*	a moth	Blastobasidae	7	Common
45.004	*Platyptilia gonodactyla*	Triangle Plume	Pterophoridae	1	Common
45.013	*Stenoptilia bipunctidactyla*	Twin-spot Plume	Pterophoridae	2	Common
45.033	*Merrifieldia leucodactyla*	Thyme Plume	Pterophoridae	1	Local
45.037	*Oidaematophorus lithodactyla*	Dusky Plume	Pterophoridae	1	Local
46.001	*Schreckensteinia festaliella*	a moth	Schreckensteiniidae	1	Common
49.025	*Pandemis cerasana*	Barred Fruit-tree Tortrix	Tortricidae	2	Common
49.036	*Clepsis rurinana*	a moth	Tortricidae	3	pRDB1
49.045	*Eana osseana*	a moth	Tortricidae	63	Local
49.048	*Eana penziana bellana*	a moth	Tortricidae	122	
49.059	*Tortrix viridana*	Green Oak Tortrix	Tortricidae	1	Common
49.06	*Aleimma loeflingiana*	a moth	Tortricidae	1	Common
49.07	*Acleris rhombana*	Rhomboid Tortrix	Tortricidae	1	Common
49.077	*Acleris variegana*	Garden Rose Tortrix	Tortricidae	3	Common
49.078	*Acleris aspersana*	a moth	Tortricidae	2	Common
49.091	*Pseudargyrotoza conwagana*	a moth	Tortricidae	1	Common
49.097	*Cochylimorpha straminea*	a moth	Tortricidae	1	Common
49.137	*Cochylis dubitana*	a moth	Tortricidae	1	Common
49.139	*Cochylis atricapitana*	a moth	Tortricidae	10	Common
49.156	*Hedya nubiferana*	Marbled Orchard Tortrix	Tortricidae	1	Common
49.157	*Hedya pruniana*	Plum Tortrix	Tortricidae	18	Common
49.161	*Celypha striana*	a moth	Tortricidae	10	Common
49.166	*Celypha lacunana*	a moth	Tortricidae	5	Common
49.194	*Bactra lancealana*	a moth	Tortricidae	2	Common

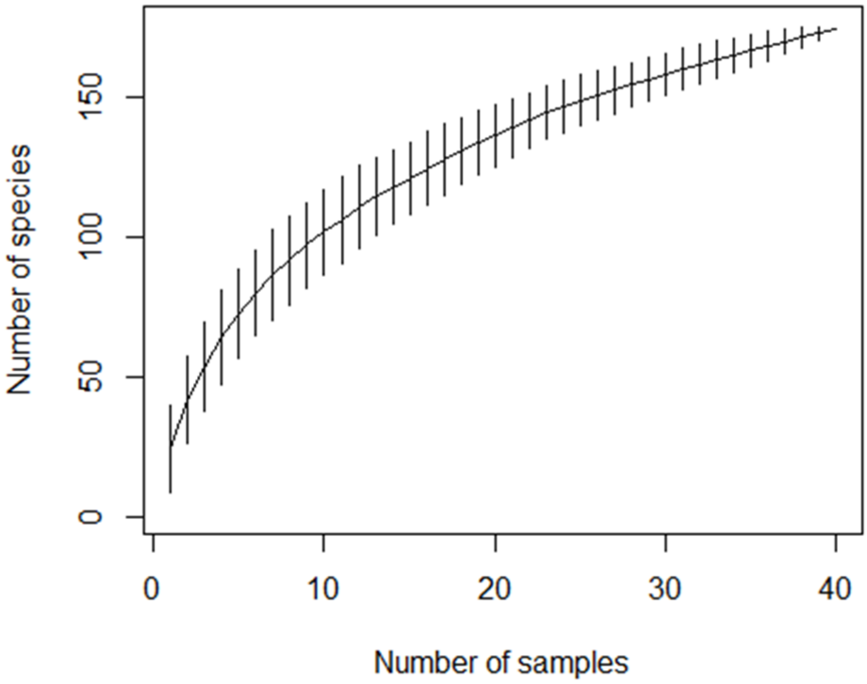
49.225	*Spilonota laricana*	a moth	Tortricidae	1	Local
49.248	*Epinotia tenerana*	Nut Bud Moth	Tortricidae	1	Common
49.265	*Eucosma cana*	a moth	Tortricidae	4	Common
49.266	*Eucosma hohenwartiana*	a moth	Tortricidae	1	Common
49.294	*Notocelia uddmanniana*	Bramble Shoot Moth	Tortricidae	3	Common
49.298	*Notocelia trimaculana*	a moth	Tortricidae	9	Common
49.325	*Cydia ulicetana*	a moth	Tortricidae	1	Common
49.345	*Lathronympha strigana*	a moth	Tortricidae	1	Common
62.035	*Acrobasis advenella*	a moth	Pyralidae	7	Common
62.037	*Acrobasis marmorea*	a moth	Pyralidae	2	Local
62.058	*Phycitodes binaevella*	a moth	Pyralidae	4	Common
62.059	*Phycitodes saxicola*	a moth	Pyralidae	3	Local
63.003	*Pyrausta cingulata*	a moth	Crambidae	7	Nationally Scarce B
63.005	*Pyrausta despicata*	a moth	Crambidae	174	Common
63.006	*Pyrausta aurata*	a moth	Crambidae	3	Common
63.007	*Pyrausta purpuralis*	a moth	Crambidae	30	Common
63.021	*Anania terrealis*	a moth	Crambidae	1	Nationally Scarce A
63.034	*Udea prunalis*	a moth	Crambidae	1	Common
63.062	*Scoparia subfusca*	a moth	Crambidae	10	Common
63.064	*Scoparia ambigualis*	a moth	Crambidae	196	Common
63.066	*Scoparia pyralella*	a moth	Crambidae	48	Common
63.067	*Eudonia lacustrata*	a moth	Crambidae	1	Common
63.069	*Eudonia angustea*	a moth	Crambidae	1	Common
63.073	*Eudonia truncicolella*	a moth	Crambidae	55	Common
63.074	*Eudonia mercurella*	a moth	Crambidae	4	Common
63.08	*Chrysoteuchia culmella*	Garden Grass-veneer	Crambidae	47	Common
63.081	*Crambus pascuella*	a moth	Crambidae	5	Common
63.084	*Crambus ericella*	a moth	Crambidae	35	Nationally Scarce A
63.086	*Crambus lathoniellus*	a moth	Crambidae	62	Common
63.089	*Agriphila tristella*	a moth	Crambidae	54	Common
63.09	*Agriphila inquinatella*	a moth	Crambidae	144	Common
63.093	*Agriphila straminella*	a moth	Crambidae	48	Common
63.095	*Agriphila geniculea*	a moth	Crambidae	26	Common
63.099	*Catoptria pinella*	a moth	Crambidae	2	Common
63.1	*Catoptria margaritella*	a moth	Crambidae	4	Local
63.102	*Catoptria falsella*	a moth	Crambidae	10	Common

63.116	*Cataclysta lemnata*	Small China-mark	Crambidae	1	Common
65.003	*Watsonalla cultraria*	Barred Hook-tip	Drepanidae	3	Local
65.007	*Cilix glaucata*	Chinese Character	Drepanidae	3	Common
65.008	*Thyatira batis*	Peach Blossom	Drepanidae	1	Common
65.009	*Habrosyne pyritoides*	Buff Arches	Drepanidae	4	Common
66.01	*Euthrix potatoria*	Drinker	Lasiocampidae	4	Common
69.003	*Laothoe populi*	Poplar Hawk-moth	Sphingidae	4	Common
70.016	*Idaea aversata*	Riband Wave	Geometridae	6	Common
70.018	*Idaea straminata*	Plain Wave	Geometridae	1	Local
70.04	*Scotopteryx mucronata*	Lead Belle	Geometridae	2	Common
70.041	*Scotopteryx luridata*	July Belle	Geometridae	24	Common
70.054	*Xanthorhoe montanata*	Silver-ground Carpet	Geometridae	1	Common
70.059	*Camptogramma bilineata*	Yellow Shell	Geometridae	8	Common
70.061	*Epirrhoe alternata*	Common Carpet	Geometridae	2	Common
70.063	*Epirrhoe galiata*	Galium Carpet	Geometridae	178	Local
70.074	*Hydriomena furcata*	July Highflyer	Geometridae	15	Common
70.075	*Hydriomena impluviata*	May Highflyer	Geometridae	7	Common
70.078	*Thera cognata*	Chestnut-coloured Carpet	Geometridae	13	Nb
70.079	*Thera britannica*	Spruce Carpet	Geometridae	1	Common
70.081	*Thera obeliscata*	Grey Pine Carpet	Geometridae	1	Common
70.085	*Cidaria fulvata*	Barred Yellow	Geometridae	4	Common
70.087	*Cosmorhoe ocellata*	Purple Bar	Geometridae	23	Common
70.091	*Eulithis populata*	Northern Spinach	Geometridae	16	Common
70.094	*Ecliptopera silaceata*	Small Phoenix	Geometridae	1	Common
70.097	*Dysstroma truncata*	Common Marbled Carpet	Geometridae	2	Common
70.099	*Colostygia olivata*	Beech-green Carpet	Geometridae	48	Local
70.1	*Colostygia pectinataria*	Green Carpet	Geometridae	105	Common
70.102	*Coenotephria salicata*	Striped Twin-spot Carpet	Geometridae	1257	Common

70.111	*Asthena albulata*	Small White Wave	Geometridae	1	Common
70.123	*Triphosa dubitata*	Tissue	Geometridae	1	Local
70.133	*Perizoma alchemillata*	Small Rivulet	Geometridae	1	Common
70.141	*Gymnoscelis rufifasciata*	Double-striped Pug	Geometridae	3	Common
70.151	*Eupithecia pulchellata*	Foxglove Pug	Geometridae	2	Common
70.158	*Eupithecia pusillata*	Juniper Pug	Geometridae	49	Common
70.168	*Eupithecia nanata*	Narrow-winged Pug	Geometridae	4	Common
70.172	*Eupithecia distinctaria*	Thyme Pug	Geometridae	106	Nb
70.173	*Eupithecia centaureata*	Lime-speck Pug	Geometridae	5	Common
70.179	*Eupithecia absinthiata*	Wormwood Pug	Geometridae	3	Common
70.187	*Eupithecia icterata*	Tawny Speckled Pug	Geometridae	3	Common
70.192	*Aplocera plagiata*	Treble-bar	Geometridae	12	Common
70.207	*Lomaspilis marginata*	Clouded Border	Geometridae	8	Common
70.222	*Petrophora chlorosata*	Brown Silver-line	Geometridae	55	Common
70.223	*Plagodis pulveraria*	Barred Umber	Geometridae	2	Local
70.226	*Opisthograptis luteolata*	Brimstone Moth	Geometridae	3	Common
70.236	*Ennomos erosaria*	September Thorn	Geometridae	1	Common
70.238	*Selenia lunularia*	Lunar Thorn	Geometridae	3	Local
70.241	*Crocallis elinguaria*	Scalloped Oak	Geometridae	14	Common
70.252	*Biston betularia*	Peppered Moth	Geometridae	2	Common
70.258	*Peribatodes rhomboidaria*	Willow Beauty	Geometridae	64	Common
70.265	*Alcis repandata*	Mottled Beauty	Geometridae	1	Common
70.27	*Ectropis bistortata*	Engrailed	Geometridae	5	Common
70.277	*Cabera pusaria*	Common White Wave	Geometridae	3	Common
70.28	*Lomographa temerata*	Clouded Silver	Geometridae	2	Common
70.283	*Campaea margaritaria*	Light Emerald	Geometridae	9	Common
70.284	*Hylaea fasciaria*	Barred Red	Geometridae	1	Common
70.287	*Charissa obscurata*	Annulet	Geometridae	137	Local
70.297	*Pseudoterpna pruinata*	Grass Emerald	Geometridae	8	Common
71.02	*Pterostoma palpina*	Pale Prominent	Notodontidae	1	Common
71.021	*Ptilodon capucina*	Coxcomb Prominent	Notodontidae	2	Common
71.025	*Phalera bucephala*	Buff-tip	Notodontidae	7	Common

72.002	*Rivula sericealis*	Straw Dot	Erebidae	1	Common
72.019	*Spilosoma lutea*	Buff Ermine	Erebidae	3	Common
72.02	*Spilosoma lubricipeda*	White Ermine	Erebidae	1	Common
72.031	*Tyria jacobaeae*	Cinnabar	Erebidae	7	Common
72.036	*Nudaria mundana*	Muslin Footman	Erebidae	49	Local
72.043	*Eilema depressa*	Buff Footman	Erebidae	1	Local
72.044	*Eilema griseola*	Dingy Footman	Erebidae	4	Common
72.045	*Eilema lurideola*	Common Footman	Erebidae	209	Common
72.053	*Herminia tarsipennalis*	Fan-foot	Erebidae	1	Common
73.032	*Colocasia coryli*	Nut-tree Tussock	Noctuidae	15	Common
73.045	*Acronicta rumicis*	Knot Grass	Noctuidae	1	Common
73.061	*Stilbia anomala*	Anomalous	Noctuidae	57	Local
73.084	*Bryophila domestica*	Marbled Beauty	Noctuidae	1	Common
73.096	*Hoplodrina octogenaria*	Uncertain	Noctuidae	2	Common
73.097	*Hoplodrina blanda*	Rustic	Noctuidae	57	Common
73.102	*Rusina ferruginea*	Brown Rustic	Noctuidae	111	Common
73.109	*Thalpophila matura*	Straw Underwing	Noctuidae	93	Common
73.114	*Euplexia lucipara*	Small Angle Shades	Noctuidae	4	Common
73.128	*Amphipoea oculea*	Ear Moth	Noctuidae	7	Common
73.131	*Luperina testacea*	Flounced Rustic	Noctuidae	13	Common
73.146	*Photedes captiuncula*	Least Minor	Noctuidae	4	RDB3
73.154	*Apamea remissa*	Dusky Brocade	Noctuidae	96	Common
73.158	*Apamea sordens*	Rustic Shoulder-knot	Noctuidae	9	Common
73.162	*Apamea monoglypha*	Dark Arches	Noctuidae	84	Common
73.169	*Mesapamea secalis*	Common Rustic	Noctuidae	13	Common
73.17	*Mesapamea didyma*	Lesser Common Rustic	Noctuidae	2	Common
73.174	*Oligia latruncula*	Tawny Marbled Minor	Noctuidae	2	Common
73.238	*Mniotype adusta*	Dark Brocade	Noctuidae	9	Common
73.252	*Tholera cespitis*	Hedge Rustic	Noctuidae	48	Common
73.253	*Tholera decimalis*	Feathered Gothic	Noctuidae	1	Common
73.254	*Cerapteryx graminis*	Antler Moth	Noctuidae	58	Common

73.255	*Anarta trifolii*	Nutmeg	Noctuidae	1	Common
73.261	*Polia nebulosa*	Grey Arches	Noctuidae	2	Common
73.271	*Ceramica pisi*	Broom Moth	Noctuidae	23	Common
73.273	*Hada plebeja*	Shears	Noctuidae	48	Common
73.279	*Hecatera bicolorata*	Broad-barred White	Noctuidae	1	Common
73.289	*Mythimna pudorina*	Striped Wainscot	Noctuidae	2	Local
73.293	*Mythimna impura*	Smoky Wainscot	Noctuidae	6	Common
73.298	*Mythimna ferrago*	Clay	Noctuidae	4	Common
73.317	*Agrotis exclamationis*	Heart and Dart	Noctuidae	7	Common
73.32	*Agrotis clavis*	Heart and Club	Noctuidae	4	Common
73.329	*Ochropleura plecta*	Flame Shoulder	Noctuidae	2	Common
73.331	*Diarsia dahlii*	Barred Chestnut	Noctuidae	1	Local
73.333	*Diarsia mendica*	Ingrailed Clay	Noctuidae	45	Common
73.334	*Diarsia rubi*	Small Square-spot	Noctuidae	5	Common
73.338	*Lycophotia porphyrea*	True Lover's Knot	Noctuidae	117	Common
73.341	*Standfussiana lucernea*	Northern Rustic	Noctuidae	88	Local
73.342	*Noctua pronuba*	Large Yellow Underwing	Noctuidae	114	Common
73.345	*Noctua comes*	Lesser Yellow Underwing	Noctuidae	36	Common
73.348	*Noctua janthe*	Lesser Broad-bordered Yellow Underwing	Noctuidae	2	Common
73.353	*Xestia baja*	Dotted Clay	Noctuidae	18	Common
73.355	*Xestia castanea*	Neglected Rustic	Noctuidae	2	Local
73.357	*Xestia xanthographa*	Square-spot Rustic	Noctuidae	8	Common
73.36	*Xestia ditrapezium*	Triple-spotted Clay	Noctuidae	1	Local
73.361	*Xestia triangulum*	Double Square-spot	Noctuidae	2	Common
74.003	*Nola cucullatella*	Short-cloaked Moth	Nolidae	1	Common



Appendix 2. Species accumulation curve for samples taken from Hutton Roof and Farleton Knott in June and July 2021.

Appendix 3. Moth species lists for the calcareous grassland and limestone pavement habitats and the abundance of each caught within the respective habitats. Species may occur in both habitats.

Grassland species list		Pavement species list	
Taxon	**Abundance**	**Taxon**	**Abundance**
Acompsia cinerella	2	*Acrobasis advenella*	2
Acrobasis advenella	5	*Acrobasis marmorea*	2
Agriphila inquinatella	56	*Acronicta rumicis*	1
Agriphila straminella	41	*Agriphila inquinatella*	28
Agriphila tristella	8	*Agriphila straminella*	4
Agrotis clavis	3	*Agrotis clavis*	1
Agrotis exclamationis	7	*Anania terrealis*	1
Alcis repandata	1	*Anarta trifolii*	1
Aleimma loeflingiana	1	*Apamea monoglypha*	52
Apamea monoglypha	27	*Apamea remissa*	48
Apamea remissa	42	*Apamea sordens*	4
Apamea sordens	5	*Aplocera plagiata*	4

Aplocera plagiata	8
Aproaerema sangiella	7
Asthena albulata	1
Biston betularia	1
Blastobasis lacticolella	5
Blastodacna hellerella	1
Bryotropha senectella	3
Bryotropha similis	1
Cabera pusaria	3
Campaea margaritaria	6
Camptogramma bilineata	2
Catoptria margaritella	1
Celypha lacunana	3
Celypha striana	9
Ceramica pisi	11
Cerapteryx graminis	2
Charissa obscurata	11
Chrysoteuchia culmella	40
Cidaria fulvata	2
Cochylis atricapitana	4
Coenotephria salicata	36
Coleophora albicosta	1
Coleophora mayrella	2
Coleophora striatipennella	2
Colocasia coryli	5
Colostygia olivata	13
Colostygia pectinataria	43
Cosmorhoe ocellata	2
Crambus ericella	32
Crambus lathoniellus	33
Crambus pascuella	2
Crocallis elinguaria	4
Diarsia mendica	23
Dysstroma truncata	1
Eana osseana	27
Eana penziana bellana	30
Ectropis bistortata	2
Eilema griseola	1
Eilema lurideola	70
Elachista adscitella	42
Elachista triseriatella	59
Epirrhoe galiata	34
Eucosma cana	4
Eudonia lacustrata	1
Eudonia mercurella	4
Eudonia truncicolella	2
Eulithis populata	6
Eupithecia absinthiata	2

Aproaerema sangiella	2
Argyresthia dilectella	2
Bactra lancealana	1
Biston betularia	1
Blastobasis lacticolella	1
Bryophila domestica	1
Bryotropha senectella	2
Campaea margaritaria	2
Camptogramma bilineata	2
Cataclysta lemnata	1
Catoptria falsella	3
Celypha lacunana	2
Celypha striana	1
Ceramica pisi	12
Charissa obscurata	81
Chrysoteuchia culmella	7
Cidaria fulvata	2
Cilix glaucata	2
Clepsis rurinana	3
Cochylimorpha straminea	1
Cochylis atricapitana	5
Coenotephria salicata	136
Coleophora albicosta	8
Coleophora mayrella	1
Colocasia coryli	10
Colostygia olivata	34
Colostygia pectinataria	53
Cosmorhoe ocellata	5
Crambus ericella	5
Crambus lathoniellus	29
Crambus pascuella	3
Crocallis elinguaria	3
Cydia ulicetana	1
Diarsia mendica	22
Dichomeris marginella	1
Eana osseana	2
Eana penziana bellana	85
Ectropis bistortata	1
Eilema depressa	1
Eilema lurideola	131
Elachista adscitella	47
Elachista atricomella	1
Elachista triseriatella	13
Epirrhoe alternata	1
Epirrhoe galiata	107
Eucosma hohenwartiana	1
Eudonia truncicolella	1
Eulithis populata	10

Eupithecia centaureata	2
Eupithecia distinctaria	31
Eupithecia nanata	1
Eupithecia pusillata	1
Euplexia lucipara	1
Euthrix potatoria	2
Gymnoscelis rufifasciata	1
Habrosyne pyritoides	2
Hada plebeja	19
Hedya pruniana	11
Herminia tarsipennalis	1
Hoplodrina blanda	24
Hoplodrina octogenaria	2
Idaea aversata	3
Idaea straminata	1
Korscheltellus fusconebulosa	2
Lomaspilis marginata	4
Lomographa temerata	2
Lycophotia porphyrea	18
Mesapamea secalis	3
Mniotype adusta	3
Monochroa cytisella	4
Mythimna ferrago	2
Mythimna impura	1
Mythimna pudorina	2
Neofaculta ericetella	1
Noctua pronuba	13
Nola cucullatella	1
Notocelia trimaculana	4
Notocelia uddmanniana	2
Nudaria mundana	37
Ochropleura plecta	1
Oidaematophorus lithodactyla	1
Oligia latruncula	1
Opisthograptis luteolata	1
Opostega salaciella	2
Pandemis cerasana	1
Paraswammerdamia nebulella	2
Parornix devoniella	1
Peribatodes rhomboidaria	33
Petrophora chlorosata	33
Phalera bucephala	5
Photedes captiuncula	1
Phyllonorycter salicicolella	1
Plagodis pulveraria	1
Plutella xylostella	1
Polia nebulosa	2
Pseudoterpna pruinata	4

Eupithecia absinthiata	1
Eupithecia centaureata	3
Eupithecia distinctaria	73
Eupithecia nanata	6
Eupithecia pulchellata	2
Eupithecia pusillata	6
Euplexia lucipara	3
Euthrix potatoria	2
Gracillaria syringella	1
Gymnoscelis rufifasciata	1
Habrosyne pyritoides	2
Hada plebeja	29
Hecatera bicolorata	1
Hedya nubiferana	1
Hedya pruniana	7
Hoplodrina blanda	32
Hydriomena impluviata	7
Hylaea fasciaria	1
Idaea aversata	2
Korscheltellus fusconebulosa	1
Laothoe populi	4
Lathronympha strigana	1
Lomaspilis marginata	4
Lycophotia porphyrea	20
Merrifieldia leucodactyla	1
Mesapamea secalis	4
Mniotype adusta	6
Monochroa cytisella	3
Monopis laevigella	1
Mythimna ferrago	2
Mythimna impura	2
Nematopogon schwarziellus	1
Neofaculta ericetella	1
Noctua pronuba	20
Notocelia trimaculana	5
Notocelia uddmanniana	1
Nudaria mundana	12
Ochropleura plecta	1
Oligia latruncula	1
Opisthograptis luteolata	1
Paraswammerdamia nebulella	6
Peribatodes rhomboidaria	30
Petrophora chlorosata	22
Phalera bucephala	2
Photedes captiuncula	3
Phycitodes binaevella	4
Phycitodes saxicola	3
Plagodis pulveraria	1

Ptilodon capucina	1	*Plutella xylostella*	2
Pyrausta despicata	149	*Pseudargyrotoza conwagana*	1
Pyrausta purpuralis	26	*Pseudoterpna pruinata*	3
Rusina ferruginea	70	*Pyrausta aurata*	1
Scoparia ambigualis	114	*Pyrausta cingulata*	6
Scoparia pyralella	25	*Pyrausta despicata*	8
Scoparia subfusca	2	*Pyrausta purpuralis*	4
Scotopteryx luridata	20	*Rivula sericealis*	1
Scotopteryx mucronata	1	*Rusina ferruginea*	41
Scrobipalpa artemisiella	1	*Schreckensteinia festaliella*	1
Selenia lunularia	2	*Scoparia ambigualis*	54
Spilosoma lubricipeda	1	*Scoparia pyralella*	23
Spilosoma lutea	2	*Scoparia subfusca*	8
Standfussiana lucernea	14	*Scotopteryx luridata*	4
Teleiodes vulgella	1	*Scotopteryx mucronata*	1
Thalpophila matura	60	*Scrobipalpa artemisiella*	4
Thera britannica	1	*Selenia lunularia*	1
Thera cognata	5	*Spilonota laricana*	1
Thera obeliscata	1	*Spilosoma lutea*	1
Thyatira batis	1	*Standfussiana lucernea*	53
Tyria jacobaeae	5	*Stenoptilia bipunctidactyla*	1
Xestia baja	2	*Teleiodes vulgella*	1
Xestia triangulum	1	*Thalpophila matura*	20
		Thera cognata	7
		Tortrix viridana	1
		Tyria jacobaeae	2
		Udea prunalis	1
		Xanthorhoe montanata	1
		Xestia baja	7
		Xestia ditrapezium	1
		Xestia triangulum	1

Appendix 4. List of Macro-moths used in the trait analysis including their larval hostplant groups, overwintering stage, larval feeding specificity, voltinism, forewing length and the number of habitats they occur in (Cook *et al.,* 2021).

Binomial	**Vernacular**	**Hostplant group**	**Feeding specificity**	**Overwintering stage**	**Voltinism**	**Forewing length**	**Habitat occurence**
Acronicta rumicis	Knot Grass	Herb/Trees and shrubs	Polyphagous	Pupa	Multivoltine	18	4
Agrotis clavis	Heart and Club	Herbs	Polyphagous	Larva	Univoltine	16	2
Agrotis exclamationis	Heart and Dart	Herbs	Polyphagous	Larva	Multivoltine	17	3
Alcis repandata	Mottled Beauty	Herb/Trees and shrubs	Polyphagous	Larva	Univoltine	22.5	4
Anarta trifolii	Nutmeg	Herbs	Polyphagous	Pupa	Multivoltine	16	1
Apamea monoglypha	Dark Arches	Grasses	Oligophagous	Larva	Univoltine	22.5	6

Apamea remissa	Dusky Brocade	Grasses	Oligophagous	Larva	Univoltine	18	3
Apamea sordens	Rustic Shoulder-knot	Grasses	Oligophagous	Larva	Univoltine	17.5	2
Aplocera plagiata	Treble-bar	Herbs	Oligophagous	Pupa	Multivoltine	20.5	3
Asthena albulata	Small White Wave	Trees and shrubs	Polyphagous	Pupa	Univoltine	10	1
Biston betularia	Peppered Moth	Trees and shrubs	Polyphagous	Pupa	Univoltine	25	2
Bryophila domestica	Marbled Beauty	Lichen and algae	Oligophagous	Larva	Univoltine	13	2
Cabera pusaria	Common White Wave	Trees and shrubs	Polyphagous	Pupa	Multivoltine	16	2
Campaea margaritaria	Light Emerald	Trees and shrubs	Polyphagous	Larva	Multivoltine	22	2
Camptogramma bilineata	Yellow Shell	Herbs	Polyphagous	Larva	Univoltine	14.5	5
Ceramica pisi	Broom Moth	Herb/Trees and shrubs	Polyphagous	Pupa	Univoltine	18	6
Cerapteryx graminis	Antler Moth	Grasses	Polyphagous	Egg	Univoltine	14.5	3
Charissa obscurata	Annulet	Herb/Trees and shrubs	Polyphagous	Larva	Univoltine	16.5	3
Cidaria fulvata	Barred Yellow	Trees and shrubs	Oligophagous	Egg	Univoltine	13	2
Cilix glaucata	Chinese Character	Trees and shrubs	Oligophagous	Pupa	Multivoltine	11.5	1
Coenotephria salicata	Striped Twin-spot Carpet	Herbs	Oligophagous	Larva	Univoltine	13.5	5
Colocasia coryli	Nut-tree Tussock	Trees and shrubs	Polyphagous	Pupa	Multivoltine	15.5	2
Colostygia olivata	Beech-green Carpet	Herbs	Oligophagous	Larva	Univoltine	14	5
Colostygia pectinataria	Green Carpet	Herbs	Polyphagous	Larva	Multivoltine	13.5	6
Cosmorhoe ocellata	Purple Bar	Herbs	Oligophagous	Larva	Multivoltine	14	6
Crocallis elinguaria	Scalloped Oak	Trees and shrubs	Polyphagous	Egg	Univoltine	20	2
Diarsia mendica	Ingrailed Clay	Herb/Trees and shrubs	Polyphagous	Larva	Univoltine	15	5
Dysstroma truncata	Common Marbled Carpet	Herb/Trees and shrubs	Polyphagous	Larva	Multivoltine	16.5	4
Ectropis bistortata	Engrailed	Trees and shrubs	Polyphagous	Pupa	Multivoltine	18.5	2
Eilema depressa	Buff Footman	Lichen and algae	Polyphagous	Larva	Univoltine	16	3
Eilema griseola	Dingy Footman	Lichen and algae	Polyphagous	Larva	Univoltine	16.5	5
Eilema lurideola	Common Footman	Lichen and algae	Polyphagous	Larva	Univoltine	15.5	3
Epirrhoe alternata	Common Carpet	Herbs	Polyphagous	Pupa	Multivoltine	13.5	6
Epirrhoe galiata	Galium Carpet	Herbs	Oligophagous	Pupa	Multivoltine	14	4
Eulithis populata	Northern Spinach	Trees and shrubs	Polyphagous	Egg	Univoltine	15.5	4
Eupithecia absinthiata	Wormwood Pug / Ling Pug	Herb/Trees and shrubs	Polyphagous	Pupa	Univoltine	12	5
Eupithecia centaureata	Lime-speck Pug	Herb/Trees and shrubs	Polyphagous	Pupa	Multivoltine	11	3
Eupithecia distinctaria	Thyme Pug	Herbs	Monophagous	Pupa	Univoltine	9	2

Eupithecia nanata	Narrow-winged Pug	Trees and shrubs	Monophagous	Pupa	Multivoltine	10.5	3
Eupithecia pulchellata	Foxglove Pug	Herbs	Monophagous	Pupa	Univoltine	11	5
Eupithecia pusillata	Juniper Pug	Trees and shrubs	Oligophagous	Egg	Univoltine	10	3
Euplexia lucipara	Small Angle Shades	Herb/Trees and shrubs	Polyphagous	Pupa	Univoltine	15.5	4
Euthrix potatoria	Drinker	Grasses	Polyphagous	Larva	Univoltine	28	6
Gymnoscelis rufifasciata	Double-striped Pug	Herb/Trees and shrubs	Polyphagous	Pupa	Multivoltine	9	4
Habrosyne pyritoides	Buff Arches	Trees and shrubs	Oligophagous	Pupa	Univoltine	18.5	2
Hada plebeja	Shears	Herbs	Polyphagous	Pupa	Univoltine	15.5	2
Hecatera bicolorata	Broad-barred White	Herbs	Oligophagous	Pupa	Univoltine	14	1
Herminia tarsipennalis	Fan-foot	Trees and shrubs	Polyphagous	Larva	Univoltine	14.5	1
Hoplodrina blanda	Rustic	Grass/Trees and shrubs	Polyphagous	Larva	Univoltine	14.5	2
Hoplodrina octogenaria	Uncertain	Herbs	Polyphagous	Larva	Univoltine	15	4
Hydriomena furcata	July Highflier	Trees and shrubs	Polyphagous	Egg	Univoltine	16	5
Hydriomena impluviata	May Highflier	Trees and shrubs	Monophagous	Pupa	Univoltine	14.5	2
Hylaea fasciaria	Barred Red	Trees and shrubs	Oligophagous	Larva	Univoltine	19	3
Idaea aversata	Riband Wave	Herbs	Polyphagous	Larva	Univoltine	15	4
Korscheltellus fusconebulosa	Map-winged Swift	Herbs	Polyphagous	Larva	Univoltine	20	5
Laothoe populi	Poplar Hawk-moth	Trees and shrubs	Oligophagous	Pupa	Univoltine	38	3
Lomaspilis marginata	Clouded Border	Trees and shrubs	Oligophagous	Pupa	Univoltine	12.5	5
Lomographa temerata	Clouded Silver	Trees and shrubs	Oligophagous	Pupa	Univoltine	14	2
Lycophotia porphyrea	True Lover's Knot	Trees and shrubs	Oligophagous	Larva	Univoltine	13.5	4
Mesapamea secalis	Common Rustic	Grasses	Polyphagous	Larva	Univoltine	14	3
Mniotype adusta	Dark Brocade	Herb/Trees and shrubs	Polyphagous	Larva	Univoltine	19.5	5
Mythimna ferrago	Clay	Grass/Herb	Polyphagous	Larva	Univoltine	16.5	3
Mythimna impura	Smoky Wainscot	Grasses	Polyphagous	Larva	Univoltine	16	6
Mythimna pudorina	Striped Wainscot	Grasses	Oligophagous	Larva	Univoltine	17.5	3
Noctua pronuba	Large Yellow Underwing	Grass/Herb/Trees and shrubs	Polyphagous	Larva	Univoltine	23.5	5
Nola cucullatella	Short-cloaked Moth	Trees and shrubs	Oligophagous	Larva	Univoltine	9	1
Nudaria mundana	Muslin Footman	Lichen and algae	Oligophagous	Larva	Univoltine	11	2
Ochropleura plecta	Flame Shoulder	Herbs	Polyphagous	Pupa	Multivoltine	13.5	4
Oligia latruncula	Tawny Marbled Minor	Grasses	Oligophagous	Larva	Univoltine	12	2

Opisthograptis luteolata	Brimstone Moth	Trees and shrubs	Polyphagous	Pupa	Multivoltine	17.5	2
Peribatodes rhomboidaria	Willow Beauty	Trees and shrubs	Polyphagous	Larva	Multivoltine	20.5	1
Petrophora chlorosata	Brown Silver-line	Herbs	Monophagous	Pupa	Univoltine	16.5	4
Phalera bucephala	Buff-tip	Trees and shrubs	Polyphagous	Pupa	Univoltine	28	2
Photedes captiuncula	Least Minor	Grasses	Polyphagous	Larva	Univoltine	8	2
Plagodis pulveraria	Barred Umber	Trees and shrubs	Monophagous	Pupa	Univoltine	18	2
Polia nebulosa	Grey Arches	Herb/Trees and shrubs	Polyphagous	Larva	Univoltine	23.5	1
Pseudoterpna pruinata	Grass Emerald	Trees and shrubs	Oligophagous	Larva	Univoltine	16.5	5
Ptilodon capucina	Coxcomb Prominent	Trees and shrubs	Polyphagous	Pupa	Multivoltine	19.5	3
Rivula sericealis	Straw Dot	Grasses	Polyphagous	Larva	Multivoltine	14	6
Rusina ferruginea	Brown Rustic	Herb/Trees and shrubs	Polyphagous	Larva	Univoltine	16	4
Scotopteryx luridata	July Belle	Herb/Trees and shrubs	Oligophagous	Larva	Univoltine	17	4
Scotopteryx mucronata	Lead Belle	Herb/Trees and shrubs	Oligophagous	Larva	Univoltine	17	4
Selenia lunularia	Lunar Thorn	Trees and shrubs	Polyphagous	Pupa	Univoltine	19	2
Spilosoma lubricipeda	White Ermine	Herb/Trees and shrubs	Polyphagous	Pupa	Univoltine	20.5	3
Spilosoma lutea	Buff Ermine	Herb/Trees and shrubs	Polyphagous	Pupa	Univoltine	19.5	2
Standfussiana lucernea	Northern Rustic	Herbs	Polyphagous	Larva	Univoltine	19	2
Thalpophila matura	Straw Underwing	Grasses	Oligophagous	Larva	Univoltine	18.5	3
Thera britannica	Spruce Carpet	Trees and shrubs	Polyphagous	Larva	Multivoltine	15	2
Thera cognata	Chestnut-coloured Carpet	Trees and shrubs	Monophagous	Larva	Univoltine	12.5	4
Thera obeliscata	Grey Pine Carpet	Trees and shrubs	Polyphagous	Larva	Multivoltine	15	3
Thyatira batis	Peach Blossom	Herb/Trees and shrubs	Oligophagous	Pupa	Univoltine	17.5	2
Tyria jacobaeae	Cinnabar	Herbs	Polyphagous	Larva	Univoltine	20	3
Xanthorhoe montanata	Silver-ground Carpet	Herbs	Polyphagous	Larva	Univoltine	15.5	4
Xestia baja	Dotted Clay	Herb/Trees and shrubs	Polyphagous	Larva	Univoltine	19	4
Xestia ditrapezium	Triple-spotted Clay	Herb/Trees and shrubs	Polyphagous	Larva	Univoltine	18	3
Xestia triangulum	Double Square-spot	Herb/Trees and shrubs	Polyphagous	Larva	Univoltine	18	1

Appendix 5. LMM output testing the effect of vegetation variables on 19 macro-moth trait CWMs. Unit was included as the random effect for each model and df was estimated by Satterthwiate's method. Significant values are highlighted in bold.

Vector	Fixed Effect	df	F-value	p-value
Specificity monophagous	Negative indicator plant species	1, 33.068	4.68	**0.038***
	Positive indicator plant species	1, 33.163	0.15	0.701
	Non-indicator plant species	1, 36.289	7.24	**0.011***
	Number of forbs in flower	1, 31.700	0.02	0.881
	Vegetation height	1, 36.499	1.95	0.171
	Cover of woody plants	1, 37.176	10.41	**0.003****
	Cover of bryophytes	1, 30.621	0.09	0.762
	Cover of ferns	1, 30.643	0.10	0.748
	Cover of grass	1, 30.511	0.56	0.462
Specificity oligophagous	Negative indicator plant species	1, 35.265	0.30	0.585
	Positive indicator plant species	1, 35.634	5.36	**0.026***
	Non-indicator plant species	1, 38.453	5.21	**0.028***
	Number of forbs in flower	1, 32.935	1.18	0.286
	Vegetation height	1, 38.514	6.40	**0.016***
	Cover of woody plants	1, 39.488	0.97	0.328
	Cover of bryophytes	1, 32.556	2.61	0.116
	Cover of ferns	1, 32.488	0.06	0.813
	Cover of bare ground	1, 30.951	0.06	0.808
Specificity polyphagous	Negative indicator plant species	1, 36.823	2.20	0.146
	Positive indicator plant species	1, 37.309	4.86	**0.034***
	Non-indicator plant species	1, 39.571	10.11	**0.003****
	Number of forbs in flower	1, 34.625	1.26	0.270
	Vegetation height	1, 39.422	4.34	**0.043***
	Cover of woody plants	1, 39.975	0.04	0.836
	Cover of bryophytes	1, 33.060	1.85	0.183
	Cover of ferns	1, 32.842	0.03	0.870
	Cover of grass	1, 32.741	0.13	0.722
Forewing length	Negative indicator plant species	1, 35.101	0.71	0.404
	Positive indicator plant species	1, 35.141	0.73	0.399
	Non-indicator plant species	1, 38.516	4.74	**0.036***
	Flowering herbaceous plant species	1, 32.414	1.15	0.291
	Vegetation height	1, 38.203	2.08	0.158
	Cover of woody plants	1, 39.295	1.63	0.209
	Cover of bryophytes	1, 32.237	0.05	0.825
	Cover of ferns	1, 32.435	1.02	0.320
	Cover of forbs	1, 34.843	0.04	0.847
Univoltine moth species	Negative indicator plant species	1, 33.130	11.62	**0.002****
	Positive indicator plant species	1, 33.173	0.85	0.362
	Non-indicator plant species	1, 35.959	0.00	0.983
	Number of forbs in flower	1, 32.976	1.18	0.285
	Vegetation height	1, 36.183	0.47	0.498

	Cover of woody plants	1, 36.742	2.07	0.158
	Cover of bryophytes	1, 31.043	0.43	0.517
	Cover of ferns	1, 31.074	0.37	0.470
	Cover of grass	1, 30.952	0.36	0.555
Multivoltine moth species	Negative indicator plant species	1, 33.130	11.62	**0.002****
	Positive indicator plant species	1, 33.173	0.85	0.362
	Non-indicator plant species	1, 35.959	0.00	0.983
	Number of forbs in flower	1, 32.976	1.18	0.285
	Vegetation height	1, 36.183	0.47	0.498
	Cover of woody plants	1, 36.742	2.07	0.158
	Cover of bryophytes	1, 31.043	0.43	0.517
	Cover of ferns	1, 31.074	0.37	0.470
	Cover of grass	1, 30.952	0.36	0.555
Overwintering as larvae	Negative indicator plant species	1, 35.268	1.92	0.174
	Positive indicator plant species	1, 35.501	0.56	0.461
	Non-indicator plant species	1, 38.227	4.42	**0.042***
	Number of forbs in flower	1, 33.692	2.57	0.119
	Vegetation height	1, 38.337	0.01	0.904
	Cover of woody plants	1, 39.023	0.69	0.411
	Cover of bryophytes	1, 32.503	0.39	0.539
	Cover of ferns	1, 32.470	0.05	0.800
	Cover of grass	1, 32.352	1.85	0.183
Overwintering as pupae	Negative indicator plant species	1, 33.364	3.08	0.088
	Positive indicator plant species	1, 33.394	0.81	0.373
	Non-indicator plant species	1, 36.001	3.60	0.066
	Number of forbs in flower	1, 32.298	3.65	0.065
	Vegetation height	1, 36.219	0.68	0.416
	Cover of woody plants	1, 36.728	3.62	0.065
	Cover of bryophytes	1, 31.427	0.21	0.646
	Cover of ferns	1, 31.459	0.04	0.833
	Cover of grass	1, 31.343	2.07	0.160
Larval hostplant grasses	Negative indicator plant species	1, 35.149	0.41	0.526
	Positive indicator plant species	1, 35.439	3.29	0.078
	Non-indicator plant species	1, 38.397	2.32	0.136
	Number of forbs in flower	1, 33.379	0.53	0.474
	Vegetation height	1, 38.428	1.40	0.243
	Cover of woody plants	1, 39.183	0.85	0.363
	Cover of bryophytes	1, 32.067	4.96	**0.033***
	Cover of ferns	1, 32.013	0.42	0.523
	Cover of grass	1, 31.890	1.93	0.174
Larval hostplant herbaceous plants	Negative indicator plant species	1, 33.621	0.59	0.446
	Positive indicator plant species	1, 33.706	0.01	0.923
	Non-indicator plant species	1, 36.408	0.00	0.944
	Number of forbs in flower	1, 32.140	1.81	0.188
	Vegetation height	1, 36.653	1.61	0.212

	Cover of woody plants	1, 37.480	2.73	0.107
	Cover of bryophytes	1, 31.685	0.19	0.669
	Cover of ferns	1, 31.774	0.11	0.745
	Cover of bare ground	1, 30.824	3.75	0.062
Larval hostplants trees and shrubs	Negative indicator plant species	1, 32.038	1.89	0.178
	Positive indicator plant species	1, 32.252	0.87	0.358
	Non-indicator plant species	1, 36.015	5.65	**0.023***
	Number of forbs in flower	1, 29.840	0.32	0.574
	Vegetation height	1, 36.291	0.01	0.944
	Cover of woody plants	1, 37.567	0.73	0.397
	Cover of bryophytes	1, 29.281	1.91	0.178
	Cover of ferns	1, 29.351	0.49	0.487
	Cover of bare ground	1, 27.988	0.32	0.574
Larval hostplants lichen and algae	Negative indicator plant species	1, 35.948	0.07	0.799
	Positive indicator plant species	1, 36.434	0.26	0.614
	Non-indicator plant species	1, 39.237	2.69	0.109
	Number of forbs in flower	1, 33.668	7.38	**0.010***
	Vegetation height	1, 39.116	1.66	0.205
	Cover of woody plants	1, 39.849	2.44	0.126
	Cover of bryophytes	1, 32.051	0.09	0.769
	Cover of ferns	1, 31.879	0.63	0.432
	Cover of grass	1, 31.763	4.32	**0.046***
Woodland moth species	Negative indicator plant species	1, 34.424	0.29	0.592
	Positive indicator plant species	1, 34.559	0.01	0.926
	Non-indicator plant species	1, 37.567	0.34	0.564
	Number of forbs in flower	1, 32.929	0.20	0.657
	Vegetation height	1, 37.692	0.03	0.853
	Cover of woody plants	1, 38.391	0.02	0.899
	Cover of bryophytes	1, 31.781	1.14	0.293
	Cover of ferns	1, 31.775	0.03	0.873
	Cover of grass	1, 31.650	7.37	**0.012***
Heathland moth species	Negative indicator plant species	1, 39.956	0.43	0.514
	Positive indicator plant species	1, 39.999	2.41	0.128
	Non-indicator plant species	1, 39.748	3.99	0.052
	Number of forbs in flower	1, 38.637	0.13	0.720
	Vegetation height	1, 39.967	7.21	**0.010***
	Cover of woody plants	1, 38.737	8.75	**0.005****
	Cover of bryophytes	1, 37.086	0.60	0.442
	Cover of ferns	1, 36.101	0.98	0.328
	Cover of grass	1, 36.002	6.94	**0.012***
Moorland moth species	Negative indicator plant species	1, 32.098	2.84	0.102
	Positive indicator plant species	1, 32.000	0.40	0.532
	Non-indicator plant species	1, 35.868	0.06	0.803
	Number of forbs in flower	1, 29.972	1.53	0.226
	Vegetation height	1, 35.603	0.52	0.475

	Cover of woody plants	1, 36.828	1.84	0.183
	Cover of bryophytes	1, 29.643	3.75	0.062
	Cover of ferns	1, 29.928	0.35	0.559
	Cover of forbs	1, 31.820	2.14	0.154
Grassland moth species	Negative indicator plant species	1, 35.389	1.90	0.176
	Positive indicator plant species	1, 35.853	0.49	0.488
	Non-indicator plant species	1, 38.957	0.01	0.915
	Number of forbs in flower	1, 33.113	0.01	0.909
	Vegetation height	1, 38.869	0.10	0.757
	Cover of woody plants	1, 39.696	0.03	0.853
	Cover of bryophytes	1, 31.496	1.83	0.186
	Cover of ferns	1, 31.355	0.35	0.558
	Cover of grass	1, 31.231	0.47	0.500
Wetland habitat species	Negative indicator plant species	1, 37.512	2.46	0.125
	Positive indicator plant species	1, 37.941	0.83	0.367
	Non-indicator plant species	1, 39.726	0.66	0.423
	Number of forbs in flower	1, 35.575	2.52	0.122
	Vegetation height	1, 39.589	0.52	0.474
	Cover of woody plants	1, 39.997	0.92	0.343
	Cover of bryophytes	1, 34.175	0.31	0.581
	Cover of ferns	1, 33.954	0.15	0.701
	Cover of grass	1, 33.868	0.30	0.589
Coastal habitat species	Negative indicator plant species	1, 33.348	3.03	0.091
	Positive indicator plant species	1, 33.426	0.14	0.708
	Non-indicator plant species	1, 36.360	0.08	0.778
	Number of forbs in flower	1, 32.075	0.19	0.664
	Vegetation height	1, 36.567	0.77	0.384
	Cover of woody plants	1, 37.188	1.62	0.212
	Cover of bryophytes	1, 31.062	0.17	0.679
	Cover of ferns	1, 31.086	0.03	0.867
	Cover of grass	1, 30.960	7.32	**0.011***
Montane and upland moth species	Negative indicator plant species	1, 39.736	0.50	0.482
	Positive indicator plant species	1, 39.904	0.09	0.763
	Non-indicator plant species	1, 39.879	2.95	0.094
	Number of forbs in flower	1, 38.079	0.02	0.901
	Vegetation height	1, 39.959	2.53	0.12
	Cover of woody plants	1, 39.085	1.04	0.314
	Cover of bryophytes	1, 36.518	5.01	**0.031***
	Cover of ferns	1, 35.772	0.25	0.622
	Cover of grass	1, 35.642	0.53	0.471