

Grizzled Skippers
(*Pyrgus malvae*) under
threat: Investigating
impacts of climate and
land-use change on an
early successional
habitat UK specialist

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Thesis Abstract

Grizzled Skippers under threat: Investigating impacts of climate and land-use change on an early successional UK specialist

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The interacting forces of land-use and climate change are having unpredictable and idiosyncratic effects on species, both globally and within the United Kingdom. For example, there are some cases where previously threatened species are now expected to benefit from climate change, an outcome which could alleviate pressure on conservation resources and planning.

In our study, we examined one such case; *Pyrgus malvae*, a warm-preferring butterfly and specialist of semi-natural ephemeral habitats in the south of England, which has been in long term decline. Declines were likely driven by habitat loss, but the species was predicted to expand northward under warming temperatures. However, in our investigations of long term abundance records, we found that *P. malvae* declines in the UK were steeper in the north and west of its range, and independent of climate effects, which negates the likelihood of imminent northward expansion.

We then surveyed habitat patches and undertook analysis into signs of higher specificity towards the north or west, and found that habitat requirements were largely similar across its England range. Furthermore, we discovered that many 'significant' determinants of presence and abundance were related to physical structures associated with warm microclimates, reinforcing the already known importance of microclimates for the species.

Having explored the risk to habitat quality for individual populations from habitat degradation, we then investigated the threats to metapopulations from land-use change and habitat loss to continued succession using Individual Based Modelling. We found that increased scrub encroachment in patches decreased overall time spent in habitat (i.e. opportunities for breeding and population growth), and movements between patches (i.e. impacting rescue effects and recolonisations). Additionally, intervention to protect individual sites at expense of others could have positive or negative effects on patch network connectivity, or time spent in habitat. Division of resources between sites should therefore consider desired outcomes at the landscape level.

Based on our own findings, and existing literature, we have made some recommendations on implementing Key Performance Indicators ([KPIs](#)) for *P. malvae* for conservation

assessment and standardisation to combat gradual loss of populations around the country, which would increase the likelihood of collapse of population networks. More sustainable approaches to conservation will likely be needed in an environment with changing climate, longer growing seasons, higher nutrient deposition, and increasing land-use demands, in order to prevent further losses of *P. malvae* and species like it.

CHAPTER 1

General Introduction

In this thesis, I explore the interacting pressures of climate change and land-use change on a threatened butterfly species in the UK, *Pyrgus malvae*. The UK, like many parts of Europe, has undergone a relatively recent and dramatic transformation in its landscape structure, resulting in the loss of much of its natural habitat and by association, the declines of once abundant animal and plant species.

P. malvae is a valuable case study of a species driven into long-term decline by land-use changes, including agricultural intensification, abandonment, and eutrophication, but which was expected to benefit from warming temperatures as a thermophilic species historically restricted to warmer southern regions in England and Wales.

The species therefore is an interesting example of a species where, in a world where climate change is considered to be a threat for many species, a changing climate may instead mediate the effects of land-use change. Warming temperatures could, in this case, halt or reverse declines of a threatened species, and facilitate its range expansion north into regions previously thought to be climatically unsuitable. However, no signs of recovery or northern expansion have been thus far observed in the butterfly within the UK.

Understanding why, against expectations, *P. malvae* does not appear to be benefitting in terms of abundance or range extent from climate change will provide valuable insights for conservation and predicting species response to compounding drivers of decline. For example, there are many species which are expected to need to track their shifting climate envelope. Is this species' lack of expansion a sign that, within the UK, habitat fragmentation and barriers to movement could impede or prevent climate-niche-tracking? This is a particularly pressing concern for sedentary specialists with small populations, like *P. malvae*, which are already likely to be more vulnerable to declines.

Here, I aim to explore generally whether this species is showing early signs precipitating northern expansion, effects of climate on population size trends, signs of its habitat suitability requirements being mediated (i.e. relaxed) by climate change, and the species' connectivity between habitat patches in a changing landscape.

1.1. Land-use and Biodiversity in the UK

Many of the targets for biodiversity and habitat creation within the UK are based on the landscape in the past century, prior to recent declines. However, the conventional idea of the 'historical landscape' of the UK, and mainland Europe, is actually fairly recent and bears little resemblance to the changing Holocene and pre-Neolithic era assemblages, dominated by open and closed forest and tundra (Poschlod and WallisDeVries 2002).

Much of the land cover in the UK in the 1800s was semi-natural and the result of anthropogenic land management techniques. Semi-natural grasslands were created by humans clearing and grazing forests in what is now the UK and central Europe for the purposes of agriculture at least 4000 years Before Present (BP) (Poschlod and WallisDeVries 2002). Prior to the period of the Roman Empire, areas of what were previously grazed forests are believed to have been converted into pasture, while arable field rotation systems were established for food crops as well as hay making, used for draught horses and cattle (Green 1990). Patches of semi-natural grassland were often connected through the practice of transhumance shepherding, which involved moving herds between upland and lowland pasture depending on the time of year (Davies 1941, Poschlod and WallisDeVries 2002).

Meanwhile, many broad-leaf dominated woodlands, particularly in the south-east of Britain, were brought into coppice from the Middle Ages to meet demands for fuel and building materials (Fuller and Warren 1993). Coppicing typically involves regular cutting of trees and intervening periods of regrowth from the cut stumps, in order to produce renewable and easily transportable wood. The practice would often involve rotational cutting, resulting in a mixture of stages of growth within a single woodland. The practice of coppicing reached the north and west of Britain by the 18th century (Fuller and Warren 1993). These traditional practices of the time, amongst others, created a heterogeneous landscape, consisting of a range of seral stages and habitat structures. Prior to the 1900s, semi-natural grassland was believed to cover over 6.5 mha of the land (Fuller 1987), and coppiced woodland over 230kha (Fuller and Warren 1993).

Although land management practices varied over time through the Middle Ages, the late 19th century brought a period of rapid change, driven by globalisation of trade and the industrial revolution (Green 1990, Poschlod and WallisDeVries 2002). The countryside was shaped by land practices motivated by production and profit, and new technologies and transport transformed those practices over the 20th century. By the late 19th century,

policies, market demands, international trade and developing technologies manifested as changes in land management and consequently, the physical landscape (Green 1990, Fuller and Warren 1993). The establishment of the railways in mid-1800s facilitated rapid large scale transport, coupled with cheap imports of crops and wool from abroad (e.g. North America), forcing farming systems to become more efficient to stay profitable (Poschlod and WallisDeVries 2002). Increases in efficiency resulted from farm specialisation, larger fields (Robinson and Sutherland 2002), mechanisation (Whetham 1970, Brassley 2000), pesticide use, applications of mineral fertilisers (Skinner et al. 1997), stationary paddocks (Walton 1919, Davies 1941, Stoate et al. 2001), and higher performance breeds of cattle (Whetham 1970). These factors tend toward producing landscapes of intensively managed monocultures (Wilson et al. 1999, Walker et al. 2009), with little retention of any semi-natural habitats, or corridors between semi-natural habitat patches. At the same time, an increased focus on coal and coke as fuel resources, as opposed to coppice products (Fuller and Warren 1993, Crossley 2005), drove a transition from coppice management to management of high non-native conifer forests, particularly in north and western Britain (Máliš et al. 2021). This became a major change in land-use with the establishment of the Forestry Commission in the early part of the 20th century (Atkinson and Townsend 2011).

By the late 20th century, the agricultural and silvicultural practices that had previously shaped the majority of the landscape into 'semi-natural habitats' had been largely abandoned (Fuller and Warren 1993, Poschlod and WallisDeVries 2002). Semi-natural habitats, which are generally characterised by lower nutrient concentrations, open vegetation structures, and warm microclimates, have since been largely lost because of conversion, development, loss of grazing pressure, and abandonment (Hooftman and Bullock 2012). Agricultural intensification only accelerated in the post-WWII era, as policy at the UK and European level encouraged self-reliance and increasing food production (Stoate et al. 2001, Robinson and Sutherland 2002). The Agricultural Act of 1947, and the subsequent Common Agricultural Policy ([CAP](#)) of the European Union, subsidised farmers to compete with cheap imports and resulted in drastic increases in yield, and even cases of surplus (Winter 1991, Howden et al. 2013). Both arable and pasture fields were managed intensively, with high nutrient deposition and stocking densities (Howden et al. 2013), and the increase in land-use area efficiency led to abandonment of less profitable areas (Smart et al. 2005). The previously managed semi-natural areas soon underwent natural processes of succession, and the extent of semi-natural grasslands had declined to 0.6 mha by 1980 (Fuller 1987), mirrored by a decline to less than 50kha of coppiced woodland (Fuller and

Warren 1993). Aside from direct management, other factors are likely to have contributed to loss of semi-natural habitats, including increasing nutrient deposition from rising agricultural run-off and atmospheric nitrogen oxides (Diekmann and Falkengren-Grerup 2002, Smart et al. 2005), and the loss of wild grazers such as rabbits, which were hit by a devastating myxomatosis epidemic beginning in the 1950s (Sumption and Flowerdew 1985).

The dramatic transformation of the UK landscape in the 20th century consequently altered the flora and fauna composition of the country. Many historically abundant species are associated with the then-wide-spread areas of semi-natural habitats. However, since the baselines of biodiversity in the UK were largely established in the 20th century (UK Government 1994, IUCN 2001), we have witnessed dramatic and rapid declines (Lawton et al. 2010, Hayhow et al. 2016). Declines are associated with a range of drivers (Smart et al. 2005, Watling and Donnelly 2006, Burns et al. 2016), but generally understood to be have been primarily driven by land-use change (Burns et al. 2016). It should be noted, nonetheless, that the accepted baselines are based upon relatively recent data, and can strongly influence our perception of 'declines'. Additionally, techniques for monitoring species and biodiversity have varied over time (e.g. UKBMS), and we have only recently begun standardised data collection (Didham et al. 2020). Fluctuations in time and space of species further complicate the assessment of overall trends, particular in short term data which is influenced by the length of monitoring window (Fox et al. 2019, Didham et al. 2020). This is particularly relevant in light of the rapid environmental changes of the 20th century (Poschlod and WallisDeVries 2002).

Today, once widespread semi-natural habitats have become so rare and fragmented, that they and their associated fauna are primary conservation targets, both nationally and internationally (Fuller 1987, Lawton et al. 2010, Hayhow et al. 2016). Declining and rare habitats and species were identified and given conservation priority within the Biodiversity Action Plan of 1984 (UK Government 1994, Biodiversity Reporting and Information Group 2011). Sites containing priority habitats or priority species were designated, primarily as Sites of Special Scientific Interest (SSSI), from 1949 onwards (Adams 1984). Today, the majority of priority habitats are located within Special Sites of Scientific Interest ([SSSIs](#)) or similar site denominations, most likely because semi-natural habitats have clearly deteriorated in areas without protection (Lawton et al. 2010). As a result of dedicated projects, and management resulting from Agri-Environment Schemes ([AES](#)), the cover and condition of some priority habitats in the UK have improved since the 1970s (Adams 1984,

Defra 2021). Some habitat types, such as calcareous grassland, appear to have benefited from conservation more than others, notably including orchards and lowland broad-leaved woodland (Gaston et al. 2006, Thomas et al. 2015). The disparity in recovery could result from factors such as financial incentives, ease of physical access, and costs and complexity of management regimes (Kleijn and Sutherland 2003, Atkinson and Townsend 2011, Quine et al. 2011, Ridding et al. 2015).

The nature of land-use change has also produced a fragmented landscape, driven by opportunistic and historically non-regulated conversion of land parcels in individual projects, and by natural processes (Hooftman and Bullock 2012). Connectivity through the landscape was rarely a consideration in early protection efforts, which were often necessarily also opportunistic, and preceded much of the evidence we have today regarding the importance of connectivity. Consequently, parcels of habitat being isolated within the landscape has reduced robustness of metapopulations (i.e. networks of populations of a species), and made individual populations more vulnerable to local extinctions with lower likelihood of rescue effects or recolonisations (Lawton et al. 2010). Shifts in assemblages are known to lead to less robust ecosystems, which are more likely to undergo system collapses (Fox and Harpole 2008, Genung et al. 2020), particularly where there are increasingly unstable or dynamic conditions (e.g. climate change) (Masson-Delmotte et al. 2021). Furthermore, barriers to movement that arise in a fragmented landscape, such as urban infrastructure, could be particularly threatening for species which are sedentary, or poor dispersers.

The landscape level movements and distribution of a species is impacted by both its intrinsic dispersal behaviour, and on the spatial arrangement and quality of the landscape matrix. Species with greater dispersal capacity, or more generalist requirements to allow occupation of different habitat types (Angert et al. 2011, Baguette et al. 2013), are theoretically less impacted by habitat fragmentation than weaker dispersers or habitat specialists. This trend has been observed in assemblages of butterfly species (Warren et al. 2001, Platts et al. 2019). However, the nature of the landscape itself can also influence metapopulation dynamics. More hostile environments between habitat patches, such as urban areas, can have mixed effects on inter-patch connectivity associated with higher mortality but more rapid movement (Nowicki et al. 2014), as can greater structural contrast at habitat boundaries. Although responses to habitat edges are highly species specific, a stark habitat contrast at boundaries can lower an individual's likelihood of exiting a patch (Ries and Debinski 2001, Schultz et al. 2012), and therefore moving through the landscape.

Some theoretical studies have found higher likelihoods of exiting habitat patches when introducing buffer zones at the margins of habitat (Cantrell and Cosner 1999).

A species' ability to move through the landscape, and subsequently its inter-patch connectivity, has significant implications for metapopulation dynamics (Baguette et al. 2013). Higher connectivity between patches generally increases robustness of metapopulations to local extinctions from disturbance events (Lande 1993), and enables source-sink dynamics which can maintain smaller populations at strategically important locations. Source-sink dynamics are particularly important for species relying on ephemeral habitats, as core populations can be lost rapidly (Lawton et al. 2010), requiring the ability to establish populations elsewhere to compensate. Such inter-patch connectivity is also necessary to maintain genetic diversity, particularly at patches with smaller breeding populations (Lande 1988). In addition to the traditional benefits of higher connectivity, species ability to disperse through the landscape is likely to be fundamental for successful adaptation to climate change, by tracking their shifting climate envelopes (Lenoir and Svenning 2015).

Habitat fragmentation can have unpredictable, idiosyncratic effects on species, but further research into responses, for example in *P. malvae* where studies on movement are limited, can help us to better predict effects of land use change, and plan conservation efforts accordingly; a field in which emerging mechanistic modelling approaches hold great potential (Keith et al. 2008, Evans et al. 2019a).

Land-use processes in the UK are generally driven by the private sector and encouraged by the broader public sector demands. They are thus hard to halt or reverse by decisions in the public sector alone, often needing cooperation from the private sector. This may be more difficult because conservation approaches for semi-natural habitats generally have low Return On Investment (ROI) financially, with few obvious avenues for profit. Uptake therefore usually requires legislation and possibly financial compensation, which can be complicated, unpopular, and difficult to enforce. The goal of much conservationism in the UK seems to be to return to the ecosystems widespread in the early 1900s. However, these landscapes were heavily influenced by continuous human activity, so conservation actions often require regular active intervention, and are frequently resource-intensive (Lawton et al. 2010). It therefore seems unlikely that we can return to previous land-use approaches under business-as-usual scenarios, particularly given land-use demands of our current population.

Changes in the broad schemes of land-use are not the only drivers of habitat change. There are many more factors driving declines in biodiversity globally and within the UK (Baillie et al. 2004, Hayhow et al. 2016), including warming and climate volatility (Burns et al. 2016), fragmentation of landscapes (Watling and Donnelly 2006), nutrient deposition (Smart et al. 2005), application of pesticides and herbicides (Skinner et al. 1997), and novel invasive species (Wagner 2020). The rapidity of environmental change is compounded by the number of simultaneous and interacting pressures, hindering the natural world from adapting or acclimatising. There are therefore many UK species at risk of eventual extinction (Hayhow et al. 2016), a process which could also result in our country's wildlife homogenising.

Human impacts on natural systems can interact in a number of ways, often with idiosyncratic and unpredictable consequences for species than can be both detrimental or beneficial (Franco et al. 2006, Wallisdevries and Van Swaay 2006, Oliver et al. 2015, Burns et al. 2016). Species which are most adaptable with generalist requirements generally have a competitive advantage in systems in disequilibrium with several novel selection pressures (van Swaay et al. 2006, Diamond et al. 2011), albeit with some exceptions (Van Dyck et al. 2009). Species which are endemic, sedentary, and reliant on ephemeral, man-made (i.e. semi-natural) habitats (Robinson and Sutherland 2002, van Swaay et al. 2006, Wilson et al. 2007) are disproportionately in decline within the UK. However, the changing environment may also provide some new opportunities for species, even those currently threatened, and we need to be able to look forward to predict and prepare for future scenarios. One key example is climate isotherms shifting polewards in tandem, which could allow for expansion of some species current geographical ranges, but could be counteracted by land-use and fragmentation.

1.2. Climate change and Impacts

While human activities have been shaping the physical landscape for millennia, the phenomenon of anthropogenic climate change is far more recent (Masson-Delmotte et al. 2021), but no less impactful on the natural world. We have observed global temperature increases in recent decades at a rate unprecedented in over 2000 years (Allen et al. 2018, Masson-Delmotte et al. 2021), almost certainly driven by anthropogenic green-house gas ([GHG](#)) emissions (Masson-Delmotte et al. 2021). Within the UK, temperatures and rainfall appear to be increasing in comparison to the 19th and 20th centuries (Jenkins et al. 2008), and the growing season in 2011-2020 is estimated to be 17% longer in duration than in

1961-1990 (Menzel and Fabian 1999, Carey et al. 2008). Despite increasing rainfall (Jenkins et al. 2008), occurrence and intensity of droughts have also increased (Dai 2013, Vicente-Serrano et al. 2014, Masson-Delmotte et al. 2021). Increased frequency and intensity of extreme weather events such as droughts (Otto et al. 2017, Masson-Delmotte et al. 2021), can themselves, in combination with changes in land management, trigger disturbance events, (e.g. wildfires in heathland) (Tedim et al. 2018, Duane et al. 2021). Additionally, climate zones have shifted polewards (Belda et al. 2016, Masson-Delmotte et al. 2021), and the global growing season is lengthening with an additional two growing degree days per decade (Dunn et al. 2020, Masson-Delmotte et al. 2021). Patterns of climate change such as these have direct and indirect implications for wildlife and natural communities.

One or more aspects of climate are often key determinants of species' spatial distributions and the timing of key events in their life histories (Roy and Sparks 2000, Thomas 2010), and changes in climate can therefore have dramatic ecological impacts. Changes we have seen so far have manifested ecologically in a number of ways, including; shifts in species distribution and abundance (Parmesan and Yohe 2003, Maggini et al. 2011, Lenoir and Svenning 2015), novel species interactions (Pateman et al. 2012, Ockendon et al. 2014, Pearce-Higgins et al. 2015), phenological shifts and subsequent asynchrony (Parmesan and Yohe 2003, Parmesan 2007), and changes in the composition of communities (Saura et al. 2014, Nieto-Sánchez et al. 2015).

Within the UK, we have witnessed patterns of climate effects in invertebrates (e.g. Lepidoptera), which are often considered early indicators of climate responses given their sensitivity to climate, rapid life cycles, and widely available records of presence and abundance. The northern range limits of some species previously limited to the south of England and Wales are shifting north (Davies et al. 2005, Mair et al. 2012, O'Connor et al. 2014). However, the rate of expansions vary between species with different levels of mobility, specialisation and exposure (Pöyry et al. 2009, Chen et al. 2011b, Dickinson et al. 2014). Generally, greater shifts have occurred in high-dispersal generalists (Dennis et al. 2004, Menéndez et al. 2006), but see Mair et al. (2014). A fragmented landscape puts slow dispersers and sedentary specialists at a further disadvantage. These species in particular are at risk of not being able to track their climate envelope, particularly when areas of suitable habitat are not connected.

Furthermore, species shifting at different rates may cause novel interactions of species previously separated in space, possibly resulting in hybridisation (e.g. the Brown Argus

(*Aricia agestis*) and Northern Brown Argus (*Aricia artaxerxes*) (Mallet et al. 2010), predation, or competitive exclusion. Parallels can be seen in the novel interactions between species whose potentially interacting life cycle stages were previously separate in time (Roy and Sparks 2000), and conversely, emerging asynchrony between some species with symbiotic relationships (e.g. hostplants and insects) (Parmesan 2007).

Furthermore, climate can itself impact on structure of the landscape; most immediately through changing plant communities, which are affected by drought, rainfall, and growing degree days. Such impacts will likely have bottom-up effects in the trophic chain, and especially for those communities associated with highly specific plant assemblages. One potentially major consequence of lengthening growing seasons and reductions in the number of days with ground frost is greater accumulation of above ground vegetation biomass (Wallisdeevries and Van Swaay 2006, Piao et al. 2020). In combination with a lack of natural or domestic grazing pressure and increased nutrient (e.g. nitrogen) deposition (Smart et al. 2004), warming temperatures are likely to accelerate shifts towards plant communities dominated by stress-intolerant, fast growing, tall vegetation (Dennis et al. 2004, Smart et al. 2005).

This is likely to homogenise habitats given enough time (Keith et al. 2009, Newbold et al. 2015). For specialist species, or species relying on a range of habitat types within their lifetime (Lawton et al. 2010), acceleration of eutrophication by climate change is particularly concerning. These species may already be under greater threat from habitat fragmentation (Davies et al. 2005). We are also seeing some species' performance and/or interactions being mediated by climate. Brown Argus (*A. agestis*), for example, was previously restricted to *Helianthemum nummularium*, but has been observed expanding into areas dominated by *Geranium molle* when summer temperatures increased and enabled the species to persist and reproduce (Pateman et al. 2012).

A changing climate introduces a new level of complexity to understanding and protecting our ecosystems, because the physical environment is not currently at equilibrium, and it is unclear what the eventual 'equilibrium' will be. With multiple, interacting pressures acting on multiple species at once, identifying and simultaneously addressing the major drivers of biodiversity decline is a major challenge in conservation today.

1.3. Early Successional Habitats and Associated Specialists

One key group of semi-natural habitats are those of early successional stages. Although once widespread across the UK and much of Europe (Fuller and Warren 1993, Poschlod and WallisDeVries 2002), they have become some of the most threatened (Hayhow et al. 2016). Early stages of succession can be created through intense weather events (e.g. drought) (Gibson and Brown 1992, Walker et al. 2004, Bonari et al. 2017, Stuhldreher and Fartmann 2018), but also occur in areas with high numbers of wild grazing animals (Ripple et al. 2015, Murphy et al. 2016). The habitat structure and associated fauna of UK early successional habitats have largely been by-products of agriculture and silviculture (Green 1990, Fuller and Warren 1993). Although the UK now has a restricted fauna of native grazing species (Mitchell and Kirby 1990, Hodder et al. 2009), widespread deforestation followed by maintenance of herds of domestic grazers (Green 1990) and use of coppicing techniques (Fuller and Warren 1993) produced a mosaic of habitat structures, and halted the processes of succession (i.e. establishment of woody vegetation and tall swards) in many areas. Consequently, early successional habitats were widespread, which were generally species rich and characterised by high cover of bare ground, short swards, and sparse overhead canopies (Fuller and Warren 1993, Biodiversity Reporting and Information Group 2011, Bullock et al. 2011). Prior to intensive human intervention in the Neolithic era, these habitats are thought to have been present but uncommon within the landscape (Green 1990, Poschlod and WallisDeVries 2002).

As one of the habitat types most directly dependent on human intervention, early successional habitats were among the first reported to be impacted by abandonment of the traditional management techniques which shaped the UK landscape for millennia (Fuller and Warren 1993, Poschlod and WallisDeVries 2002). Their loss is significant because of their previous cover, steep declines, and the number and abundance of species relying on them (Fuller and Warren 1993, Poschlod and WallisDeVries 2002, Thomas et al. 2015). Early successional habitats are also of note scientifically; because of their sensitivity, they can provide essential data for recognition and prediction of impacts from climate change (Oliver et al. 2009, Hodgson et al. 2015). Their warm microclimates can serve as stepping stones for species' dispersal at cool range boundaries in higher latitudes and elevations, and will likely play a crucial role in facilitating range shifts in response to climate change (Thomas et al. 1999, Krämer et al. 2012, Hannah et al. 2014, Lawson et al. 2014).

Early successional habitats and their associated microclimates therefore provide useful microcosms to examine and explore early signs of response to climate change.

Early successional habitat provides unique locations and breeding opportunities for many xerophilous invertebrates which are disproportionately in decline within the UK and across Europe (Thomas et al. 2015). The habitats are crucial for several invertebrates with specialist requirements not just in terms of plant species present, but also vegetation structure, nutritional and physical status (e.g. nitrogen content, leaf area) (Brereton 1997). As traditional management became economically non-viable, much of this habitat was lost. Nonetheless, some new areas have been inadvertently created (Biodiversity Reporting and Information Group 2010, Wildlife and Countryside LINK 2015) through the abandonment of industrial sites, and some have been restored from conservation action (Walker et al. 2004, Oatway 2018).

Despite these new habitats, the net loss of early successional stages over the past century is thought to be the driver of declines of many invertebrate species, many of which in the UK are limited to the south because of climate suitability (Thomas et al. 2015). These species have been hypothesised to benefit from a warming climate, because of their climate niche potentially expanding geographically, and potential opportunities to exploit later seral stages. Testing this hypothesis is useful from a conservation standpoint for individual threatened species, and also for climate change ecology generally. It may answer: whether these specialist species are tracking the climate, and if not, why not; what is the resilience of specialists in an unstable system; whether specialists can occupy new habitat niches; and how will fragmentation of their landscape play into their ability to adapt and cope with climate change.

1.4. Future of UK Landscape and Biodiversity

The national and global pressures that drove many of the most dramatic changes in UK land-use (such as intensive monoculture) are only likely to increase over time (Foley et al. 2005), and the environment continues to change in terms of substrate, flora and fauna community composition, and climate (Smart et al. 2004, Keith et al. 2009, Bodirsky et al. 2012, de Jong et al. 2013, Pimm et al. 2014, Piao et al. 2020, Masson-Delmotte et al. 2021). Attempts to return to a previous style of landscape management strategy in small protected areas are unlikely to be enough to maintain biodiversity. It seems likely that new approaches to manage semi-natural habitats sustainably will be required to compensate for these new conditions (Sutherland et al. 2008, Lawton et al. 2010).

Our land-use is intrinsically tied to our population size and resource usage, and global human population size is expected to increase to 10 billion by 2050 (United Nations Department of Economic and Social Affairs 2019). As a consequence, demand for housing, infrastructure, food production and energy generation are also expected to rise (Foley et al. 2011, Masson-Delmotte et al. 2021). Particularly in a post-EU political climate, and with ongoing pressures on supply chains, there is again increasing emphasis for the UK to become more self-sufficient, and rely less on imports (Garnett et al. 2020). The Cambridge Institute for Sustainability Leadership (CISL) estimated in 2014 that meeting demands of a growing population and sustainability aims would require more land than previously expected to be available by 2030 (Montague-Fuller 2014). Tackling this challenge alone will require rigorous strategic planning and investment. The demands of growing population size are apparently in direct opposition to goals of sparing land for nature, and competition for land is likely to grow. Land is therefore likely to be assigned multiple uses, but from a political stand point, the environment is often seen to give little measurable short term returns. Compared with pressing human needs, management for biodiversity may then take lower immediate priority.

World events, including 'Brexit', a global pandemic, and ongoing financial instability, further compound this issue. The recent departure from the EU and linked environmental regulations have further exposed the landscape to gaps in regulation and policy that could be exploited with devastating and long-lasting impacts, or become opportunities for strengthening environmental protections (Gravey 2019). The Local Nature Recovery Strategies ([LNRS](#)) scheme (Defra 2018), for example, is one of the UK government's latest measures to tackle the biodiversity crisis within the Environment Bill (British Parliament 2021), and will aim to provide local strategies in collaboration with public, private and voluntary sectors. However, with cuts to funding, and the loss of ecologists from key roles in local authorities (Oxford 2013, Montague-Fuller 2014), there remain concerns about the capacity of such schemes to meet targets on biodiversity and species abundance.

Beyond land-use change, climate change, and associated threats to biodiversity, are also unlikely to reduce over the next century (Masson-Delmotte et al. 2021). Under even the lowest [GHG](#) emission scenario, with net negative CO₂ emissions after 2050, global surface temperatures are expected to rise by more than 1° by 2100 (Masson-Delmotte et al. 2021). Projections of rainfall are less certain; for example, some models estimate decreased summer precipitation in the UK by 2080 (Masson-Delmotte et al. 2021), but recent trends suggest a trend of positive anomalies in summer rainfall (Met Office Hadley Centre 2019).

There is little dispute over a projected increase in temperature, but there is less certainty in regional and seasonal rates of increase (Masson-Delmotte et al. 2021), which introduces further uncertainty into estimating ecological impacts. Ongoing, and likely accelerating climate change, will put further pressure on both natural systems and human inhabitants. There may need to be major changes in patterns of global and local land-use for food production, especially to cope with increasing demands of refugee migration, overseas aid, and emergency aid.

Although many species are at risk of extinction if drivers go unmitigated (Pimm et al. 2014, Dirzo et al. 2014, Fox et al. 2015), our understanding of these threats does enable us to intervene more effectively. While climate change trajectories are difficult to influence geopolitically, and even in the best case scenario are expected to continue for many decades (Masson-Delmotte et al. 2021), landscape management is more actionable. Strategic planning could involve: land sparing vs sharing; Local Nature Recovery Schemes; improved technology; strict legal protections for existing sites; Agri-Environment Schemes; and legally enforced targets for environment outcomes (Foley et al. 2011, Montague-Fuller 2014, Karner et al. 2019, British Parliament 2021). Several strategies already exist in the UK (e.g. Nature Recovery Networks ([NRNs](#))), but effective implementation relies on up-to-date information from the field, a balance of decision-making that reflects different viewpoints and expectations, and the establishment of measurable targets.

Current farming practices do not encourage optimum levels of grazing pressure and coppicing for maintenance of semi-natural habitats. Combined with effects of warming climate and nitrogen deposition (Smart et al. 2004, Masson-Delmotte et al. 2021), species relying on early successional habitat are therefore threatened. For species most vulnerable, more research and active management will be needed, in addition strategic decision-making about where and how to convert habitat. Conservation of such species is likely to need long-term solutions that minimise need for regular intervention, e.g. topsoil stripping, or regular rotations, mowing and removing cuttings (Fuller 1987, Walker et al. 2004). Research about drivers of decline in our most threatened groups is particularly important at this moment in time, and will almost certainly become even more so in future. Understanding the responses to climate change displayed by individual species, assemblages, and habitats is vital for the development of guidance on how to implement, and assess, their conservation.

1.5. Grizzled Skipper: Threats and Trends

The Grizzled Skipper (*Pyrgus malvae*) is a spring-flying butterfly (Figure 1.1) first formally recorded in Western Europe in 1747 (Brereton 1997), and is widespread across the continent (Brereton et al. 1998, Asher et al. 2001). Occupying a range of habitat types, it is primarily restricted to habitats containing its larval hostplants (Brereton 1997), members of the *Rosaceae* family, in open microhabitat structures, primarily because of their higher temperatures but also potentially due to higher nitrogen content (Brereton 1997).



Figure 1.1 Overhead view of a Grizzled Skipper (*Pyrgus malvae*) basking

The butterfly was one of several expected to expand its range over time given its estimated climatic niche (Settele et al. 2008), but has nonetheless declined by over 50% in occurrence, and over 35% in abundance in the UK between 1976 and 2014 (Hayhow et al. 2016). Additionally, *P. malvae* is currently limited to central and southern England and Wales, and has shown no signs of expansion thus far (Hayhow et al. 2016), possibly due to an inability to disperse between fragmented patches of early successional habitat (Brereton et al. 1998). As a well recorded, early successional sedentary specialist, with a rapid life cycle, sensitive to temperature, and existing within a fragmented ecosystem (Brereton et al. 1998), this species is therefore an ideal case study for investigating the interacting pressures of climate and land-use change.

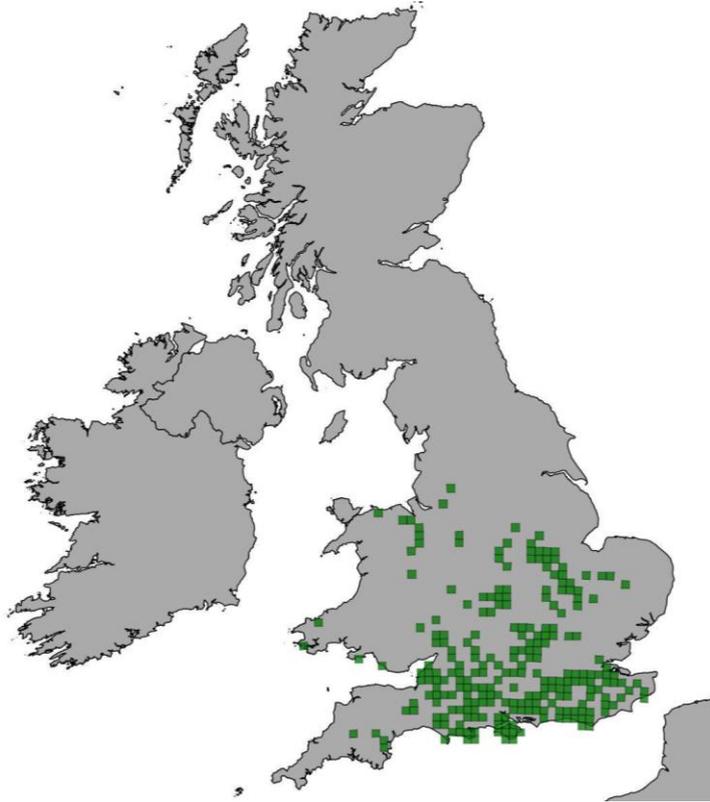


Figure 1.2 Distribution of UK *Pyraus malvae* records in 10 km x 10 km grid squares (green squares) between 2007 and 2021, obtained from the National Biodiversity Network Atlas [Accessed March 2022]. Outline of UK landmass shown as in grey.

1.5.1. Life History

The flight period of *P. malvae* historically spans from April to June, but can begin earlier in warmer spring conditions (Brereton 1997, de Schaetzen et al. 2018), and the butterfly has been known to have a partial second generation in particularly warm summer conditions (Brereton 1997). During its instar stages, the larva feeds on multiple species of the plant family *Rosaceae* (Brereton 1997), during which time it creates tents for protection from predators and shelter. Overwintering as a pupa (Asher et al. 2001), several days of high temperatures trigger metamorphosis and emergence as an adult (Brereton 1997). Both sexes feed throughout the day from various spring-flowering nectar sources. Male and females can occupy different micro-distributions when food-plant density is low, with males tending to cluster around scrub where they undertake patrols, and females moving more freely near nectar and egg laying opportunities (Brereton 1997). After mating, females will conduct an ‘image search’ for egg laying opportunities, seeking patches of bare ground or stone and suitable hostplants within the *Rosaceae* family, including wild (*Fragaria vesca*) and barren strawberry (*Potentilla sterilis*), agrimony (*Agrimonia eupatoria*),

creeping cinquefoil (*Potentilla reptans*), and salad burnet (*Sanguisorba minor*), in addition to plants less commonly used for egg laying, such as meadowsweet (*Filipendula ulmaria*) and bramble (*Rubus fruticosus*) (Brereton 1997). Local preferences for particular hostplants have been suggested colloquially, but no formal investigation has yet been undertaken. When she has inspected and found a suitable plant, she will usually lay eggs singly. The larvae have been found in *ex situ* experiments to require multiple plants for healthy development (Brereton 1997), but reasons for this are not clear, although are possibly related to plant chemical defences or nutritional quality.

1.5.2. Habitat Requirements

P. malvae has been found in a number of different habitats provided they contain certain key habitat elements; scrub, patches of bare ground, nectar, and suitable hostplants (Krämer et al. 2012, Streitberger and Fartmann 2013). Habitat types include calcareous and acidic grassland, heathland, coppiced woodland, woodland glades and rides, and disused industrial areas (e.g. quarries) (Brereton et al. 1998, de Schaetzen et al. 2018). Deforestation and subsequent traditional management techniques created and maintained large areas of habitat in the UK and Europe in an artificial early successional stage (Fuller and Warren 1993, Poschlod and WallisDeVries 2002), providing the ideal breeding conditions for the butterfly and other specialists like it, such as the Small Blue butterfly (*Cupido minimus*). The butterfly tends to use a variety of habitat structures (Brereton 1997), selecting bare ground for egg laying, nectar for continuous feeding, tall vegetation for perching, and scrub for shelter and patrolling. The species therefore benefits from mosaics of habitat, potentially complicating habitat management recommendations.

1.5.3. Changes in Habitat Availability and its Drivers

As previously mentioned, changes in land management techniques in the past century produced a fragmented landscape for *P. malvae*, and other early successional specialists (Brereton et al. 1998, Lawton et al. 2010). From the 1800s, falling market demand for products of coppicing and greater demand for timber drove a dramatic shift in silviculture to tall stands of non-native species with closed canopies and few clearings, and few glades or open rides (Fuller and Warren 1993). Agriculture similarly intensified post-World War II because of an increased government focus on self-sufficiency, improving technology and fertilisers and pesticides, and increasing farm sizes (Robinson and Sutherland 2002). Many previously semi-natural grasslands became improved arable and pasture fields (Green 1990, Poschlod and WallisDeVries 2002), with little to no structural diversity or hedgerows,

and other less profitable land parcels were abandoned and left to natural succession (Lawton et al. 2010). Changes in agricultural policy coincided with crashes in rabbit populations from the spread of myxomatosis (Sumption and Flowerdew 1985), which released many areas from natural grazing pressure, and consequently accelerated rates of succession and transition to rank grasses over open herb-rich swards (Stoate et al. 2001), with little suitable breeding habitat for *P. malvae*.

Unnatural early-successional habitats also emerged following abandonment of quarries and industrial areas (Biodiversity Reporting and Information Group 2010), but these too require some form of management or intervention to prevent natural succession (Brereton 1997). Some of these areas were also bought and converted to developed land, further contributing to loss of habitat and fragmentation of the landscape (Robins et al. 2013).

1.5.4. Conservation

Despite declines being first reported in the late 20th century, with national declines in range of over 30% in the UK between 1940 and 1982, *P. malvae* has only quite recently received statutory protection (Brereton et al. 1998). The species was added to the Biodiversity Action Plan as a priority species in 2006 during a review (Biodiversity Reporting and Information Group 2007), and has since been incorporated into the country-level England and Wales successors to the UK Biodiversity Action Plan ([BAP](#)) (British Parliament 2006, National Assembly for Wales 2016). *P. malvae* is a Section 41 Species in the Natural Environment and Rural Communities Act of 2006, and a Section 7 Species of the Environment (Wales) Act of 2016, which require that priority species be considered and protected by local authorities when land is considered for development. *P. malvae*'s European status is currently listed as 'Not threatened' (Council Directive 1992), likely due to the butterfly being widespread across Central, Western, and Southern Europe, as well as in parts of China (de Schaetzen et al. 2018). However, *P. malvae* is listed as endangered in North Rhine-Westphalia and near-threatened across Germany, and declines in Europe have also been reported (Streitberger and Fartmann 2013, de Schaetzen et al. 2018), such as an over 50% decline in the Netherlands between 1970 and 1998 (Brereton et al. 1998). Therefore, the species' status may change in coming years.

As a priority species, and specialist of priority habitats, *P. malvae* has benefitted from many government-funded conservation actions, for example through the SSSI scheme. Many of *P. malvae*'s known UK populations within traditional habitat types (e.g. grassland, woodland, heathland) are often within [SSSIs](#) or other protected locations (Lawton et al.

2010), though this is not necessarily the case for disused industrial locations, such as a quarries or railways (Brereton 1997). Through schemes such as Countryside Stewardship (CS), and Habitat Action Plans (HAPs) (UK Biodiversity Steering Group 1995), a range of techniques have been employed to revert improved agricultural land including: reseeding grassland seedbanks; cutting; grazing; nutrient stripping; and biological control (e.g. grass suppression using yellow rattle) (Pers. Obs.) (Brereton et al. 1998, Slater 2007).

The butterfly has also specifically been the target of reintroduction and habitat creation projects (Brereton 1997). Projects were particularly focussed in northern areas where populations were small and vulnerable to extinction. For example, *P. malvae* was recently reintroduced to Derbyshire as a part of a several year project (Butterfly Conservation 2018), before the 2020 Covid-19 pandemic impeded progress. Previous reintroduction attempts were undertaken in Lancashire, although they were ultimately unsuccessful (Coleman 2017). Additionally, recent habitat creation at a restored quarry near Newark, Nottingham, resulted in a 2021 sighting of the butterfly, where it had nearly been lost in the 1990s (Churcher 2021a).

However, some habitats used by *P. malvae* have not recovered to the same extent at semi-natural grassland and heathland (Ridding et al. 2015). Low-land broadleaved woodland SSSI have a relatively low proportion of sites in 'good' or 'recovering' condition (Defra 2021). Additionally, uptake of management schemes for woodland is generally lower than for grassland areas, potentially because of the relative cost and difficulty in accessing sites (Atkinson and Townsend 2011), which are frequently isolated and surrounded by privately owned agricultural land.

1.5.5. Future Threats and Opportunities

Climate change, as for many species, presents both opportunities and threats for *P. malvae* (Settele et al. 2008). As a species largely believed to be restricted to habitat patches with the warmest microclimates in its early development stages (Brereton 1997, Streitberger and Fartmann 2013), habitat previously unsuitable due to seral stage or topography was theorised to become available for *P. malvae* in warmer summer climates (Settele et al. 2008, Oliver et al. 2009, Krämer et al. 2012). However, *P. malvae* occupies a fragmented landscape, and north-south connectivity between semi-natural habitats is likely limited (Travers et al. 2021), raising concerns over the already sedentary butterfly's ability to track a shifting climate envelope. There is therefore also the risk of warming conditions in the south that could eventually make the southern-most parts of the range climatically

unsuitable (Settele et al. 2008), trapping the species in a contracting area of suitable habitat over time. However, this is not an imminent threat in the UK which is towards the north of the overall range limit.

Because climate can affect a single species in a number of ways, depending on life stage and specific climate variable, predicting net impacts on *P. malvae* is difficult; for example, will warmer summers open up new breeding habitat opportunities, or will wetter, warmer conditions year round lead to higher disease, phenological asynchrony, and changes in habitat structure?

There are several avenues for possible investigation of this species. Assuming climate change could open up new habitats for *P. malvae*, we might expect to see precursors to northern expansion at the current cool range limit, where temperature is most likely a limiting factor. We could make predictions as to whether the species' habitat requirements are becoming less stringent in line with expected effects of a warming climate, and use this information to more effectively plan conservation efforts and priority actions. We can also explore the potential impacts of continued succession on connectivity, to inform strategic investment of conservation effort to encourage population network connectivity and a robust metapopulation.

1.6. Research rationale: Aims, Objectives, and Research Questions

This study focuses on *P. malvae* as a case study for habitat specialists expected to benefit from climate change based on prior knowledge of their climate envelope, and exploring whether climate has the potential to mitigate impacts of land-use change on threatened species. In addition to further understanding about species like these, this project also aims to inform and aid conservation planning of *P. malvae* itself, as a priority species.

In this project, I attempt to answer the following questions in each of the chapters of the thesis:

1. Are population size trends of *P. malvae* more positive in the north compared to the south, indicating early signs of northern expansion, and how much of the long-term trends are explained by climate?
2. What are predictors of habitat suitability for *P. malvae* in the UK, and do they vary with geographical location or habitat type?

3. Do *P. malvae* exhibit edge avoidant responses to boundaries of grassland and scrub/woodland, and does scrub encroachment at the borders of habitat patches impact on connectivity and landscape scale movement?

In the general discussion of this thesis, I will then propose a framework for how the answers to these questions could be used by conservation organisations, such as Butterfly Conservation, to devise Key Performance Indicators ([KPIs](#)) to quantitatively measure and report on progress in the conservation of *P. malvae*, and other key species of conservation interest.

CHAPTER 2

Grizzled Skippers stuck in the south: Population level responses of an early successional specialist butterfly to climate across its UK range over 40 years

This chapter is adapted from a published article by the same title in *Diversity and Distributions*, of which I was the first author.

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Declaration of Contributions: All authors collaborated on study design, and reviewed and edited the manuscript. Myself and Dr. Jenny Hodgson conducted the data analysis and created the figures. We thank Nick Isaac for his modelling expertise and advice on study design.

Abstract

Climate change has been predicted to facilitate poleward expansion of many early successional specialist invertebrates. The Grizzled Skipper, *Pyrgus malvae*, is a threatened butterfly in long-term decline that has not met expectations of northern expansion in Britain, possibly indicating that climate change has not improved northern habitat suitability, or that another driver (e.g. land-use change) is masking its effects.

Here we explore the effect of climate on population size trends over four decades, and whether any regions show an improving population trend that may be a precursor to northern expansion. Examining detailed spatio-temporal abundance data can reveal unexpected limitations to population growth that would not be detectable in widely-used climate envelope models.

Mixed models were used to investigate *P. malvae* population size in relation to time and monthly climate measures across its UK range since 1976, based on repeated transect walks.

We found that *P. malvae* population size declined more over time in the north and west of its UK range than in the south and east, and was negatively related to high December temperature and summer rainfall. However, the effect sizes of temperature and rainfall were minimal.

The last 40 years of climate change have not ameliorated climate suitability for *P. malvae* at its range edge, contrary to expectations from spatial-only climate envelope models. The clear long-term downward trends in population size are independent of climate change and we propose probably due to habitat deterioration.

Our findings highlight potential hazards in predicting species range expansions from spatial models alone. Although some climate variables may be associated with a species' distribution, other factors may be more dominant drivers of trends and therefore more useful predictors of range changes.

Key Words:

Climate Change, Conservation, Lepidoptera, Range changes, Modelling

2.1. Introduction

Temperatures have been increasing globally since the mid-20th century (Intergovernmental Panel on Climate Change, 2014; Met Office, 2019), with increasing regularity of extreme heat and drought summer events, and longer growing seasons (Met Office, 2019; Menzel et al., 2020). It has been predicted that in a scenario of ambient warming, species' geographical ranges may shift in order to track their climate envelopes, predominantly polewards and to higher altitudes (Parmesan et al., 1999; Root et al., 2003). For early successional specialists that frequently require warmer microclimates within their range, range changes may result from an ability to occupy later seral stages under warming conditions, hereby becoming less specialised and less reliant on early successional habitats (Thomas, Rose, Clarke, Thomas, & Webb, 1999; Komonen, Grapputo, Kaitala, Kotiaho, & Päävinen, 2004; O'Connor, Hails, & Thomas, 2014). Less specialised habitat requirements may enable species to expand their cover within and beyond current population boundaries (Settele et al., 2008; Thomas et al., 2001). Some early successional species, such as the Brown Argus butterfly (*Aricia agestis*), appear to have already broadened their habitat niche as a result of warmer summers, and expanded polewards (Pateman et al.

2012). However, one early successional specialist that has not responded to climate change as expected is *Pyrgus malvae*, the Grizzled Skipper butterfly, that has declined in the UK by 55% between 1976 and 2018 (Brereton et al., 2019).

Expectations of range expansions and shifts are not unique to early successional specialists (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Davis & Shaw, 2001), but in particular *P. malvae*, like other southern restricted and warm-preferring species, is expected to benefit from warming temperatures in large part due to its requirements for warm microclimates for oviposition and development during temperature-sensitive immature stages (Weiss et al. 1988, Krämer et al. 2012). As early successional specialists like *P. malvae* often rely on the presence of warm microclimates to persist in cooler areas, such as at higher altitudes or more poleward locations, their habitat breadth in those cooler locations may be narrower than in warmer areas in southern Europe (van Swaay, Warren, & Loïs, 2006). Therefore, an increase in temperature in the northern parts of *P. malvae*'s range may increase breeding habitat availability, and facilitate increases in abundance and subsequent range expansions. However, contrary to predictions of poleward expansion under a warming climate, no indication of natural northern expansion has been observed in *P. malvae* (National Biodiversity Network 2020), and declines have been observed that on average do not appear to have slowed in the last decade, despite warming conditions (Brereton et al., 2019; Fox et al., 2015). Similar observations of species not fully tracking their expanding range limits have been made across several taxonomic groups and countries (Devictor et al., 2012; Warren et al., 2001; Vanderwal et al., 2013; Bertrand et al., 2016)

Although there has not yet been evidence of northern expansion by way of colonisations beyond the current north range edge, investigating changes in abundances of northern populations could provide insight into the likelihood of imminent expansion. Increasing abundances close to the range edge of *P. malvae* have been found previously to represent

an intermediate step prior to colonisation (Maggini *et al.*, 2011). Therefore, investigating whether *P. malvae* abundance is showing increases at poleward range limits over time could provide an early indication of increasing climate suitability as would be expected from spatial-based predictions. Spatial-based predictions alone may not be able to fully capture limitations to expansion, such as dispersal capacity and biotic habitat requirements, so assessing trends over time and space may offer a more accurate reflection of potential range changes. In addition, exploring the effects of climate variables on population abundance could provide further insight into the role that climate plays in influencing long-term trends, and differences in regional trends if they are found.

2.1.1. Aims

Here we aim to explore the effect of climate on long-term population size trends, and whether UK Butterfly Monitoring Scheme ([UKBMS](#)) indices of population size at [UKBMS](#) sites are decreasing at differing rates between regions. Population size trends differing with latitude/longitude is of interest as relatively positive trends in population size may be a precursor to northern expansion (Mair *et al.*, 2014; Maggini *et al.*, 2011).

We hypothesise that if climate change is ameliorating declines in *P. malvae* in the UK, climate predictors will account for a large portion of variation in abundance otherwise explained by time, thereby emerging as a dominant driver of long-term trends. In addition, if climate is the limiting factor for northern range expansion, but range edge conditions are becoming more suitable under climate change, abundance will have relatively positive long-term trends at higher latitudes.

2.2. Methods

Pyrgus malvae is found in early seral stages of grassland, woodland, and brownfield habitats (Brereton, Bourn, & Warren, 1998) in the UK. However, its range has contracted, having lost its northern most population in York in the 1990s, and having gone locally extinct in several counties, including in Derbyshire in 2007, where it is currently the focus of reintroduction efforts (Butterfly Conservation, 2018). Another reintroduction was attempted at Gait Barrows in Lancashire in 2002 (geographical locations shown for reference in Figure 2.1), where it had occupied habitat in the early 20th century, but the population is believed to have gone extinct in 2007 (Coleman 2017).

The UK Butterfly Monitoring Scheme is a long-term coordinated recording scheme for butterflies in which a core component is a network of more than 2000 sites at which adult butterflies are counted weekly over the flight season between April and September (Brereton et al., 2019; Pollard & Yates, 1993). The weekly butterfly counts are used to produce annual indices that account for missing weeks, and this index can be used as a proxy for a species' population size at a site (Rothery and Roy 2001). Henceforth, 'Population Index' is used to mean the *P. malvae* annual abundance index at a given [UKBMS](#) transect site, which is calculated from a generalised additive model (Rothery & Roy, 2001). Mixed models were used to investigate *P. malvae* population size in relation to year and relevant monthly climate measures across its UK range in the survey period of 1976-2016.

Climate data were obtained from Met Office data at 5 x 5 km resolution, as monthly mean temperature, and monthly rainfall values (mm) (Perry 2005). Each population index value was matched to the climate data from its own 5 km square, for the months from June of the previous year to May of the year of the record (inclusive). This time window was chosen to span the life stages of a single generation from the larval period to the following

flight period. Mean monthly temperature and rainfall were chosen for ease of interpretation and generality (Pollard 1988, Palmer et al. 2015). Preliminary investigation of three-month pooled climate values did not produce notably different or more significant effects on population index than monthly mean temperature and rainfall (Appendix 1).

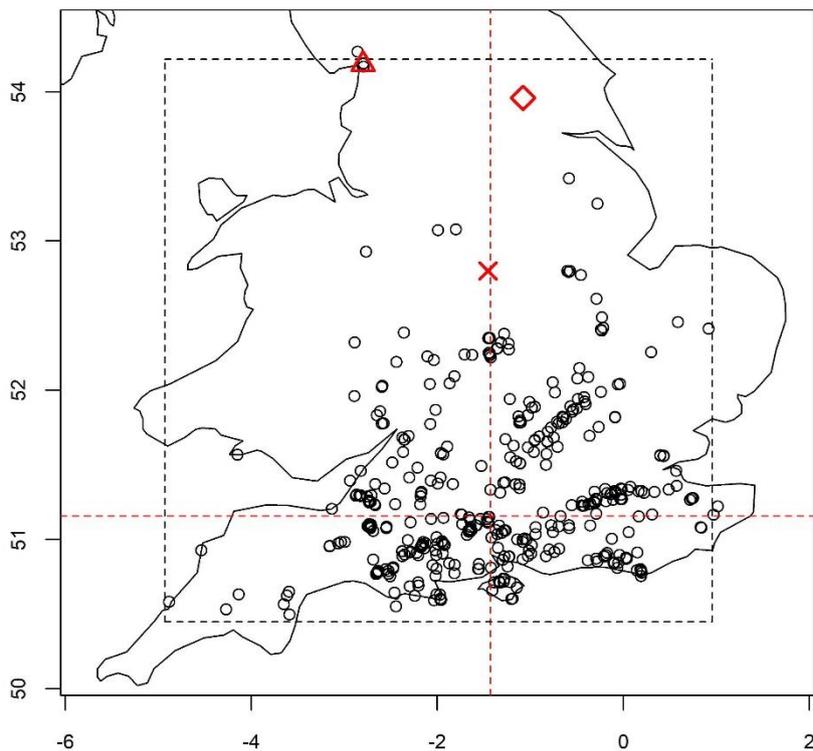


Figure 2.1 Map showing the geographical distribution of UKBMS sites included within analyses, where each site is represented by a black circle. The black dashed lines depict the total range of all UKBMS sites with Grizzled Skipper (*Pyrgus malvae*) records between 1976 and 2016. The red dashed lines depict the median latitude and longitude of all records used in analyses. Locations of *P. malvae* extinctions and reintroductions are shown as red symbols; the Derbyshire reintroduction site (cross), Lancashire reintroduction site (triangle), Yorkshire extinction site (diamond).

A total of 483 sites, mapped in Figure 2.1, were available that had at least one year with sufficient data to produce an annual population index during the survey period, and fell within a 5 km grid square with Met Office data. Year-site combinations with *P. malvae*

presence but with too few visits to estimate a population index (according to [UKBMS](#) criteria) were omitted.

Generalised linear mixed effects models were run using the R package 'lme4' (Bates et al. 2015). The error family used was negative binomial to account for a high proportion of zeros in the population index data (38%). To prevent convergence issues, all predictor variables were standardised by subtracting the mean of each variable, and dividing by the standard deviation.

In all models, to account for pseudo-replication, as sites were visited repeatedly, and for stochastic variation between years and regions across the country, year, site number, and 50 km x 50 km grid squares (Total: 59) were introduced as random factors. Our approach did not account for population size in the previous year, because of the limited number of [UKBMS](#) records with visits to the same site the prior year. 50 x 50 km square was selected as the appropriate size in order to minimise the number of grid squares with very few sites, and at a high enough resolution to isolate geographic aggregations of sites with unusually high residual errors from the model when 50 x 50 km square is not included as a random effect. Model fit was evaluated using [AIC](#) comparisons, and validated by assessing heterogeneity in residuals.

We ran three sets of statistical models to elucidate the effects of climate vs potentially co-varying effects of geography. The final minimum adequate model was then used to explore the impact of climate on long term population index trends.

i. Non-climate predictors

To assess how population size has changed over time across the UK geographical range, irrespective of climate, models were first run containing only year, latitude and longitude as fixed effects. A model was run for each of these fixed effects independently, and then with all effects, and two way interactions, with [AIC](#) stepwise regression to obtain the Minimum Adequate Model ([MAM01](#)).

The initial Maximal Model (MM01) therefore can be described as:

<i>Equation</i> 2.1	$\begin{aligned} \text{Population Index} &\sim \text{Year} + \text{Longitude} + \text{Latitude} \\ &+ \text{Year} * \text{Longitude} + \text{Year} * \text{Latitude} + \text{Longitude} * \text{Latitude} \\ &+ (1 50 \text{ km grid-square} \div \text{Site}) + (1 \text{Year}) \end{aligned}$
------------------------	--

Upon running the final model, we observed a large difference between the real and predicted population index values at the beginning of the recording period in the north west of the study area. As we believed this to be due to data scarcity for this space and time, we reran a model omitting data prior to 1990, and the outputs were qualitatively unchanged (Appendix 2).

ii. Climate predictors

To explore the effect of climate in each month independently, and to avoid auto-correlation between months, individual models were run for each monthly climate value as the only fixed effect, for both temperature and rainfall (24 total models).

An example of one such model can be described as:

<i>Equation</i> 2.2	$\begin{aligned} \text{Population Index} &\sim \text{Previous July Temperature} \\ &+ (1 50 \text{ km grid-square} \div \text{Site}) + (1 \text{Year}) \end{aligned}$
------------------------	--

All variables found to have a significant effect were included in a single model, with no interactions, to better identify variables that may be accounting for similar variation in population index. The least significant fixed effect was removed in a step-wise manner to minimise [AIC](#), and arrive at the minimum adequate model for climate effects ([MAM02](#)).

iii. All predictors

To assess how much of the trends over time and geography observed in [MAM01](#) (Section i.) can be explained by climate effects, all monthly climate measures included in [MAM02](#) were added to model [MAM01](#), to create the third maximal model MM03. Stepwise [AIC](#) regression was used subsequently to determine the final minimum adequate model, with both climate and non-climate predictions ([MAM03](#)).

The initial maximal model (MM03) can be described as:

Equation 2.3	$\begin{aligned} &\text{Population Index} \sim \text{Year} + \text{Longitude} + \text{Latitude} \\ &+ \text{Year} * \text{Longitude} + \text{Year} * \text{Latitude} + \text{Previous December Temperature} \\ &+ \text{Previous June Rainfall} + \text{Previous July Rainfall} + \text{February Rainfall} \\ &+ (1 50 \text{ km grid-square} \div \text{Site}) + (1 \text{Year}) \end{aligned}$
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iv. Predicting indices under different climate conditions

Having established the minimum adequate model containing both climate and non-climate predictors ([MAM03](#)), we explored the extent to which fixing local (5 x 5 km) climate conditions at the mean climate values for the first five years of the study (1976-1980) would have hypothetically altered temporal trends, and population indices in the longer term. A comparison of trends under observed and fixed climate conditions was made for a subset of sites at a range of latitude and longitude values within the *P. malvae* UK range (Figure 2.2, Appendix 3).

In addition, to further investigate possible trends in climate suitability for *P. malvae* over space and time, we estimated climate suitability using just climate effect coefficients from [MAM03](#) and mean climate values for four regions within the study area, the dimensions of which are presented in Figure 2.1. The outputs are presented in Appendix 4. For further details on data processing, modelling and visualising procedures, see Appendix 21.

2.3. Results

Population index henceforth refers to the *P. malvae* annual abundance index at a given [UKBMS](#) transect site. For models involving only non-climate predictors (Methods Section i.), year, in isolation, had a significant negative effect on population index (Est. coef = -0.16, Std. error = 0.05, $p = 0.001$), but no effect was observed of latitude (Est. coef = -0.19, Std. error = 0.11, $p = 0.088$) or longitude (Est. coef = 0.06, Std. error = 0.11, $p = 0.588$) in isolation. The minimum adequate model [MAM01](#) included interactions between year and latitude, and year and longitude (ΔAIC from the next best fitting model (Year only) = -31.6).

Table 2.1 The coefficients of fixed climate effects, and model weightings from a subset of models run with the same response data (Population index).

Each row shows the outputs of a model using a unique combination of fixed effects. Models included are; a) MAM01 minimal adequate model with only non-climate effects, b) MAM02 minimal adequate model with only significant climate effects, and c) MM03 maximal model with non-climate and significant climate effects, and subsequent models with a singular climate effect removed (i-iii). Models ordered in table by AICc weighting.

Model	Intercept	Longitude	Latitude	Year	Long:Year	Lat:Year	Feb Rain	July Rain	June Rain	Dec Temp	df	AICc	Delta AIC
MM03	0.95	0.05	-0.21	-0.17	0.11	-0.13	0.07	-0.06	-0.08	-0.17	14	23921.1	0
MAM03	0.95	0.06	-0.22	-0.18	0.11	-0.13	0.08		-0.09	-0.17	13	23922.3	1.16
(i)	0.95	0.03	-0.22	-0.16	0.11	-0.13		-0.07	-0.10	-0.17	13	23922.7	1.51
(ii)	0.95	0.06	-0.22	-0.17	0.11	-0.13	0.09	-0.08		-0.18	13	23923.7	2.58
(iii)	0.94	0.07	-0.19	-0.18	0.11	-0.13	0.08	-0.06	-0.09		13	23927.9	6.75
MAM01	0.94	0.06	-0.20	-0.19	0.12	-0.14					10	23941.3	20.14
MAM02	0.93						0.09	-0.09	-0.09	-0.18	9	23954.6	33.44

The interaction of longitude and year was positive (Est. coef = 0.12, Std. error = 0.03, $p < 0.001$), and latitude and year was negative (Est. coef = -0.14, Std. error = 0.03, $p < 0.001$). These interactions suggest, in the absence of other unknown variables correlated with spatial gradients, that trends in population index over time are more negative in the north and west (**Error! Reference source not found.**, geographical differences illustrated in Figure 2.3).

When considering effects of climate one by one (Methods Section ii.), we found significant negative effects of December and January temperature, and previous June and previous July rainfall, and a positive effect of February rainfall (Appendix 1). Not all of these effects remained significant when added to a single model; the effects of January temperature, February rainfall and previous July rainfall were the least robust (Appendix 1; **Error! Reference source not found.**).

The fit of the minimal adequate non-climate model ([MAM01](#)) was improved by the inclusion of December temperature, and February, June, and July rainfall effects (ΔAIC from [MAM01](#) = -20.2, **Error! Reference source not found.**). Interestingly, neither July nor February rainfall effect was significant when both were included in the model, but when either variable was singly removed, the remaining variable became significant, and the fit of the model was slightly improved (**Error! Reference source not found.**). However, neither resultant model was a notably better fit than the other ($\Delta AIC = 0.4$; **Error! Reference source not found.**), and there was little change in the effect size or significance of other variables. For the purposes of reporting, the final model ([MAM03](#)) included climate effects of December temperature, February and June rainfall.

The inclusion of climate slightly reduced the effect size of longitude and latitude on trends over time (**Error! Reference source not found.**), but the effect size of climate itself remained small overall (Figure 2.2). In the final model ([MAM03](#)), a one degree increase in December temperature was estimated to account for a log decrease of 0.08 in population index (**Error!**

Reference source not found.). Similarly, a 5cm increase in June rainfall accounted for a log decrease of 0.09 in population index. In contrast, a 5cm increase in February rainfall accounted for a log increase of 0.08 in population index (Error! Reference source not found.).

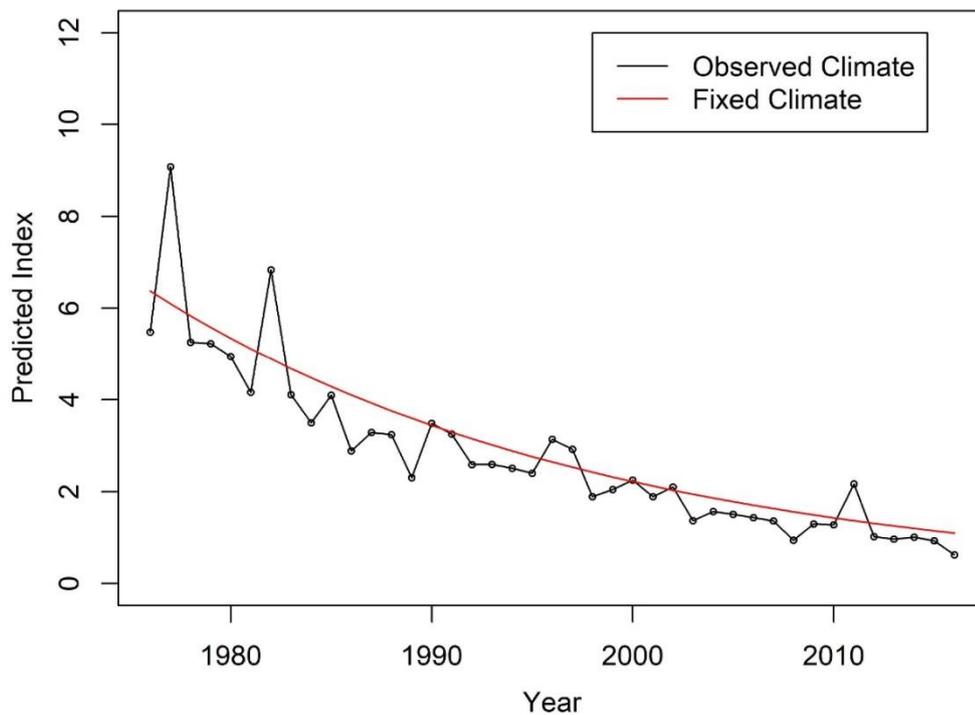


Figure 2.2 Temporal trend in modelled *P. malvae* UKBMS index at a centrally located UKBMS site (Trench Wood) between 1976 and 2016 under scenarios of fixed and changing climate conditions. Indices are predicted from the minimal adequate model of climate and non-climate effects (MAM03), without including random effects. Modelled index values when climate parameters are kept fixed at mean values from 1976-1980 are shown by the red line, while modelled index values when climate parameters represent actual climate data for the focal 5 x 5 km square are shown by the black line.

The effect size of climate is shown in Figure 2.2 for one site centrally located within *P. malvae*'s UK range (Site Number 2345, Trench Wood), but equivalent figures for a group of sites across the range can be found in Appendix 3. Comparing modelled population indices based on either observed annual climatic values, or fixed climatic conditions from 1976-1980 revealed a minimal effect of climate in long term population index trends. Climate's small effect size suggests that climate in isolation explains very little of the index declines observed over time (Figure 2.2). Correspondingly, there are similar trajectories of modelled index values

regardless of whether climate parameters are fixed or change as observed. Also, when we plot combined climate suitability based on [MAM03](#), we found no significant trends over time in any of the four regions mapped (Appendix 4).

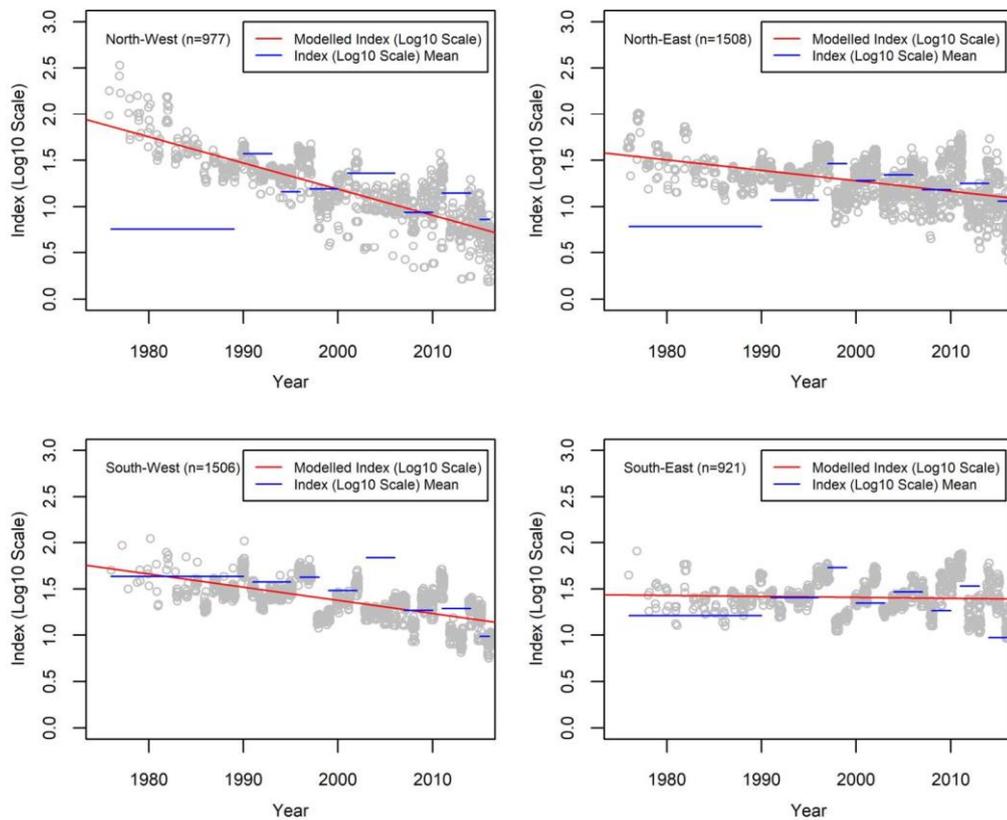


Figure 2.3 Modelled temporal trends of *P. malvae* index divided into North-West, North-East, South-West and South East regions by the median latitude (51.16) and longitude (-1.43) values of UKBMS sites with records. The modelled log index values for each UKBMS record are shown by grey circles, with jitter of ± 0.2 so points can be more clearly seen. These indices are fitted values (before including random effects) from the minimal adequate model of non-climate and climate effects (MAM03), including year, latitude, longitude, and climate effects. Blue lines show the logarithmic mean of observed indices for four time slices in each region, each covering one of eight quantiles of the data. To clarify modelled trends, linear regression between predicted log index values and year are shown by the red lines. Number of UKBMS records (n) in each region is displayed in each graph.

No patterns in residuals were immediately observable when plotting model residuals against year, latitude, longitude, or climate values not included in that model, so no evidence was found for a change in the nature or size of the effect of temperature at different rainfall levels, or vice versa, or over time and space.

2.4. Discussion

In this investigation, we explored spatial, temporal and climatic effects at a 5 km resolution on *P. malvae* population size at monitored [UKBMS](#) sites, in order to increase understanding of the role of geography and climate in the long-term trends of the declining butterfly. We used a mixed model approach to control for increasing survey effort over time, and stochastic variation between years and regions. We observed no significant positive effects of temperature on population index; population index henceforth refers to the *P. malvae* annual abundance index at a given [UKBMS](#) transect site. In the best fitting model, December temperature and June rainfall had significant negative effects on population index, while February rainfall had a positive effect on population index. However, the effect sizes of all climate variables were very small (**Error! Reference source not found.**). Climate effects manifested between years and across space, but there was little, if any, long term trend in any of the above climate variables (Appendix 5). In addition, when modelling population index purely as the product of climate effects from the final model, climate suitability did not significantly change over time, which was a consistent finding in all four regions shown in Figure 2.3 (Appendix 4). As such, the climate effects were largely independent of overall declines in population size which occurred more steeply in the north and west of the range than in the south and east. Our result contradicts predictions of northern expansion for this warm-preferring invertebrate species based on a climate envelope approach (Settele et al. 2008), but is consistent with reports of southward constrictions in *P. malvae*'s range over time (Mair et al., 2012).

2.4.1. Climate Effects

We found no significant positive impacts of temperature on population index in any month (Appendix 1), which would not suggest that the *P. malvae* is overall benefitting from climate warming during its temperature sensitive life stages.

To the contrary, we observed a negative effect of December temperatures on population index, which corroborated established detrimental effects of warm winters on a variety of invertebrates (Wallisdevries and Van Swaay 2006, McDermott Long et al. 2017). Suggested mechanisms for which include higher fungal infection rates (Harvell et al. 2002, Radchuk et al. 2013), and phenological asynchrony (Parmesan, 2007) at higher temperatures. One study posited that warmer winters impacted Lepidoptera species overwintering in temperature-sensitive immature life-stages more negatively than those overwintering as adults (Wallisdevries and Van Swaay 2006). WallisDeVries & van Swaay theorised that warmer winters result in reduced vegetation die-back, and earlier and longer growing seasons. Consequently, as live vegetation generates cooler microclimates than bare ground or dead vegetation (Stoutjesdijk and Barkman 1992), species with life-stages restricted to warm microclimates during the spring may be negatively impacted by warm winters through this indirect mechanism.

However, early successional specialists, such as *P. malvae*, frequently rely on warm microclimates even when immature life-stages occur after spring (Brereton et al., 1998; de Schaetzen, van Langevelde, & WallisDeVries, 2018; Asher et al., 2001), particularly in cooler locations (e.g. at cool range margins). Early successional specialists may therefore also be impacted by greater total vegetative biomass, and cooler microclimates, resulting from longer and earlier growing seasons following warmer winters. Similarly, populations of temperature-sensitive species in general at their cool range edges could be affected by cooling of microclimates relied upon for refuge from cooler ambient conditions (Oliver, Hill, Thomas, Brereton, & Roy, 2009).

Lusher vegetation growth may also be a potential mechanism underlying the observed negative effects of June rainfall on *P. malvae* abundance (Appendix 1), because late instar caterpillars are feeding in June; similar effects have been observed previously in *P. malvae*

(Pollard, 1988; Roy, Rothery, Moss, Pollard, & Thomas, 2001; WallisDeVries, Baxter, & van Vliet, 2011). Alternatively, higher rates of rainfall in summer months may reduce the number of egg laying opportunities for females during their flight period, particularly in years and locations with later flight seasons for *P. malvae*. Given that a model not including the effect of February rainfall was of a similar fit to the minimal adequate model with February rainfall ([MAM03](#)), we are cautious about the implications of this effect. The reported effect of February rainfall may be an artefact of its correlation with July rainfall in this data set, given a negative effect of summer rainfall on *P. malvae* abundance having precedence in the literature (Pollard, 1988; Roy et al., 2001; WallisDeVries, Baxter, & van Vliet, 2011).

2.4.2. Role of climate in declines

While the climate effects were significant, the effect sizes were small, and they did not account for long-term trends in population index, or for geographical differences in those trends. Modelling population index over time revealed similar long term trends in both unchanging, and observed climate scenarios (Figure 2.2). Climate's limited role in long-term trends may result from an absence of significant trends in combined climate suitability between 1976 and 2016 in *P. malvae*'s UK range (Appendix 4). Climate did appear to play a larger role in short term yearly variation (Figure 2.2). Similar findings regarding climate driving short term variation in abundance between years in a related species, *Pyrgus armoricanus*, were also recently reported, in conjunction with a limited effect of temperature on colonisation and extinction dynamics relative to the effects of connectivity and host plant density (Fourcade, Ranius, & Öckinger, 2017).

Furthermore, inclusion of climate predictors in the final model did not qualitatively change the effects of interactions between geography and time on *P. malvae* population index (**Error! Reference source not found.**), suggesting the climate effects are not the drivers of steeper temporal declines in the north and west than the south and east respectively.

Correspondingly, climate suitability does not show differing temporal trends in any of the geographic subsets shown in Figure 2.3 (Appendix 4).

Although this study's scope does not extend to estimating *P. malvae* population sizes under future climate scenarios, Met Office predictions (Met Office Hadley Centre 2019) of generally dryer summers may lead to increases in population sizes, while warmer winters may lead to decreases. Some multispecies studies have reported *P. malvae* as 'a climate change loser' (Brereton *et al.* In submission), but our results suggest that *P. malvae* is neither a winner nor loser from recent climate change. It is possible that simple temporal correlations could misattribute a species' long-term declines to any climate variable that also has a strong trend; this underlines that both space-only and time-only analyses have potential pitfalls.

2.4.3. Drivers of decline

We show strong evidence of long-term abundance declines between 1976 and 2016, especially in the northern and western parts of the UK range. We argue that any simple climate mechanism behind these declines would have been identified with our statistical tests, and therefore are left with the conclusion that a non-climatic driver is behind the declines, most likely habitat loss and degradation (Brereton *et al.*, 1998).

Early successional semi-natural habitats (e.g. chalk downland, coppice woodlands), once widespread across the UK and central Europe (Fuller & Warren, 1993; Green, 1990; Wesche, Krause, Culmsee, & Leuschner, 2012), have undergone large scale losses resulting from agricultural intensification (Walker *et al.* 2009, Ridding *et al.* 2015), especially since the Second World War (Green 1990, Robinson and Sutherland 2002). Corresponding declines have been observed in specialist invertebrates (Kuussaari, Heliölä, Pöyry, & Saarinen, 2007; Wenzel, Schmitt, Weitzel, & Seitz, 2006), including southern restricted butterfly species (Thomas *et al.*, 2015). Furthermore, the quality of remaining habitat has deteriorated in places due to abandonment and changes in natural grazing pressure, such as those resulting from losses of

rabbit populations to myxomatosis (Sumption & Flowerdew, 1985; Travers, Eldridge, Val, & Oliver, 2019).

In recent decades, some semi-natural grasslands have been restored or improved through rabbit population recoveries (Thomas, Simcox, & Hovestadt, 2011), and agri-environment scheme introductions, with some proven benefits to butterflies (Brereton, Roy, Middlebrook, Botham, & Warren, 2011; Davies, Wilson, Brereton, & Thomas, 2005). However, early successional deciduous woodland habitat quality continues to show an overall decline in the UK, owing to management costs and logistic difficulties. (Keith et al., 2009; Atkinson and Townsend 2011; Kirby et al., 2017). Contrastingly, coppiced woodland status varies between regions of Central Europe, as a result of silvicultural intensification and abandonment (Bergmeier, Petermann, & Schröder, 2010), leaving the future status of *P. malvae*'s habitat availability uncertain.

Additionally, north-west populations may have been more sensitive to changes in habitat quality than those in the south-east, particularly at the historical northern cool range margin. Populations at cool range margins can be more reliant on warm microclimates than those in the centre (Hodgson et al. 2015, Suggitt et al. 2018), so shifts to later successional stages may be more detrimental to cool range-edge based populations. *P. malvae* has also been shown to have higher habitat specificity at sites with higher rainfall, potentially amplifying detrimental effects of succession (Mair et al. 2012).

This brings us back to the idea that climate warming (in general, but especially in winter and spring) can lead to accelerated vegetation growth in temperate climates and reduce bare ground availability, essentially accelerating succession (Zhou *et al.*, 2001). Some early-successional species may be affected more by this than by the opposing effect that ambient warming makes even tall vegetation warmer. This makes it particularly difficult to plan for the conservation of early successional habitat specialists, which tend to be threatened across

Europe (van Swaay *et al.*, 2006; Kuussaari *et al.*, 2007) as well as in the UK (Thomas *et al.*, 2015; Thomas, 1993). We might expect each species to respond idiosyncratically to climate change at its cool range margin, depending on the precise balance of the opposing effects.

Habitat availability and climate suitability interact, so for species like *P. malvae*, it is a conservation priority to boost populations by improving habitat condition, both for the direct benefits obtained, and to indirectly allow the species to track climate if and when suitability improves. There is increasing empirical evidence that climate-driven range shifts are slower or impossible if there is insufficient habitat availability (Platts *et al.*, 2019; Devictor *et al.*, 2012). For *P. malvae*, overall declines in population size over time, and more negative trends in the north than the south, as was observed (Figure 2.3), suggests a low likelihood of poleward expansion in the near future (Maggini *et al.*, 2011). Nevertheless, alleviating the non-climatic threats to the species could lead to an expansion of range as well as abundance. This could be important for the global status of the species because as the entirety of the UK is still northerly within *P. malvae*'s overall range, and it may be suffering from heatwaves or droughts at its extreme southern limits.

The complex interactions between habitat and climate discussed so far complicate predictions of habitat suitability when considering range shifts. Species distribution models based only on spatial data (e.g. occurrence) may not fully account for other habitat requirements that limit the potential for a species to exploit opportunities in otherwise climatically suitable habitats. Predictions of range shifts/expansions are particularly vulnerable in a non-equilibrium system, such as one undergoing changes in climate and land management as is the case in many systems across the globe (Elith & Leathwick, 2009). The findings of this study reinforce the need to consider other key habitat requirements and dispersal/colonisation limitations when planning conservation actions that attempt to consider the effects of climate change on range

changes (Devictor *et al.*, 2012; Greiser, Hylander, Meineri, Luoto, & Ehrlén, 2020; Platts *et al.* 2019; Oliver, Thomas, Hill, Brereton, & Roy, 2012).

CHAPTER 3

*Assessing habitat suitability for *Pyrgus malvae**

Abstract

The Grizzled Skipper is in decline within the UK, particularly in the north and west of its range, likely driven by habitat loss and degradation. The butterfly's habitat requirements are well understood in grassland and heathland, but less is known about whether habitat requirements differ between the north and the south, or between grassland and woodland, the two most common UK habitat types for the species. Geographically different habitat requirements could be responsible for steeper declines in the north, with implications for future range expansion under climate change.

We aim to investigate predictors of habitat suitability, and whether their effects interact with geography and nearby woodland cover.

Habitat data were collected using quadrats at 33 sites containing a UKBMS transect, and used as predictors for averaged section-level *P. malvae* presence and count (2014-2019) in generalised linear models. Latitude, longitude, and woodland cover were incorporated into models individually to investigate their interactions with habitat effects.

Shade and sward height were among the variables most consistently retained in low-AIC models, both with negative effects on occupancy and/or abundance. Habitat effects did not consistently differ with latitude or longitude. Non-live cover (i.e. dead vegetation and bare ground) had a positive effect on presence and abundance which became negative in areas with higher wood cover, once woodland cover was considered.

Habitat variables significantly affecting presence and abundance and consistently improving model fit were predominantly related to habitat structure and microclimate. Specifically, less shaded areas with shorter swards, higher non-live cover, and a higher

dead-vegetation-to-bare-ground ratio were linked to higher abundance and presence, assuming low nearby woodland cover. Our findings are in line with current consensus on habitat requirements, and indicate that recommendations for habitat structure are generally applicable across the UK range. Our findings also reinforce the threat from loss of early successional habitats to abandonment and intensification, the structural features of which appear to be the most robust predictors of presence and abundance from our measurements.

Key Words:

Grizzled Skipper, Habitat suitability, Microhabitat, early successional specialists

3.1. Introduction

Climate change is expected to cause isotherms to shift polewards (Masson-Delmotte et al. 2021), which could drive range shifts and expansions for a number of species at their cool range limits. One notable group of such species are several invertebrates which are found in Southern and Central Europe, and meet their northerly range limit within the UK, often due to their requirements for warmer temperatures (Thomas 1993, Thomas et al. 2015). These species' distributional responses to climate change provide a unique opportunity to test expectations of warming conditions releasing northern populations from cool temperature limits inland, and allowing species to expand their ranges along a latitudinal and elevational gradient (Parmesan et al. 1999).

Although climate change may facilitate polewards and elevational range expansions, habitat fragmentation poses a major barrier for some species (Warren et al. 2001), particularly those with specialist requirements and limited dispersal capacity. While we have observed latitudinal and elevational shifts in a number of species, particularly invertebrates (Parmesan et al. 1999, Thomas et al. 2001a, Chen et al. 2011b), rates of range shifts are highly variable and likely dependent on a number of factors (Warren et al. 2001, Hill et al. 2002, Fourcade et al. 2017, Platts et al. 2019). Barriers to expansion from habitat fragmentation are particularly concerning for specialists (Dover and Settele 2009), a group already disproportionately at risk from land-use change (Robinson and Sutherland 2002, van Swaay et al. 2006).

Climate change therefore poses a risk to those southerly species that are unable to track their shifting climate envelopes. Although it has been theorised that species' warm trailing range edges are likely to shift more slowly than cold leading edges under climate change,

with some real world examples, (Chen et al. 2011a), there have been instances of warm range edges shifting at similar rates (Franco et al. 2006, Freeman et al. 2018). For species where the latter is true, barriers to movement, including from habitat fragmentation, could cause range extents to shrink as populations are lost from increasingly climatically unsuitable areas (Settele et al. 2008).

Many invertebrate species restricted to southern UK regions, while occupying a wide range of latitudes in central Europe and elsewhere, are limited to warmer microclimates towards their cooler latitudinal and elevational limits within the UK, manifesting as higher habitat specificity towards their cold range edge (Thomas et al. 2001a, Oliver et al. 2009), and in areas with cooler ambient conditions (Thomas et al. 1999, Davies et al. 2006). Examples of warm microclimates include early successional open habitat structures (Thomas 1993), and southern facing slopes (Lawson et al. 2014). Restrictions to microhabitats such as these have been found to considerably limit the functional area of available habitat (Oliver et al. 2009). Invertebrate species' reliance on warm microclimates are often determined by requirements of early life stages, which are generally the stages least mobile, and most sensitive to temperature in terms of survival outcomes and rates of development (Weiss et al. 1988, Bourn and Thomas 2002, Roy and Thomas 2003, WallisDeVries 2006). Females of some species, such as *Pyrgus malvae* and *Hesperia comma*, additionally often preferentially select for structures associated with warm microclimates when egg laying (Brereton 1997, Streitberger and Fartmann 2013, Lawson et al. 2014).

Warmer ambient conditions could enable individuals in cooler regions to exploit areas of habitat beyond those associated with the warmest microclimates (Thomas et al. 2001a, Oliver et al. 2009). Being able to occupy a wider range of topographies could increase the amount of functional habitat available, potentially increasing connectivity within habitat networks and carrying capacity of individual patches. But beyond this, climate change could allow use of ranker vegetation types which have become increasingly common in the UK due to changes in land management (Green 1990, Hooftman and Bullock 2012), and relax management requirements in sites they already occupy. In addition, because these cool regions are likely to disproportionately be found towards the north of species' ranges, climate change could also facilitate northern expansion for southern habitat specialists (Thomas et al. 2015).

P. malvae is among the southern early-successional habitat specialists which were expected to benefit and expand their range under warming summer conditions (Settele et

al. 2008), potentially even halting and reversing the drastic long-term declines in abundance and occupancy we have observed since the 1970s (Brereton et al. 1998, Asher et al. 2001, Fox et al. 2015, Bell et al. 2021). However, as established in the previous chapter (Bell et al. 2021), although it is difficult to make conclusions on short term trends in a species with highly stochastic variation between years (Didham et al. 2020), declines do not appear to have halted in recent years. Furthermore, long term trends appear to be independent of climate effects, suggesting that habitat remains the dominant driver of trends (Bell et al. 2021). In addition, declines appear to be steeper in the north and west of its range in England (Bell et al. 2021), which does not support a scenario of northward expansion which was previously expected based on spatial analysis of climate suitability (Settele et al. 2008).

Although habitat appears to currently be the main determinant of long-term trends, whether connectivity, quality, or cover, it remains possible that changes in climate have not yet been of sufficient scale to mediate overall suitability at the northern limits of *P. malvae*'s range (Bell et al. 2021). Future scenarios of continued climate change may yet facilitate range expansion (Intergovernmental Panel on Climate Change 2014, Met Office Hadley Centre 2019). In the meantime, steeper declines towards the north of the range are concerning for current conservation targets for the species, and highlight possibilities of either i) greater rates of habitat loss and fragmentation, or ii) more severe effects of habitat loss and fragmentation on *P. malvae*, in the north. Better understanding of habitat requirements across the range, particularly of habitat specificity in the north, could provide invaluable insight into the drivers of the more dramatic declines, and actions which could be taken to address them.

Although the habitat requirements of *P. malvae* have been the topic of several studies within the UK and in central Europe (de Schaetzen, van Langevelde, and WallisDeVries 2018; Krämer et al. 2012; Drinkwater 2012; Seddon 2008; T. M. Brereton 1996), less is known about how habitat requirements may vary geographically, or towards range edges (Oliver et al. 2009). In addition, while differences in habitat requirement were established between heathland and grassland habitats (de Schaetzen et al. 2018), few investigations have explored how requirements could differ between grassland and open woodland habitats (but see Brereton et al. 1997). Woodland is the second most abundant habitat land class where *P. malvae* occupancy has been observed in the UK ([BNM](#), [UKBMS](#)) (Appendix 6), so different habitat requirements than in grassland would be consequential.

In order to address the long-term declines of *P. malvae* within Britain, it is imperative that we understand the habitat requirements in its major habitats and across the extent of its geographical range. This could allow land manager and practitioners to tailor their land management priorities more effectively. In our study, we aimed to identify which habitat features have a significant effect on *P. malvae*'s occupancy and abundance, and investigate whether effects vary spatially, and with different levels of woodland cover, in order to better understand the likely habitat-based drivers of decline. To achieve this, we measured a number of habitat features at locations of known *P. malvae* populations across its UK range, and subsequently identified predictors of habitat suitability through statistical analyses.

Based on the findings of our previous chapter, we initially hypothesised that;

- Both presence and abundance of *P. malvae* will be significantly affected by one or more of the habitat variables
- Effects on *P. malvae* presence and abundance from habitat features related to microclimates will change in nature and/or size geographically, with features related to warmer microclimates have more significant and/or positive effects in the west than the east, and in the north than the south.
- Habitat features related to warmer microclimates will have more positive effects on *P. malvae* presence and abundance in more heavily wooded areas than less wooded areas.

3.2. Methods

3.2.1. Site Selection

We aimed to study a selection of sites with recent records of *P. malvae* presence, including counts, and which were representative of *P. malvae*'s geographical range, and main habitat types. We designated grassland and woodland as the two main habitat types of interest regarding habitat requirements, as two of the most dominant land classes in the UK (Hayhow et al. 2016). This initial selection of habitats was corroborated by our investigation of habitat land classes in the UK Centre for Ecology and Hydrology ([UKCEH](#)) Land Class Map ([LCM](#)) (Rowland et al. 2017) where *P. malvae* was recorded, in which we found grassland and woodland habitats were most over-represented (Appendix 6).

We first identified sites with UK Butterfly Monitoring Scheme ([UKBMS](#)) transects, which are set routes where butterflies are counted using the Pollard method on a weekly basis from

April to September (Pollard and Yates 1993). [UKBMS](#) transects are divided into 'sections', usually delineated by landmarks (e.g. field boundaries), or transitions between habitats.

We aimed to obtain a cross sample of geographical locations, population sizes, and dominant habitat types (Table 3.1). Site selection criteria were: i) [UKBMS](#) records of *P. malvae* in at least three years in the period 2011-2015, ii) latitude and longitude values, and iii) site population size according to [UKBMS](#) index values (Dennis et al. 2013). Annual indices are produced from counts at each transect where there have been a sufficient number of visits during the survey season (Dennis et al. 2013). A range of population sizes was necessary to investigate the predictors of abundance in addition to occupancy. We initially selected 135 sites, and grouped them by bands of latitude (n=3) and longitude (n=2).

In order to sample transects in a mixture of habitat types, we then assigned habitat classifications to transect based on two values from the [LCM](#): i) the percentage cover of Broadleaved Woodland within each 1 km grid square containing the *P. malvae* record, and ii) the first and second most dominant land cover classes in the 100 m x 100 m grid square surrounding the centroid of each [UKBMS](#) transect, using a 25 m x 25 m resolution raster. If the greatest percentage cover (i) was in agreement with the most dominant habitat type of grassland or woodland in the 1 km grid square (ii), the habitat type was 'confirmed'. If not, or if either of the values were not available, the site was instead given a 'tentative' designation.

The initial habitat classifications of each site were then checked against visual inspections of satellite imagery around site polygons in [QGIS](#) (Google 2015, QGIS Association 2022), and G4 European University Information Systems (EUNIS) habitat classifications of the transect as reported by the [UKBMS](#). If the secondary inspection of a transect contradicted the designation using [LCM](#) data, the transect was given a 'tentative' classification. Within each population size category (Table 3.1), we aimed to select at least one site per habitat classification where available, preferentially choosing 'confirmed' habitat types, and secondarily 'tentative' habitats. A total of 33 sites were chosen out of the initial 135 for surveying (Figure 3.1).

Table 3.1 Total number of selected survey sites for *Pyrgus malvae* (Total n = 33), grouped by latitudinal (North, Central, South) and longitudinal (West, East) bands, and estimated dominant habitat type; W (Woodland), G (Grassland).

Geographical Bands	Total Number of Sites	Mean Population Index							
		1-5		5-10		11-20		21-50	
		W	G	W	G	W	G	W	G
North, West	8	1	1	3	1	2	0	0	0
North, East	1	0	1	0	0	0	0	0	0
Central, West	7	0	0	2	0	3	1	0	1
Central, East	5	1	0	1	0	0	1	0	2
South, West	4	0	0	0	0	0	0	2	2
South, East	8	0	0	1	0	2	1	1	3

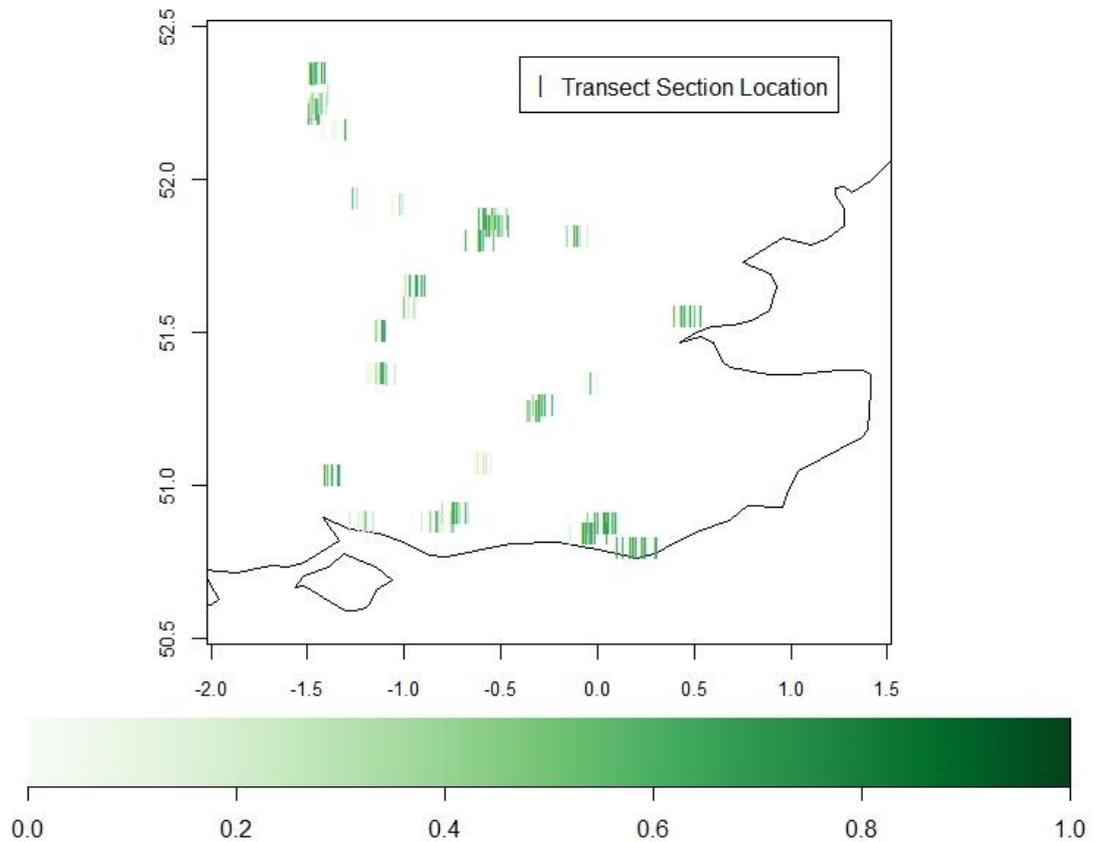


Figure 3.1 Location of UK Butterfly Monitoring Scheme Transects at which habitat surveys for *Pyrgus malvae* were undertaken in southern England. Each vertical line represents sections within transects. Black outline of landmass represents border of south-east England. Y axis; Latitude. X axis; Longitude. Colour scale represents % coverage of woodland in surrounding area (NFI), from 0 (none) to 1 (full).

3.2.2. Habitat Data Collection:

3.2.2.1. Survey Design

Having identified suitable sites, surveys to collect data on habitat features were carried out during the known flight period of *P. malvae*. Surveying spanned approximately 11 weeks, from April 23rd to July 4th 2018. Surveying began at southern sites and progressed northward in an attempt to track the *P. malvae*'s flight period. The flight period was thought to begin later at more northern sites from personal communication with various transect walkers, which was theoretically likely if ambient climates were cooler further north (Brereton 1997).

Transect routes were obtained from [UKBMS](#) maps and guided using handheld [GPS](#) (GARMIN GPSMAP 62S), and were corroborated by personal communication with the

surveyors of transects where possible. Four points were chosen randomly along the length of each section within each transect using a random number generator, at which measurements of habitat features were taken within a 1 m x 1 m quadrat. Selection of habitat features were informed by *P. malvae* breeding requirements reported by prior studies (Brereton 1997, Streitberger and Fartmann 2013, de Schaetzen et al. 2018).

3.2.2.2. Habitat Measurements

We chose habitat variables based on the literature on *P. malvae* habitat requirements, aiming to account for nectar resources, hostplants and microclimate.

Although we had designated habitat classifications for transects prior to surveying using the [UKCEH LCM](#), we found that habitat was highly heterogeneous between sections within transect. Therefore, we opted to increase the resolution of *P. malvae* abundance data from transect-level to section-level. We used the proportion of a 5m buffer region around the mapped section routes (derived from handheld [GPS](#) data collected *in situ*) which intersected National Forest Inventory ([NFI](#)) polygons categorised as 'Woodland' (Forestry Commission 2018).

We investigated agreement between proportion of woodland according to the [NFI](#) and the original habitat type categorisation based on the [UKCEH Land Cover Map \(LCM\)](#), and found that sites categorised as 'grassland' from assessment of [LCM](#) data generally had low woodland [NFI](#) percentage scores. However, many sections originally determined to be within 'woodland' sites according to [LCM](#) data and G4 assessments ([UKBMS](#)) were found to have low [NFI](#) woodland percentages, possibly resulting from patches of grassland habitat within a predominantly wooded transect. We therefore used the [NFI](#) percentage of woodland as the indicator of section habitat type as we felt this metric was at a resolution more relevant to section-level population measures than the overall sites' classification (Table 3.1).

We selected a number of habitat features to be included as predictors of *P. malvae* presence and abundance, based on requirements for microclimates, and indicators of grazing and food availability (Table 3.2). We also set requirement criteria for inclusion of habitat features within models. For inclusion, a feature required a sufficient number of successful measurements (i.e. >900 quadrats), wide distribution of data (e.g. not overly zero-inflated), and no autocorrelation or functional similarity with other features (e.g. representing the same conceptual habitat requirements). Data from habitat quadrats (Total n = 1011) were manually collated and transcribed in Microsoft Excel (Corporation Microsoft

2018) (Appendix 7). Any subsequent data tidying was carried out in R (R Core Team 2020), with further details available in Appendix 8. The final subset of habitat features included in modelling is shown in bold in Table 3.2.

Table 3.2 Habitat features for *Pyrquus malvae* measured in quadrats along all UK Butterfly Monitoring Scheme transects. Variables included in modelling highlighted in bold. Asterisks next to non-bold variables indicate reasons for not including in models.

Variable	Description
Bare ground cover (%)*	Total area percentage with no vegetation, estimated using 10cm ² quadrat divisions within the quadrat.
Dead Vegetation cover (%)*	Total area percentage with dead vegetation, estimated using 10cm ² quadrat divisions within the quadrat
Bare Ground:Dead Vegetation	The ratio of bare ground cover (%) to dead vegetation cover (%) within the quadrat
Non-live Cover (%)	Total area percentage with dead vegetation or bare-ground cover, estimated using 10cm ² quadrat divisions within the quadrat
Scrub Distance (m)**	Distance between the quadrat and the nearest patch of scrub over 1 m in height
Rubus fruticosus Distance (m)**	Distance between the quadrat and the nearest <i>Rubus fruticosus</i> plant
Dropping Presence	Presence of either rabbit or deer dropping within the quadrat, determined by visual inspection
Plant species count (n)**	Total number of unique plant species counted within the quadrat within a 90 second window
Mean Sward Height (cm)	Mean of three measurements taken with a Boorman dropdisc within the quadrat
Individual Host Plant Cover (%)***	Total area percentage of each of the following species of established hostplant for the <i>P. malvae</i> ; Agrimony, Wild Strawberry, Barren Strawberry, Creeping Cinquefoil, Tormentil and Salad burnet
Total Host Plant Cover (%)	Sum of total area percentage of all established hostplants for <i>P. malvae</i>
SMPE:PR	Ratio of Salad Burnet (SM) and Tormentil (PE) cover to Creeping Cinquefoil (PR) cover; (sections tended to be characterised by either high cover of Salad Burnet and Tormentil, or of Creeping Cinquefoil)
Overhead Shade	A visual estimate of the level of shade >2 m directly above the quadrat, categorised as 'Full' (i.e. no view of overhead sky), 'Partial' (i.e. obscured view of overhead sky), or 'None' (i.e. full view of overhead sky).
Nectar Species Count (n)	Total number of unique nectaring plant species (nectar species list based on prior literature), within the quadrat, regardless of whether flowering heads present at time of survey

* Correlated with other variables of interest

** Insufficient number of records

*** Narrow distribution of values (primarily zeroes)

3.2.3. Model Development and Selection:

3.2.3.1. Model Structure

We used a generalised linear modelling approach, with either *P. malvae* presence or abundance as the dependent variable, with a selection of habitat measurements as the independent variables. In addition to the habitat variables, we included fixed effects of a calculated spatial autocovariate, and the date of habitat data collected. We had concerns about potential spatial autocorrelation between section-level butterfly counts within transects, given the high likelihood of possible movements between sections. Therefore, we calculated a spatial autocovariate for both presence and abundance of *P. malvae*, using the ‘sf’ (Pebesma 2018), ‘rgdal’ (Bivand et al. 2020), and ‘geoR’ (Ribeiro Jr et al. 2020) packages in R; see code for further details (Appendix 8).

For occupancy models, we used a binomial variable of section-level presence. In our abundance models, we calculated a proxy of *P. malvae* abundance, which accounts for surveying intensity. In order to calculate this value, we used [UKBMS](#) section-level counts of *P. malvae* from years 2014-2019 (inclusive) and the sum of individual survey visits to a transect, to derive a value representing the relative abundance of *P. malvae* when controlling for survey effort. We logged the ‘Count(Effort)’ value to obtain a normal distribution for modelling with a Gaussian error family. We subsequently refer to this metric as ‘abundance’.

Equation 3.1	$\log \text{Count}(\text{Effort}) = \frac{\log(1 + \sum_{\text{Section}} (\text{All } P.\text{malvae counts } 2014-2019))}{\text{Section Effort} \div (\text{Section Effort})}$ <p style="text-align: center;">Where $\text{Section Effort} = \left(\text{length}(\text{Section}) \times \sum_{\text{Section}} (\text{All visits } 2014 - 2019) \right)$</p>
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All dependent variables were standardised before being used in the model, where the mean of the variable was subtracted from each value, and the result was divided by the standard deviation of the variable.

We explored data for indications of seasonal bias over time or geography in the timings or frequency of visits which may have influenced count numbers, but did not find that sites were visited more or less frequently, or at systematically different times, across latitude, longitude, or years in the [UKBMS](#) (Appendix 9).

3.2.3.2. Model Groups

For all models, we began with a maximal set of all habitat variables highlighted in bold in Table 3.1. There were a total of three groups of models, to investigate i) habitat effects in isolation, and over ii) latitude and longitude, and iii) percentage of woodland cover. The latter two model groups additionally included interaction terms between those factors and all habitat variables. Latitude and longitude interaction terms in group ii) were considered in separate models.

Each model group included models for both presence and abundance, which are described as follows.

Group 1. Base Models (No interaction terms)

P0 (Presence) & A0 (Abundance)

Group 2. Models Considering Geographical Location

PN (Presence, interactions with latitude) & AN (Abundance, interactions with latitude)

PE (Presence, interactions with longitude) & AE (Abundance, interactions with longitude)

Group 3. Models Considering Woodland Cover

PW (Presence) & AW (Abundance)

3.2.3.3. Model Validation and Selection

We used a stepwise selection approach to remove terms from the maximal models, using the 'step' function in R (R Core Team 2020). In each iteration, we removed the term whose removal resulted in the greatest decrease in [AIC](#), with interaction terms being removed before either of the corresponding standalone main habitat effects. Survey date and spatial autocovariates were not subject to removal during model selection. The low-[AIC](#) models are described for each of models in groups 1-3 in the results.

3.3. Results

3.3.1. General Findings

We found that several of the habitat variables we measured had significant effects on section-level *P. malvae* presence and abundance. Among habitat features investigated, shade was most consistently found to have a negative effect on both presence and abundance (Figure 3.2.i.b, Figure 3.2.ii.c; Table 3.3). There were other habitat features that had effects on either presence or abundance, but not both (Table 3.3). Sward height had a negative effect on *P. malvae* presence (Figure 3.2.i.a), while *P. malvae* abundance was negatively affected by a higher bare ground:dead vegetation ratio (Figure 3.2.ii.a), and positively affected by the number of nectar species present (Figure 3.2.ii.b).

The above-mentioned main effects on either presence or abundance were all generally consistent in magnitude in all models of additional interaction terms (Table 3.3; Figure 3.3.a-b). However, the effect of sward height on *P. malvae* presence became non-significant when woodland cover and interaction terms were added (Table 3.3; Figure 3.3.a). The model of *P. malvae* presence including interactions with woodland cover (PW) had very similar [AIC](#) to the presence model with no interaction terms (P0) ([AIC](#) delta < 2). The variables that were found to not improve the fit of any low-[AIC](#) model were host plant cover (Appendix 10), and the ratio of salad burnet and tormentil to creeping cinquefoil ([SMPE:PR](#)).

Table 3.3 (a/b) The significance and size of all effects in the low-AIC models discussed, for both *Pyrus malvae* presence (indicated by 'P' in the Key) and abundance (indicated by 'A' in the Key); null models with no independent variable interactions ('PO'/'AO'), and models allowing interaction terms with i) northing ('PN'/'AN'), ii) easting ('PE'/'AE'), and iii) nearby woodland cover ('PW'/'AW'). Asterisks represent significance of effects; * ($P < 0.05$), ** ($P < 0.01$), *** ($P < 0.005$). Interaction term column signifies 'Northing', 'Easting', or 'Woodland Cover'.

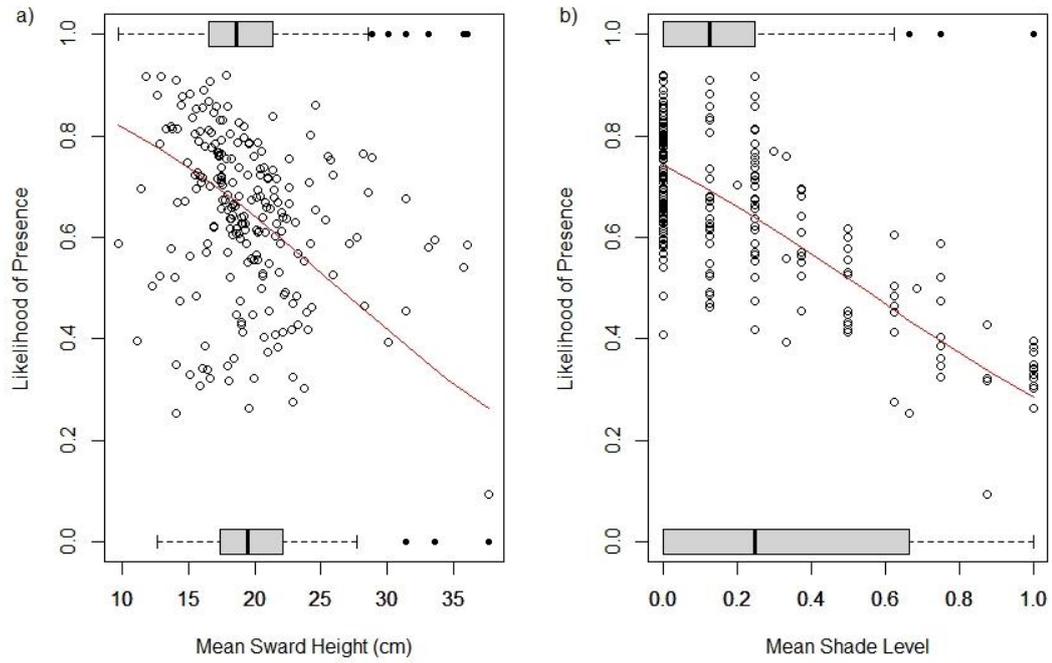
(a)

Model Key	AIC	Interaction Term	Shade	Sward height	Nectar Species	I:Nectar Species	Non-live cover	I:Non-live cover
PO	276.03		-0.62***	-0.39*				
PN	272.76	0.39*	-0.65***	-0.43*				
PE	271.76	-0.16	-0.81***	-0.47**			+0.09	+0.51**
PW	274.9	-0.19	-0.64**		+0.37*	+0.41*	+0.46	-0.44*

(b)

Model Key	AIC	Interaction Term	Shade	I: Shade	BG Ratio	I:BG Ratio	Nectar Species	I:Nectar Species	Non-live cover	I:Non-live cover	Droppings	I:Droppings
A0	849.17		-0.37**		-0.33**		+0.322**					
AN	838.04	0.49***	-0.37**		-0.29**		+0.28*	+0.27*				
AE	842.37	-0.29*	-0.29***	+0.25*	-0.34**		+0.26*					
AW	841.55	0.21	-0.38*		-0.42***	-0.24*	+0.25*		+0.19	-0.28*	+0.22	+0.42**

i)



ii)

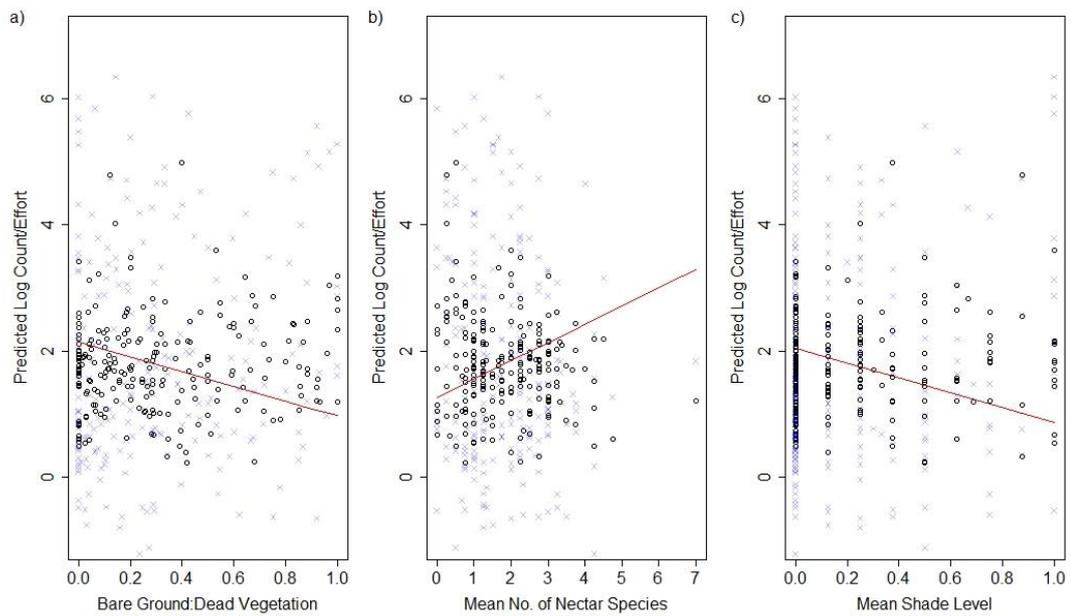


Figure 3.2 Predicted values of *Pyrgus malvae's* i) 'likelihood of presence' by model P0 (Table 3a, Line 1) and ii) 'abundance' by model A0 (Table 3b, Line 1) from non-standardised independent variables retained in the low-AIC models. Distribution of observed presence/absence values against predictors in i) are represented by boxplots with outliers, while observed abundance data points in ii) are shown as blue crosses. Mean shade level is an ordinal variable; (0 = No cover, 0.5 = Partial Cover, 1 = Full cover).

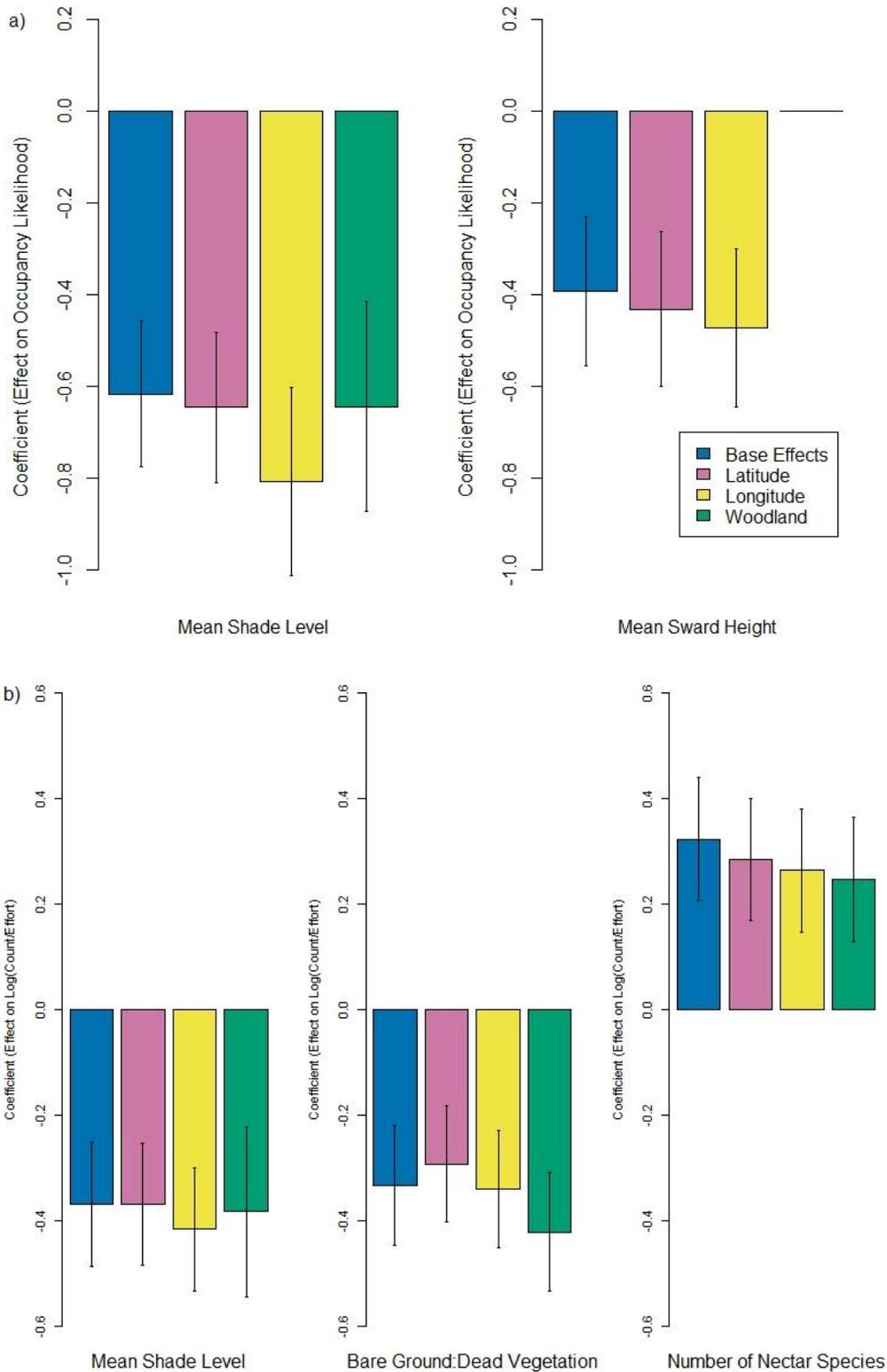


Figure 3.3 Coefficient values for *Pyrus malvae* presence and abundance (standardised) predictors retained in low-AIC models of a) PO (Table 3.3a, Line 1), and b) A0 (Table 3.3b, Line 1), when additional terms (i.e. geography or woodland cover) are considered in the models. Each bar corresponds to a coefficient value for predictor's main effect in models with interactions with an additional term included. Colour of the bar indicates the additional term, see key in plot. Absence of a bar indicates that the predictor was not retained in the low-AIC model with that term included. Error bars indicate standard error of the coefficient.

3.3.2. Models Considering Geographical Location

All main effects from the base models (A0, P0) were retained in the low-AIC models considering latitude and longitude (Table 3.3. a-b), with similar effect sizes, suggesting that the effects of shade, sward height, bare ground:dead vegetation, and the number of nectar species cannot be explained by geographical location.

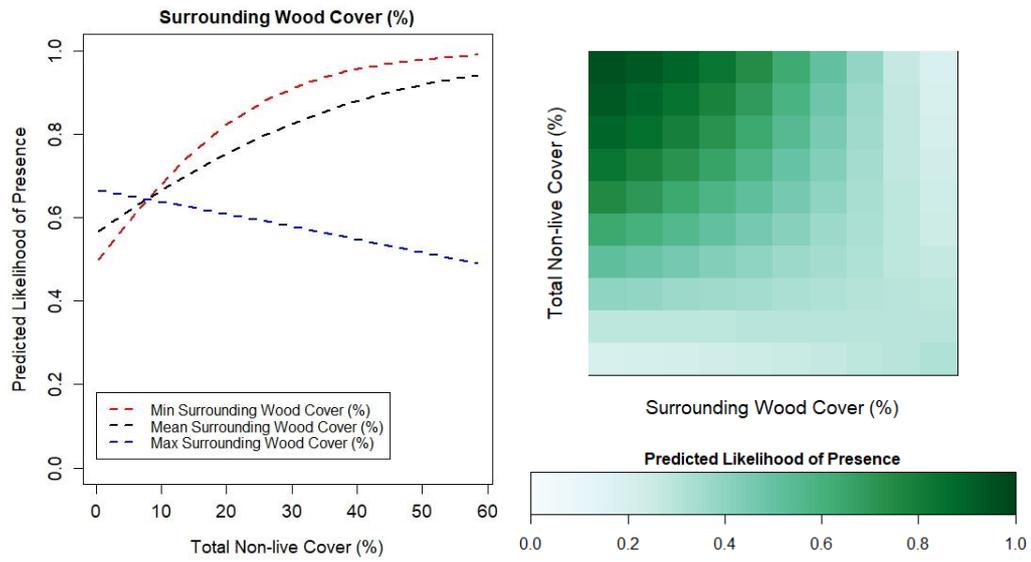
We found a number of interaction terms which were retained in low-AIC models, and main effects which become significant when geography was considered, but none for both presence and abundance models (Table 3.3.a-b.). The only interaction term retained in a model with latitude (PN, AN) was a positive effect of nectar species on abundance which became significantly more positive further north (Model AN, Table 3.3.b Line 2; Appendix 11). We also found that when considering longitude, the negative effect of shade on abundance became significantly less negative in more eastern areas (Model AE Table 3.3.b Line 3; Appendix 11). Additionally, we observed a significant positive effect of non-live cover on presence when easting was considered, which became more positive further east (PE, Table 3.3.a Line 3; Appendix 11).

3.3.3. Models Considering Woodland Cover

Notably, when considering woodland cover, non-live cover had a significant positive effect on both abundance and presence (Table 3.3.a, b Line 4), and a significant negative interaction term with woodland cover (Figure 3.4). The interaction effect size was sufficiently large that at the lowest woodland cover values, non-live cover had a net positive effect on presence and abundance, but at the highest woodland coverage, non-live cover had a net negative effect on both (Figure 3.4).

There were several predictors common to both abundance (AW) and presence models (PW) that considered woodland cover (i.e. shade, nectar species, non-live cover), but some interaction terms were unique to one model or the other. We found that the positive effect of rabbit droppings, and the negative effect of the proportion of bare ground to dead vegetation, on abundance were both amplified in woodier areas Table 3.3.b Line 4; Figure 3.4.b). Additionally, models considering woodland cover retained a positive effect of number of nectar species on both *P. malvae* presence and abundance, the latter effect increasing in woodier areas (Table 3.3.a Line 4).

a)



b)

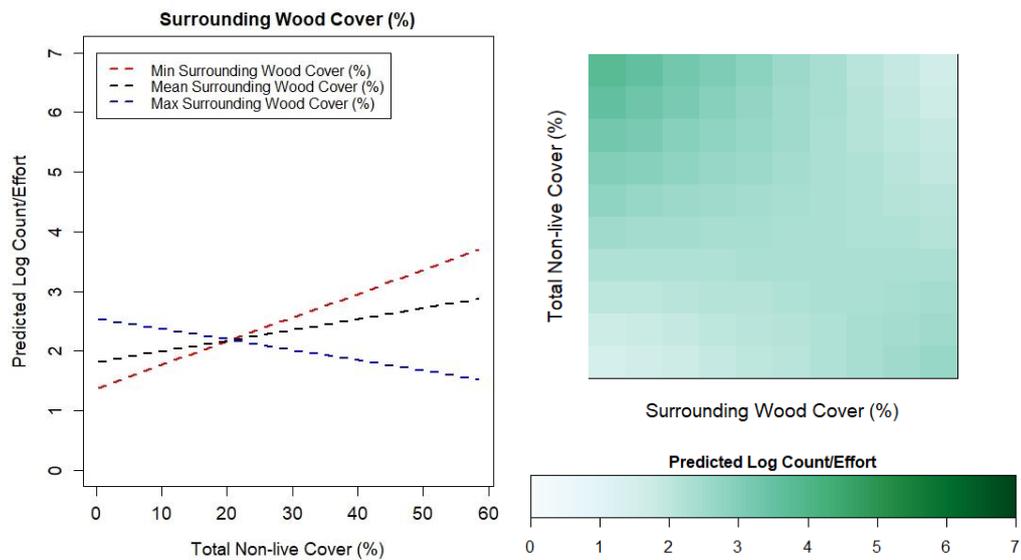


Figure 3.4 Line graphs showing the modelled effects of non-live cover on a) likelihood of presence (Model PW, Table 3a Line 4), and b) abundance (Model AW, Table 3b Line 4) of *Pyrqus malvae*, at minimum, mean, and maximum woodland cover (%) values. Accompanying the line graphs are heat maps showing the modelled effect of the interaction term between woodland cover and non-live cover. Effect size is shown at 100 combinations of the independent variables, with 10 values of each variable at regular intervals across their observed range from the empirical data.

3.4. Discussion

3.4.1. Predictors of Suitable Habitat for *P. malvae*

In this investigation, we aimed to identify habitat features that affected suitability for *P. malvae*, and whether the effects of those habitat features on presence or abundance of the butterfly changed according to geography or nearby woodland cover. A subset of our initial predictors did have a significant effect on either presence or abundance, some of which were more frequently retained in low-AIC models than others.

Several variables associated with habitat structure and microclimate had a significant effect in at least one model, of which the most common effect was 'shade', which was retained in all presence and abundance models (Table 3.3.a-b). The remaining predictors included in the final low-AIC models differed between the presence and abundance model sets ('A' vs 'P') (Table 3.3.a-b), suggesting that the significance of these predictors was more idiosyncratic, impacting on presence and abundance differently. Besides 'shade', sward height was the other predictor variable that remained in the majority of low-AIC models in the 'P' set. Predictor variables that occurred in all low-AIC models for abundance included 'bare ground:dead vegetation', and 'mean number of nectar species'.

The most consistent predictors of presence were in line with the consensus of published literature (Brereton et al. 1998, Krämer et al. 2012, de Schaetzen et al. 2018) which is that non-shaded, short-turfed areas provide warm microclimates optimal for egg laying and larval development. In contrast, predictors of abundance had a theoretical ecological basis but little precedence in the literature, with the exception of a negative effect of shade as there have been prior reports of females preferentially selecting hostplants with less shade from nearby vegetation (de Schaetzen et al. 2018). Nectar diversity could directly determine population size by providing energy for movement and reproduction, and by buffering phenological asynchrony of flowering (Parmesan 2007). However, the association could be an artefact of increased adult activity and visibility in areas with more abundant food resources (Loertscher et al. 1995, Dennis et al. 2006).

The mechanism through which the ratio of bare ground to litter (i.e. a higher proportion of bare ground compared to litter) negatively impacts abundance is unclear, but could result from dead vegetation providing more of a buffer from microclimatic variability (Stoutjesdijk and Barkman 1992) or desiccation compared to bare ground. However, any buffering effect may depend on exactly the kind of litter. The composition of non-live cover may also be correlated with other unknown environmental variables. For example, higher non-live

cover could indicate less improved soil, lower levels of irradiation from shading, or regular disturbance and/or management (e.g. wildlife disturbance).

Some habitat features did not improve the fit of any of the low-AIC models, including total hostplant cover (Appendix 10), but we do not believe that a lack of significant effect here indicates that hostplants are not important for habitat suitability. *P. malvae* has been shown to have idiosyncratic relationships between oviposition and cover of individual hostplant species due to hostplant preferences at different stages of development (Brereton et al. 1998, Krämer et al. 2012). Therefore, aggregated cover of several hostplants could be too broad to reveal significant relationships with population size or occupancy. We did undertake initial explorations of the effects of the individual hostplant species, but the majority of species had very low quadrat cover, resulting in a heavily zero-skewed distribution of cover values (Appendix 12). There was therefore less certainty in the effects of individual hostplants at high coverage percentages.

Nonetheless, the cooling effect of greater total live vegetation cover from higher host plant cover over all may counter the beneficial impact of more oviposition opportunities (Stoutjesdijk and Barkman 1992). In addition, specific qualities of individual hostplants which increase oviposition suitability, such as leaf size and height relative to the surrounding sward, have been highlighted in previous studies (Brereton 1997, Drinkwater 2012, Krämer et al. 2012, de Schaetzen et al. 2018), and could be stronger predictors of presence or abundance than cover alone.

3.4.2. Habitat Suitability Changes with Geography

In contrast to expectations of more stringent habitat requirements in the theoretically cooler northern and western sites (Thomas et al. 1999, Oliver et al. 2009, 2012b), we did not consistently find interaction terms revealing more positive effects of features related to warmer microclimates further north, or west. We found several interaction terms between habitat features and geography, but none that were consistent between presence and abundance model sets (Table 3.3.a-b. Lines 2-3). However, interaction terms which were retained in the low-AIC models, including number of nectar species and non-live cover, could highlight aspects of habitat potentially limiting to *P. malvae* population growth and/or persistence across geographic gradients. Differences in geographic requirements could result from macroclimate, habitat type, or management approaches, and determining the underlying cause would require further investigations, potentially including *in situ* experiments.

The only interaction term retained in the northing models (PN, AN) was a positive effect on abundance of an interaction between nectar species and northing. The positive effect of the number of nectar species being enhanced in the north compared to the south could suggest that there is limited availability of nectar during *P. malvae*'s flight period in northern locations. Alternatively, lower nectar diversity could be an indicator of eutrophication (Wallisdevries et al. 2012), which has been shown to be detrimental to butterflies and is associated with scrub encroachment. However, initial explorations of our data did not reveal dramatically different nectar species number values across northing or easting. One potential explanation for a more positive effect of nectar diversity in the north is a potentially higher energetic demand in generally cooler regions, leading to aggregation of adults around nectar sources. Regardless, this finding is potentially informative for habitat assessment in northern sites, and encourages site-level investigations of whether there may be sufficient nectar diversity during the *P. malvae* flight season.

By comparison, both shade and non-live cover had interaction terms with easting, which each had an effect on abundance and presence respectively (Table 3.3.a-b. Line 3). The positive effect of non-live cover on *P. malvae* presence became notably greater in the east and had a net negative effect at the most western sites, which runs counter to the theory of cooler western macroclimates necessitating warm microclimates for *P. malvae* persistence (Brereton et al. 1998, Krämer et al. 2012, de Schaetzen et al. 2018). However, it should be noted that non-live cover is a broad category covering both bare ground and litter, the composition of which could indicate different environmental conditions of varying habitat suitability not accounted for by our measured variables, such as soil type, habitat class (beyond woodland cover), or management techniques. It should also be considered that the west of the UK tends to experience wetter, milder winters than the east, and higher coverage of dead vegetation could buffer against extreme conditions faced by overwintering pupae in the east, and simultaneously increase risk of fungal infection in the west.

However, the theory of warmer microclimates being necessary in western areas was supported by the negative effect of shade on abundance which became increasingly negative in the west (Table 3.3.b, Line 3), though the finding was isolated, and effect size of the interaction was smaller than that with non-live cover (Table 3.3.b, Line 3).

In the previous chapter, we found that long-term declines in *P. malvae* abundance were steeper in the north and west of the UK range, and independent from climate effects (Bell

et al. 2021), which suggests that habitat loss and deterioration were drivers, in line with current thinking (Brereton et al. 1998, Asher et al. 2001). We initially hypothesised that differences in regional trends could be explained by stricter habitat requirements in the north and west, driven by greater reliance on warm microclimates. However, we have not found clear indications of more stringent requirements in the north or west for habitat structure associated with warm microclimates (e.g. low sward height, high non-live cover, low shade) (Thomas et al. 1999, Oliver et al. 2009), so an alternative explanation could be greater rates of habitat loss or quality deterioration in northern and western sites compared to southern and eastern sites. One example of this is the greater loss of coppiced areas in the north and west, than in the south-east (Fuller and Warren 1993). Potential explanations for regional differences in rates of habitat loss are further explored in the previous chapter (Bell et al. 2021).

We opted not to explore geographic differences in the availability of suitable habitat within this investigation, as our site selection process was biased towards favourable *P. malvae* habitat, given the pre-requisite for transect-level presence in recent years. Therefore, any findings would not be representative of the overall landscape where the species is generally in decline.

3.4.2. Habitat Suitability Changes with Woodland Cover

As an early successional habitat specialist that occurs in different habitat types, we were interested in whether habitat requirements differed between dominant land classes. Although differences in habitat requirements in grassland and heathland have been observed in central Europe (de Schaetzen et al. 2018), little appears to be known about different habitat requirements in grassland and woodland, despite both being widely regarded as the species' two principal habitats in the UK (Brereton et al. 1998).

We found that woodland cover interacted with a number of habitat features which affected presence and abundance (Table 3.3.a-b. Line 4). The most consistent interaction effect was between woodland cover and non-live cover (Figure 3.4.; Table 3.3.a-b. Line 4), where a positive effect of non-live cover at low woodland cover values became a negative effect at the upper range of woodland cover. One likely explanation is that non-live cover has a significant positive impact in unshaded areas because of warmer microclimates due to greater irradiation, but this effect is lost in wooded areas with less light exposure (Stoutjesdijk and Barkman 1992, Chen et al. 1993). It is possible that there is a quadratic relationship between non-live cover and woodland cover with a possible positive effect of

non-live cover at intermediate values, at which higher non-live cover could provide valuable warm microclimates in a more open woodland area. However, the data we collected lack resolution at intermediate woodland cover values (Appendix 13), so we were not able to find evidence for this relationship.

The majority of interaction terms retained in the low-AIC model differed between presence (PW) and abundance models (AW) (Table 3.3.a-b, Line 4). The positive effect of nectar species number on presence, but not abundance, became greater with higher woodland cover (Table 3.3.a, Line 4), possibly because of an association between low nectar diversity and eutrophication (Wallisdevries et al. 2012), which could be more detrimental or more heavily correlated in woodier areas. Nonetheless, the mechanism through which nectar species diversity appears to be important for abundance and presence remains unclear at present.

Contrastingly, the negative effect of the 'bare ground:dead vegetation' ratio on abundance became more negative with higher woodland cover (Table 3.3.b, Line 4). One explanation for a particularly negative effect of relatively higher bare ground cover, compared to dead vegetation cover, could stem from potentially lower light levels and subsequently cooler microclimates in the absence of irradiation in more heavily wooded areas. Additionally, higher relative coverage of dead vegetation could provide a buffer against more extreme variations in microclimates when there is otherwise a lack of vegetation in wooded areas (Stoutjesdijk and Barkman 1992, Chen et al. 1993), providing more suitable conditions for *P. malvae*.

It is also notable that a positive but non-significant effect of droppings presence on abundance was retained in Model 'AW' (Table 3.3.b, Line 4), and that interaction with woodland cover results in a further positive effect on abundance. A positive effect of the presence of droppings, a possible indicator of grazing pressure, is in line with previous findings of beneficial impacts of wildlife grazing and disturbance for *P. malvae* egg laying (de Schaetzen et al. 2018). Furthermore, a greater positive effect of grazing in wooded areas could suggest a particularly beneficial role of wild grazing pressure from rabbits in and around woodlands, because of the slowing effect on succession and the creation of suitable breeding microhabitats (Sumption and Flowerdew 1985, Green 1990). However, the associations of grazing with abundance or presence in this study are difficult to draw conclusions from, as they were retained only in one low-AIC model of six (Table 3.3).

3.4.3. Conclusions

Our findings seem to suggest that, at the sites surveyed, habitat features determining microclimates, overhead shade in particular, are key determining factors for *P. malvae* presence and abundance, and that non-live cover has a positive impact on abundance assuming there is sufficient light available (Table 3.3.a-b. Line 4). Additionally, while some interactions between latitude and longitude improved model fits, features associated with warmer microclimates did not appear to influence occupancy or abundance to any greater extent in the north than in the south. It therefore seems that steeper declines previously observed in the north (Bell et al. 2021) are not likely driven by more stringent habitat requirements at higher latitudes. There is some evidence for more stringent habitat requirements in wooded areas, such as nectar diversity and natural grazing pressure (Table 3.3.a-b. Line 4), but these are more idiosyncratic as retained effects differed between low-[AIC](#) presence and abundance models. Our findings generally align with conventional understanding that the *P. malvae* requires open glades and rides within woodland (Brereton et al. 1998, Asher et al. 2001), but we lack data on intermediate woodland cover to increase our certainty in requirements in less defined or intermediate habitats.

Nonetheless, our findings highlight the risk posed to *P. malvae* by continued succession to later seral stages, and the loss of open glades and rides, given the consistently negative effects of shade, particularly in comparison to our other chosen predictors of habitat suitability. The risk from shading is particularly relevant given the observed trends of woodlands becoming more closed, with denser canopies and loss of open sections. Succession rates may be increased by insufficient management resources or alternative management focuses (Green 1990, Balmer and Erhardt 2000, Kirby et al. 2017), in addition to increasing nutrient deposition (Smart et al. 2004) and a changing climate potentially conducive to increased vegetation growth (Menzel and Fabian 1999, Zhou et al. 2001, Menzel et al. 2020), making the risk to *P. malvae* increasingly relevant for the future.

CHAPTER 4

*Modelling movement of *Pyrgus malvae* between habitat patches*

Abstract

Grizzled Skippers (*Pyrgus malvae*) are in long term decline, most likely driven by habitat loss. Habitat succession, accelerated by climate change and nutrient deposition, is likely responsible for drops in habitat quality. However, the question of how habitat loss and degradation impacts on connectivity and metapopulation function is also of key interest.

To investigate this, we observed *P. malvae* movements and behaviour at five sites in Warwickshire, separated by up to 7 km and used the data to parameterise an Individual Based Model to simulate their flightpaths in the surveyed landscape. We then simulated long-term movement under hypothetical scenarios of scrub encroachment at patch edges, and human intervention to protect individual patches at the expense of others.

We determined that a Correlated Random Walk model with edge avoidance behaviour can replicate key features of *P. malvae* movement observed in the field over short time intervals, enabling longer-term simulations. We subsequently found that higher levels of scrub encroachment resulted in more time spent out of habitat and reduction in connectivity between patches. We further found individual site protection effects on overall connectivity and average time spent out of habitat was highly dependent on the size, shape and connectedness of the site protected.

Site prioritisation will therefore likely depend on goal of intervention; for example, preserving individual populations in strategic but isolated locations (e.g. for range expansion), or preserving connected sites to increase robustness of metapopulation to disturbance events and local extirpations.

Key words:

Grizzled Skipper, Individual Based Model, edge responses, land-use change, habitat succession, early successional specialists.

4.1. Introduction

We have become increasingly aware of long term declines in invertebrates around the globe over the last few decades (Van Dyck et al. 2009, Hallmann et al. 2017, Wagner 2020). A number of drivers have been identified (Robinson and Sutherland 2002, van Swaay et al. 2006, Hayhow et al. 2016); pesticides, climate change, invasive species, and habitat loss and degradation being chief among them (Wagner 2020). Invertebrate declines are of concern in and of themselves, but loss of invertebrates from the ecosystems they inhabit also carry serious implications for other species which are dependent on their interactions (e.g. Large Blue (*Phengaris arion*) and *Myrmica sabuleti*) (Conrad et al. 2006, Dirzo et al. 2014).

Some groups of invertebrates appear to be under greater immediate threat than others, in particular early successional habitat specialists (Thomas 1993, van Swaay et al. 2006, Thomas et al. 2015). Declines in these specialists are strongly linked to the wide-scale degradation and loss of early seral stages of habitat succession in many countries (Balmer and Erhardt 2000, Robinson and Sutherland 2002, Wesche et al. 2012), including the UK. Early successional habitats are reliant on traditional land management practices (Robinson and Sutherland 2002, Poschlod and WallisDeVries 2002). If not managed, these habitats are likely to become fewer, smaller, poorer quality, and more fragmented (Fuller and Warren 1993). Therefore, land management intervention is necessary to prevent further local declines and extinctions of early successional habitat specialists (Lawton et al. 2010), and eventual species loss. Further exploration of this topic can be found in Chapter 1.

While habitat quality is generally important in determining species' occupancy, population growth, and density (Thomas et al. 2001b, Curtis et al. 2015), connectivity is further required for species' longevity at the landscape level (Pickett and Thompson 1978, Thomas et al. 2001b). However, connectivity is not a one-dimensional factor; site proximity, aggregation and distribution along abiotic gradients are just some of the aspects which can influence processes such as genetic exchange and diversity, rescue of smaller vulnerable populations, and tracking shifting climate envelopes through the landscape (Lande 1988, Margules and Pressey 2000, Travers et al. 2021). The ability to rapidly colonise newly suitable patches of habitat is particularly important for species that occupy ephemeral habitats (Bennett 2003), such as those in early or late seral stages of habitat succession which are often managed in rotations (Poschlod and WallisDeVries 2002). Spatial arrangement of habitat patches is also singularly important for determining

metapopulation persistence for species with limited dispersal capacity, which may only be able to travel short distances within a generation (Pickett and Thompson 1978, Brereton 1997).

The threat posed by habitat succession to specialists through degradation of habitat quality is relatively well-studied (Fleishman et al. 2000, WallisDeVries 2006, Krämer et al. 2012, Hodgson et al. 2015), but impacts on connectivity are less so, which could limit efficacy of conservation at spatial scales above site-level. Studies such as ours could help in anticipating future novel threats under continued habitat succession, and in prioritising locations for habitat creation and protection when resources are limited. This aspect of planning is particularly relevant currently, given government targets for creation of 500,000ha hectares of natural environment by 2030 (Defra 2018). For example, scrub encroachment at the boundaries of habitat patches may affect inter-patch connectivity, and by association resilience of metapopulations to disturbance or local extinctions. These impacts could be mitigated by selective protection of individual patches within a network. For early successional habitats, intervention and management is costly (Gerber et al. 2018), and funding primarily comes from grants for conservation purposes which can be short-term and competitive (Winch et al. 2021), which often require land managers to prioritise sites for conservation efforts.

The Grizzled Skipper (*Pyrgus malvae*) is one species which could particularly benefit from research of this nature. Our investigation in Chapter 2 corroborated existing reports of *P. malvae* declines, and indicated that in contrast to expectations of northern range expansion under climate change (Settele et al. 2008), declines were steeper further north (Bell et al. 2021). We also found that climate effects were not responsible for overall long term declines, suggesting that habitat instead could be a main driver of trends. In our subsequent investigation of the impact of habitat features on occupancy and abundance of *P. malvae* (in Chapter 3), our most robust findings were the negative effects of sward height on occupancy and of overhead shade level on both abundance and occupancy. Both habitat features being linked to cooler microclimates (Stoutjesdijk and Barkman 1992) reinforced findings from prior studies of a preference for warm microclimates (Drinkwater 2012, Krämer et al. 2012, de Schaetzen et al. 2018), and highlighted potential risks to habitat quality from succession.

However, as mentioned prior, habitat quality is only one aspect of long-term persistence, with connectivity also being of high importance. With the notable exception of insights

provided by Brereton et al. (Brereton 1997), less is known about *P. malvae*'s movements within and between sites, particularly in relation to habitat edges. Brereton et al. (1997) reported that *P. malvae* is a largely sedentary species, generally moving less than 150 m a day, with occasional longer distance movements made predominantly by males. Individuals, again primarily males, were found to have moved over a kilometre between populations, occasionally traversing scrub and woodland. These movements indicate that these habitats restrict but do not prevent movement, and boundaries between grassland and woodland or scrub are somewhat permeable.

Habitat edge permeability (i.e. tendency of individuals to cross a boundary between habitat and non-habitat during an encounter) can impact in particular on migration rates and is a relevant metric when considering landscape level movements in scenarios of increasing fragmentation and decreases in patch size (Schultz et al. 2012) which are both likely under further scrub encroachment. Interchange of individuals between sites is an important component of source-sink dynamics, particularly for a species, such as *P. malvae*, reliant on transient, ephemeral habitats. Furthermore, *P. malvae* generally exist in small populations, many of which have been reported to go locally extinct and move locally between habitat patches on a yearly basis (Brereton 1997).

The degree to which individuals show an edge avoidance response (i.e. an avoidance of crossing out of habitat at a boundary) has implications for both time spent within a habitat, potentially impacting on population density and growth. The level of interchange of individuals between neighbouring sites could also affect short-term metapopulation dynamics and resilience, as well as the species' capacity to track shifting climate envelopes through the landscape. We were therefore interested in the capacity of adult *P. malvae* for movement within a single generation under different spatial configurations of habitat to understand the effect of landscape changes on patch dynamics.

Our areas of interest focused on the movements of members of a population over a single generation, and on the influence of habitat patch shapes and configuration on connectivity. Therefore, the use of spatially explicit Individual Based Models (Wilensky 1999), which have been employed in investigations of a similar nature (Evans et al. 2019a, 2020), was central in our approach. Individual Based Models simulate the explicit spatial movements and interactions of individuals among themselves, and with their environment. In our case, they can be used to replicate movements of *P. malvae* individuals and explore features of their

simulated movements over an average lifespan to a range of landscape scenarios with complex patch shapes, sizes and configurations.

In this study, we quantified the movement tendencies and edge avoidance behaviour of *P. malvae*, and subsequently parameterised Individual Based Model ([IBM](#)) simulations to make estimates of connectivity in a landscape in scenarios of increasing fragmentation and smaller patch sizes. We also examined the influences of human intervention, by comparing simulations where scrub encroachment occurs uniformly at all habitat boundaries, and where some sites are protected at the expense of others.

Based on previous reports that scrub and wooded areas inhibit movement (Brereton 1997), we expected that *P. malvae* would show edge avoidance responses (i.e. preferentially select grassland over non-grassland destinations) and follow a correlated random walk ([CRW](#)) pattern (i.e. a pattern of movement where successive steps are correlated with each other), in line with other butterfly species (Schultz 1998, Evans et al. 2019a). We also hypothesised that in simulations of greater scrub encroachment, there would be higher movement of individuals between sites and less time spent within habitat overall, even with moderate edge avoidant behaviour. Under increased scrub encroachment:

Hyp 1. Total amount of time spent in grassland will decrease

Hyp 2. Chance of reaching a different site will increase overall

We expected that under encroachment, smaller patch sizes and a potentially higher boundary-length-to-area ratio would result in a net higher likelihood of individuals encountering boundaries and leaving grassland. We expected that if a higher proportion of individuals leave grassland, a higher total number would reach new sites, and would on average spend more time out of habitat.

Finally, we expected that protecting individual sites would lessen the effects of encroachment on both time spent in habitat and connectivity, compared to a uniform encroachment scenario. For both hypotheses (Hyp 1-2), we posited that;

Hyp 3. Effects of encroachment would be greater if all patches have equal encroachment, than if individual sites are protected at the expense of greater encroachment in other sites.

4.2. Methods

4.2.1. Site Selection

We collected movement data of *P. malvae* individuals in the field at a number of sites in order to calibrate individual based models to simulate patch dynamics under different landscape scenarios. To increase likelihood of encounters, we opted to visit sites with which we were somewhat familiar with the local landscapes and micro-distributions of the species from previous visits.

Of 33 sites with *P. malvae* records which were surveyed for habitat features in 2018 (see Chapter 3), a subset of five sites were selected for this study. Only sites with high population size indices from the UK Butterfly Monitoring Scheme were considered in order to maximise likelihood of encountering individuals for observation. Although surveying only high abundance sites may introduce selection bias, surveyed patches contained compartments with variable section-level counts and mosaics of habitats. We selected multiple sites in order to minimise influences from site specific effects on behaviour, which were within a 50 km x 50 km area to allow site visits in a randomised order, to reduce seasonal effect bias between sites. Because we were particularly interested in the movement capacity of individuals under conditions in the north of the species' range, we preferentially chose from more northern sites. We chose these sites as *P. malvae* movements have only so far been recorded and published from southern populations, and we expected that flight patterns in theoretically cooler areas could provide more conservative estimates of movement speed and displacement.

The final selected sites were all located in Warwickshire (Figure 4.1):

Fenny Compton Tunnel (FC) (Grid-ref: SP4152, 20,007 m²)

Harbury Spoilbank North (HN) (Grid-ref: SP3859, 11,551 m²)

Harbury Spoilbank South (HS) (Grid-ref: SP3859, 10,773 m²)

Ufton Fields (UF) (Grid-ref: SP3761, 26,554 m²)

Bishops Hill (BH) (Grid-ref: SP3958, 68,322 m²)

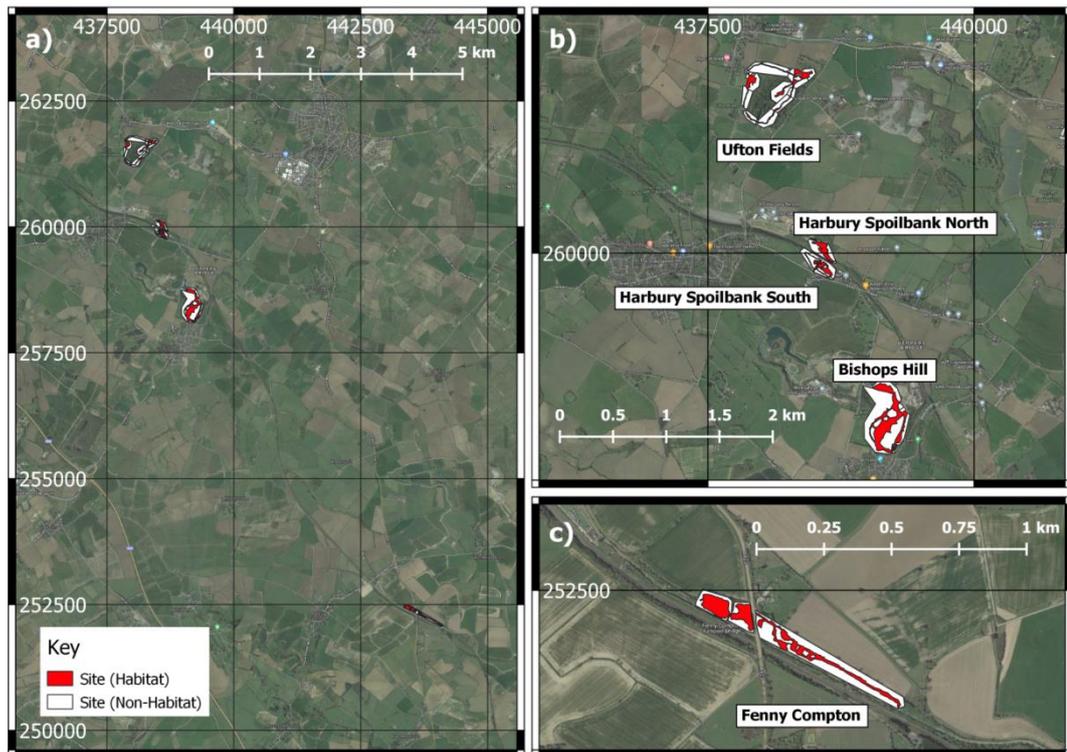


Figure 4.1 Map of all sites visited in 2019 in Warwickshire, England, map from Google Hybrid. Red polygons represent the outlines of habitat patches for *Pyrrhus malvae* in each site, white polygons represent outline of overall site (non-habitat). a) Full area encompassing all sites, b) Higher resolution outlines of four northernmost sites, c) Higher resolution outline of southernmost site. Scale bars included, overlaying grid at 2.5 km resolution.

4.2.2. Field Data Collection

4.2.2.1. Criteria for Surveying

The survey period ran for the approximate extent of the *P. malvae*'s flight period; beginning from the 29th of April 2019, and ending on the 5th of June 2019 (Total Survey Days (n) = 22). We made efforts to visit sites repeatedly through the 22 days to limit seasonal bias between sites in flight behaviour over the flight period. Survey time was divided proportionally amongst the sites based on their relative total habitat area. Butterfly tracking was conducted between 09:00 and 18:00 on days with temperatures generally above 15 °C, and wind speed not above 5 on the Beaufort scale, in line with methodology from Brereton (1997).

4.2.2.2. Tracking Butterflies

Patches of grassland, scrub or woodland, and water were initially mapped from visual inspection of satellite imagery (Google 2015), and Warwickshire's Habitat Biodiversity Audit Scheme (HBA & Local Wildlife Sites Project Partnership 2016) to guide in-field mapping of

transect routes. 'Search' transects, in a systematic 'zig-zag' walk across grassland patches, were undertaken using the Pollard walk method (Pollard and Yates 1993), with a walking speed of approximately 2 kmph and observing a 5 m area either side of the walking route. Final transect paths, and the boundaries of habitat patches were recorded in the field using a handheld [GPS](#) device (GARMIN GPSMAP 62S).

We attempted to survey patches within a site in a randomised order, to minimise potential biases on butterfly behaviour from time of day surveyed (Brereton 1997). When a *P. malvae* individual was sighted, the search transect was paused and the individual was followed (i.e. butterfly tracking) at a distance of >1 m. Numbered tracking cones were placed at the closest approximation of the butterfly's location every 20 seconds during flight, and at the last seen location. If an individual was stationary for more than 20 seconds, the next cone would be placed at the next 20 second interval after it moved from its resting location.

The butterfly was followed until lost, or until 15 markers were placed, whichever was sooner. We used a measuring tape to record the distances between consecutive cones and a compass and protractor to measure the azimuth (γ) between north and the direction from one numbered cone to the next in each flight path (i.e. step direction). After a flight path was recorded, the search transect would resume from the location at which the butterfly had been sighted. Notes on behaviour and cone placements were dictated using recording software on a smartphone (Otter AI 2021), and were manually transcribed in Audacity (v.3.0.0.) ((Audacity Team 2020)), including time stamps of *P. malvae* sightings, behaviours, and marker drops.

4.2.3. Field Data Processing

[GPS](#) data were composed of tracking data (i.e. data collected automatically at regular intervals of 20 seconds while surveying), and survey points (i.e. data manually collected with a label pertaining to sightings or marker locations), each with a time stamp. We recorded [GPS](#) survey points for the starting points (i.e. the location where an individual was first sighted) as a higher priority, and for subsequent markers when possible.

When mapping flight paths, the [GPS](#) survey point for the first marker in a flight path was used as the 'starting point'. If a [GPS](#) survey starting points was not available, a [GPS](#) tracking point at the closest time to the beginning of the flight path was used as the flight path origin. As [GPS](#) tracking points could occasionally be widely spread around the area due to

faster movement while surveying, the locations of subsequent [GPS](#) marker locations would be used to identify a proximate [GPS](#) tracking point for flight path origin.

A shapefile of starting location coordinates of all flight paths was created, and the Comma Separated Vales ([CSV](#)) file was manually edited in Microsoft Excel (Corporation Microsoft 2018), using the distances and angles between the markers to estimate the coordinates of all subsequent markers, using the following equations for x and y coordinates:

Equation 4.1	$X \text{ Coordinate} = \text{Previous Coordinate} + \sin(\gamma \text{ rad}) \times \text{Distance (m)}$
Equation 4.2	$Y \text{ Coordinate} = \text{Previous Coordinate} + \cos(\gamma \text{ rad}) \times \text{Distance (m)}$

4.2.4. Quantifying Flight Behaviour and Edge Avoidance

4.2.4.1. Description of Movements

The key parameters chosen to model movement of *P. malvae*, were i) step distance, ii) turning angle, and iii) the change in probability of choosing a step ending in grassland, as opposed to non-grassland. Step distances (i.e. distances between markers) from field data were determined to have a gamma distribution with a mean value of 2.956 m and a variance of 2.540 (Figure 4.2.a).

Turning angles were calculated from the azimuths of two consecutive markers cones, using the following equation, producing a range of values between -180 to 180.

Equation 4.3	$\begin{aligned} & \text{If } -180 \leq K \leq 180; \text{Turning Angle} = K \\ & \text{If } K > 180; \text{Turning Angle} = K - 360 \\ & \text{If } K < -180; \text{Turning Angle} = K + 360 \\ & \text{Where } K = \text{Cone } 2_\gamma - \text{Cone } 1_\gamma, \text{ and } \gamma = \text{Azimuth (from north)} \end{aligned}$
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Turning angles of the flight paths were found to fit a normal distribution, with a mean of -1.07° and a standard deviation of 76.16 (Figure 4.2b), which is consistent with a distribution of a correlated random walk ([CRW](#)).

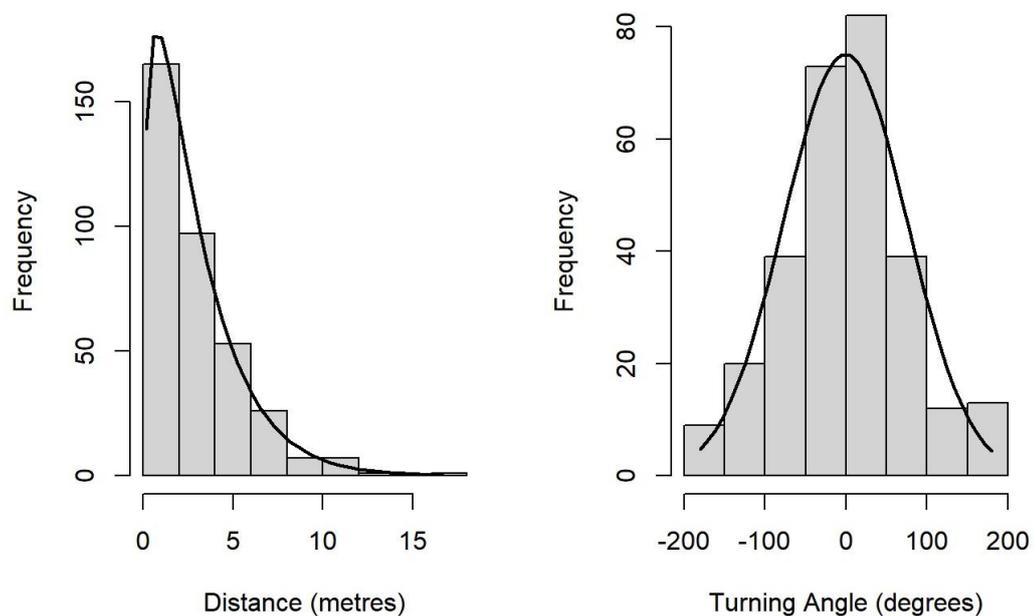


Figure 4.2 Distribution of frequencies of a) step lengths (m), and b) turning angles (degree) , taken from all observed *Pyrgus malvae* flight paths. Black solid lines represent a) Gamma and b) Gaussian distributions fitted with parameters subsequently used to calibrate individual based models.

4.2.4.2. Determining Habitat Patch Edge Avoidance

We aimed to establish whether *P. malvae* showed edge avoidance behaviour (i.e. tendency to avoid leaving grassland when encountering a boundary with non-grassland). We did this by investigating if the probability of taking a step ending in grassland as opposed to non-grassland was higher than expected based on the local proportion of grassland available. We assumed that an individual butterfly's next step length was fixed, but that the direction was influenced by the potential ending habitat type. Therefore, we took the null probability of choosing grassland habitat as the proportion of grassland habitat available in an annulus around the starting point, at a distance of the length of its next step +/- 1 m. We estimated subsequently proportions of grassland for each possible step based on marker coordinates, and habitat polygons, in [QGIS](#) (QGIS Association 2022), using the 'buffer' and 'intersect' functions.

The null probability of choosing grassland habitat (P_0) was used as an offset in a binomial logistic model where the slope was fixed at one, and the dependent variable was a binary outcome of a step ending in grassland or not. The equation for the model is as follows:

Equation 4.4	$\log\left(\frac{P_g}{1-P_g}\right) = C + \log\left(\frac{P_r}{1-P_r}\right)$
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Where P_r is the random probability of choosing grass, P_g is the observed probability of choosing grass (i.e. proportion of grass), and C is the intercept.

The model's positive intercept of 0.695 was significantly different from zero ($P = 0.018$), indicating that individuals select grassland destinations more often than expected from proportion of grassland cover, assuming that the increase in log-odds is constant at all values of proportion of grassland cover.

We then rearranged the model's equation to calculate the additional probability of selecting a destination if it was within grassland, as opposed to non-grassland, as shown here:

Equation 4.5	$P_g = e^C \times \frac{P_r}{P_r(e^C - 1) + 1}$
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The modelled intercept value of 0.695 was used to adjust the probabilities of direction selection during individual based model ([IBM](#)) simulations, depending on the habitat type in the potential 1 m² destination raster cells. The adjusted probability was incorporated to reduce the likelihood of simulated individuals leaving grassland cells when at a habitat barrier, replicating an 'edge avoidance response'.

4.2.5. Individual Based Model Development

We built an individual based model ([IBM](#)), using NetLogo software (Wilensky 1999), to simulate *P. malvae* behaviour, particularly in response to habitat edges, and explore effects of habitat changes on connectivity and movement. The landscapes for all simulations were originally based on a raster of the surveyed landscape, with cells of either grassland, or non-grassland (i.e. woodland and/or scrub), henceforth referred to as 'scrub'.

Patches of habitat within the simulation corresponded to grassland patches we had surveyed (henceforth referred to as 'habitat'), and were grouped within their original [UKBMS](#) site. The landscape raster was altered for simulated scenarios of scrub encroachment to have smaller patches of grassland habitat. Within the simulated landscape, map boundaries were treated as barriers to movement and individuals could not exit the simulation, instead being reassigned a random direction within the grid.

Butterflies were assumed to follow a correlated random walk ([CRW](#)) when not deciding whether to cross a boundary, with 'step' direction and length drawn randomly from the observed distribution of step distances and turning angles (Figure 4.2) on observed movements. When within step distance of a habitat boundary, individuals were programmed to preferentially choose destination cells within grassland during movement, as opposed to cells in woodland or scrub, using the equation for adjusted probability (Equation 4.5).

Duration of simulated 'steps' in a flight path was the mean duration of observations between markers for all flight paths (mean = 37s). These durations from observations included resting time (periods of non-movement), so rest periods during flight activity were assumed to be implicitly included within the simulation. Time steps within the individual based model are henceforth referred to as 'ticks'.

4.2.5.1. Validating short-scale movement:

[IBMs](#) were validated against observed data by running a simulation using the same starting locations as the observed paths, with 10 model replications. Simulations were run for a total duration of 518 seconds, or 14 ticks (i.e. time increments within the [IBM](#) signifying the duration of a 'step'), and comparable measures of movement were taken from the observed and simulated data. Movement metrics were then plotted and visually assessed in R (R Core Team 2020), and are depicted in the results section. These movement metrics were time spent out of habitat (i.e. proportion of simulation duration in which individuals were not in grassland), and number of individuals reaching a new site (i.e. number of individuals in a run (Total n = 1000) that moved between two sites at least once in a single simulation run).

We ran two additional short-scale simulations with grass preference intercepts (C) of 1.2, 2.4, 4.8, and 9.6, to explore the effect of edge preferences on model fit to the observed data. During validation, we found that a C value of 0.695, as produced by the statistical model (Eq. 5) overestimated movements out of habitat. We use values of $C = 4.8$ in all long-scale simulations with scrub encroachment scenarios for a more realistic depiction of emigration rates, as this value produced the closest mean movements out of habitat per tick to observed of the values tested, and had 95% confidence intervals with the greatest overlap, out of all tested C values, with the observed mean of movements.

4.2.5.2. Long Scale Movement:

We ran sets of simulations with longer run-times in order to simulate approximate lifetime movement potential. The run-time of the longer term simulations was based on number of flight hours in a day, proportion of days with suitable weather for flight, and the lifespan of *P. malvae*. The average lifespan of *P. malvae* is understood to be 5-8 days (Brereton 1997), with a peak period of activity between mid-morning and early-afternoon (09:00 and 17:00) (Brereton 1997). The proportion of days with suitable weather was assumed to be approximately 50% from the number of days on which surveying was undertaken during our data collection period in 2019 (22/45); *P. malvae* butterflies were sighted on 18 of those 22 days.

From these assumptions, each individual was estimated to be in active flight for a total of 28 hours over their lifetime on average. In the simulation, each tick represents 37 seconds, which is the mean of the duration of each tick when not accounting for periods of observation of individuals at rest. Therefore, the simulations of long-scale movement had a run time of 2,724 ticks (100,788 seconds, or 28 hours), with daily interval measurements every 389 ticks. Individuals started at random locations within habitat patches, resulting in the number of butterflies originating from the site being dependent on the habitat area within each site.

4.2.5.3. Sensitivity Analyses

Given that no data could be collected from the field on behaviour within the matrix (i.e. all grid cells not categorised as grassland), we ran five different sets of simulations with different assumptions of in-matrix movement changes, in three groups:

1. Death; butterflies die upon entering the matrix, meaning no more data was collected.
2. No Acceleration; butterfly movement was unchanged from parameters used within habitat.
3. Acceleration (a-d); butterflies increase in speed and move in a more linear manner. Achieved by halving the variance of the normal distribution determining turning angles and multiplying the mean value of the gamma distribution determining distances of steps (Figure 4.2) by a) 2, b) 4, c) 8, d) 16.

As we were also interested in the sensitivity of the long-scale simulations to edge responses, we ran long-scale simulations with a range of grass preference values (C); 0, 0.6, 1.2, 2.4, 4.8 and 9.6, as in the short-scale simulations.

4.2.5.4. Scrub Extent/Distribution:

We were interested in how extent of scrub encroachment could influence movement, given trends of increasing ‘greening’ and semi-natural habitat loss to abandonment. Additionally, we were interested in how scrub’s distribution, possibly driven by human intervention, could mitigate the effects of encroachment. Therefore, we designed two sets of landscape scenarios.

The first set of scenarios involved different extents of scrub encroachment inwards from the existing grassland edges to 1, 2, 3, 5, or 10 m, at all sites equally. Rasters for each scenario of scrub extent were derived from the original surveying landscape in R (packages used; “raster” (Hijmans 2020), “dplyr” (Wickham et al. 2020), “sp” (Pebesma and Bivand 2005, Bivand et al. 2013), “rgdal” (Bivand et al. 2020)).

The second set of scenarios assumed the number of hectares of scrub being added to the landscape is the same as would result from a ‘5 m’ scrub encroachment scenario (6.798ha) into all patches as above, but this total cover was distributed to one site at the expense of the others. For each site, a raster was created with the focal site unaffected, and total remaining scrub cover (6.798ha) split amongst the other four sites.

For all ‘long-scale’ simulations, 1000 individuals were seeded at random locations within grassland patches in the map. In a ‘run’, individuals would move through the landscape for 2,724 ticks, and then the simulation was reset to 0 ticks, and the simulation was rerun with 1000 new randomly seeded individuals. Ten simulation runs were conducted for each scrub scenario, (i.e. a unique raster). Data were collected every 389 ticks from each individual in each run on the following;

- a) original site (at beginning of run)
- b) total displacement (i.e. Euclidian distance between starting location and current location)
- c) total distance
- d) time spent outside of grassland
- e) number of entries in and out of grassland
- f) current site
- g) whether currently in grassland.

Our primary interests were in the amount of time spent in grassland, and in the number of individuals reaching a new site. We compared the mean values of each metric at the final time step for each simulation run. We then calculated 95% confidence intervals of metrics for each encroachment scenario by resampling individual metrics at the final time step (sample size = 1000) to determine a mean value. We repeated this process a total of 3000 times, with replacement, and calculated the lower 2.5% and upper 97.5% cut off value for these means ($n=3000$), as the confidence intervals.

We also ran all long-scale simulations with grass preference values (C) of 0.695, 2.4 and 4.8 to assess the sensitivity of outcomes of scrub encroachment scenarios to the strength of edge avoidance responses. Outputs can be found in Appendix 14 and Appendix 15. For further details on data processing, modelling and visualising procedures, see Appendix 22.

4.3. Results

4.3.1. Simulated Flight Patterns

4.3.1.1. Movements Outside of Habitat Patches

When comparing our estimated total displacement values from simulations of flight over the average lifespan of *P. malvae*, we found that the distribution of distances, ranging from a mean displacement of 184.1 m (when $C = 0.695$) to 120.4 m (when $C = 4.8$), was in the same magnitude of observed displacements reported by Brereton (Brereton 1997), who used a Mark-Release-Recapture approach. However, this comparison should be considered with caution as the precise time between recaptures is currently unknown from data (Brereton 1997).

4.3.1.2. Comparison of Observed and Simulated Data

4.3.1.2.1. Movement Metrics

Comparisons of observed and simulated data indicate that the simulation appears to sometimes overestimate displacement and distance travelled (Figure 4.3.a, c), particularly at later 'ticks', or time steps. The observed individuals took shorter steps (i.e. interval distances) at later time steps while they were being followed, which is likely responsible for the divergence from simulations (Figure 4.3.b). It should be noted that sample size of observed movements was also considerably smaller in later ticks (Figure 4.3.) (e.g. $n(\text{Tick } 1) = 75$, $n(\text{Tick } 14) = 4$).

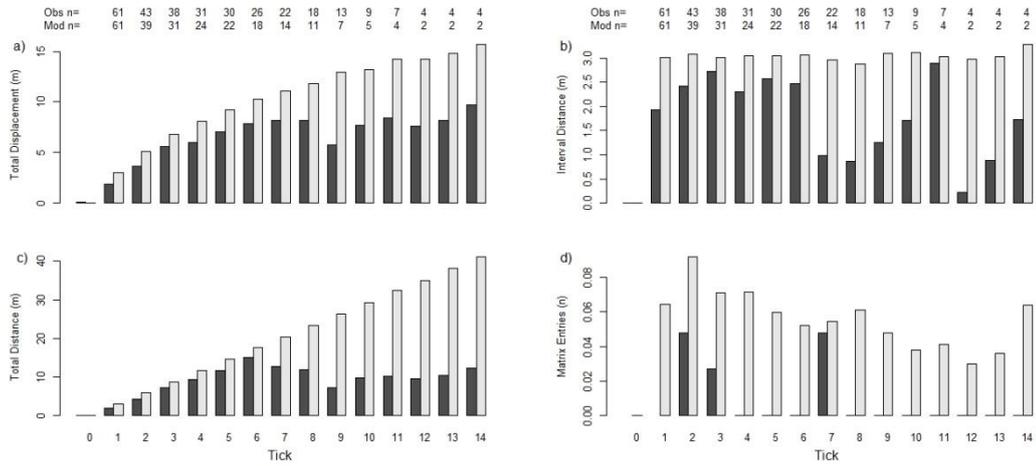


Figure 4.3 Simulated and observed mean values of *Pyrgus malvae* movement metrics over a short-time period; a) Total Displacement, b) Interval Distance, c) Total Distance, d) Matrix Entries, split by 'tick', or 37 second time step. Observed (dark grey) and simulated (light grey) flight paths of *P. malvae* shown.

4.3.1.2.2. Edge Response Comparison

In order to explore the impact of simulated edge response on movement metrics, a comparison between an IBM with a range of grass preference parameter (C) values was conducted. We found that the value of C fitted by the statistical model overestimated the overall likelihood of individuals entering the matrix in a given tick (Figure 4.4).

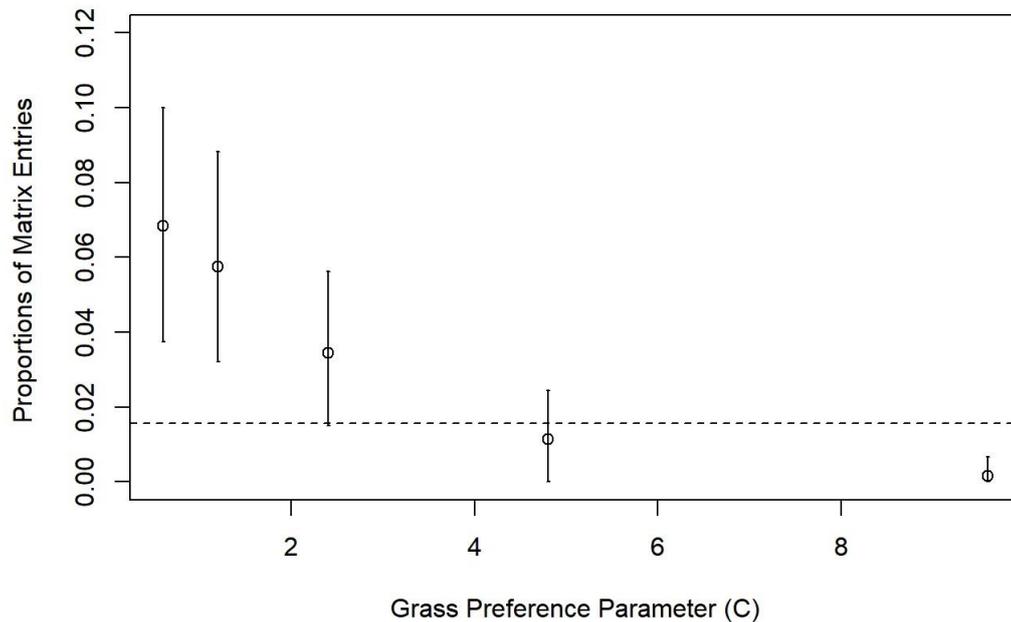


Figure 4.4 Mean proportions of *Pyrgus malvae* movements made over a short time period which resulted in entering the matrix in a random 'tick', produced by model simulations with a range of grass preference parameter (C) values. Dashed line represents the observed mean proportion of movements entering the matrix during a given tick. Error bars represent 95% confidence intervals.

Of values tested in the simulation, a \underline{C} value of 4.8 produced the most accurate likelihood of entering the matrix (Figure 4.4.), so for the purposes of realism, our remaining results and figures (Figures 4.5-4.7) focus on simulations where $\underline{C} = 4.8$. For comparisons between simulations with different \underline{C} values, see Appendix 14 and Appendix 15.

4.3.2. Sensitivity Analyses

We conducted an exploration of the effect of parameters of movement once outside of grassland habitat, by altering the mean step distance in the simulations to increase movement speed, and the variance of turning angles to make flight paths straighter. When mean step distance was unchanged in the matrix, exchanges of individuals only occurred between two of the five sites (Harbury Spoilbank North, Harbury Spoilbank South) which had a minimum separation distance of 40 m (Figure 4.1; Appendix 16). When mean step distance was doubled from observed, and turning angle variability was halved from observed, two of the other sites separated by ~ 1 km (Ufton Fields, Bishops Hill) became connected by transfer of individuals (Appendix 16). Their connection indicates that connectivity increases with acceleration in the matrix, although the remaining site (Fenny

Compton) which was at least 7 km from other sites remained isolated even with doubled movement speed (Appendix 16).

Edge response appeared to have a notable impact on both time spent within habitat and connectivity (i.e. proportion of individuals reaching a new site) (Figure 4.5). The number of individuals reaching a new site did not appear to significantly differ between simulations where $0 \leq C \leq 2.4$, then proportionally decreased with increases in C (Figure 4.5.a). In contrast, we found that time spent within habitat increased steeply with every increase in C that we simulated until it approached 1 (i.e. the entirety of the simulation's duration) (Figure 4.5.b).

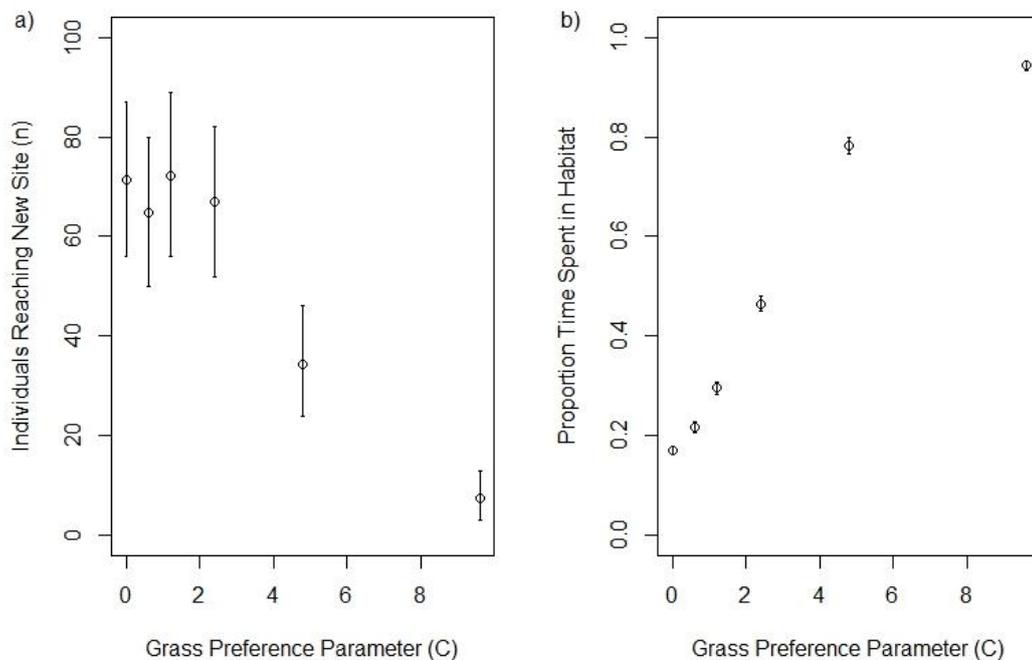


Figure 4.5 Means of simulated values of a) number of *Pyrrhus malvae* individuals having reached a different site from their starting location, and b) proportion of time spent in habitat (out of 100,788 second duration simulations), produced by long term simulations with a range of grass preference parameter (C) values and unchanged movement in the matrix. Error bars represent 95% confidence intervals.

4.3.3. Simulated Scrub Encroachment Scenarios

4.3.3.1. Scrub Extent

Largely in accordance with our first hypothesis (Hyp 1), time spent in grassland decreased linearly with the extent of scrub encroachment (Figure 4.6.a). However, while there was

little difference in the numbers of individuals reaching a new site when there were five or less metres of scrub encroachment, we saw a noticeable drop in numbers of individuals reaching new sites at ten metres of encroachment (Figure 4.6.b), contrary to our second hypothesis (Hyp 2).

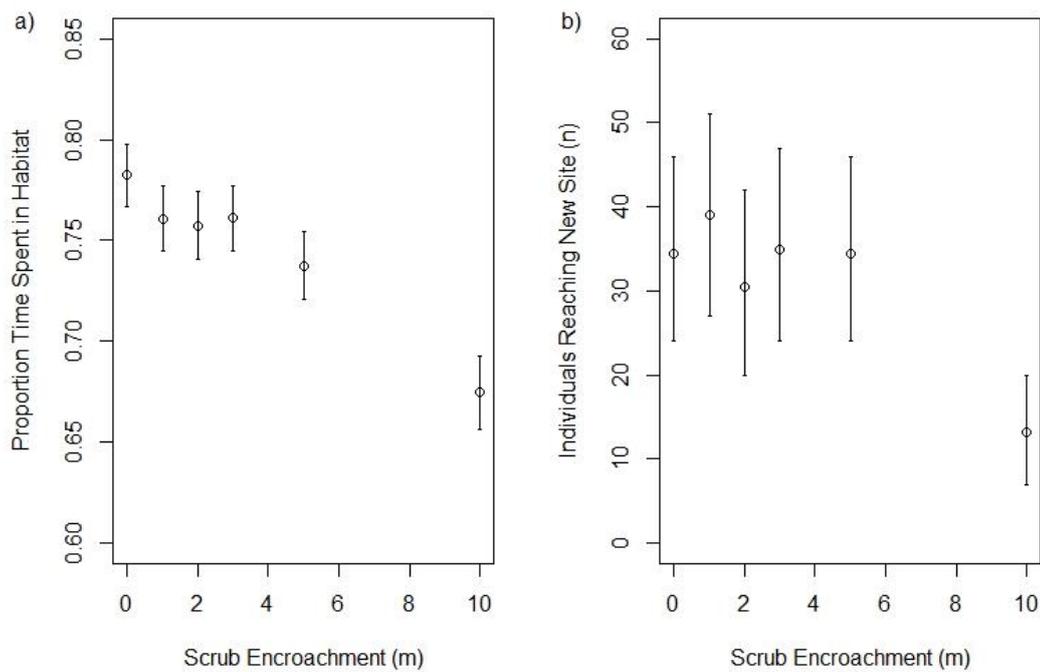


Figure 4.6 Means of simulated values of a) proportion of time spent in habitat (out of 100,788 second duration simulations) and b) number of *Pyrgus malvae* individuals reaching a different site from their starting location, produced by simulations with increasing extents of scrub encroachment. Error bars represent 95% confidence intervals.

The relationship between amount of time spent in the matrix and scrub extent appears not to change with grass preference (Appendix 14). However, the relationship between the number of individuals reaching a new site and extent of scrub encroachment was greatly mediated by the grass preference parameter (\underline{C}) value used in the simulation. When scrub encroachment was ≤ 2 m, the number of individuals reaching a new site increased considerably in simulations when \underline{C} was lower than 4.8 ($C = 0.6, 1.2$) (Appendix 14). This disparity, however, seems to diminish at higher levels of scrub encroachment.

4.3.3.2. Scrub Distribution

Having established a negative effect of scrub extent on the time spent within habitat, and on the number of individuals reaching a new site, we explored whether protecting a single site from encroachment would reduce the effect of encroachment.

We found that protecting one site could have a significant effect on time spent within habitat and individuals reaching a new site, but these effects could be positive or negative relative to the scenario of uniform encroachment of 5 m (Figure 4.7).

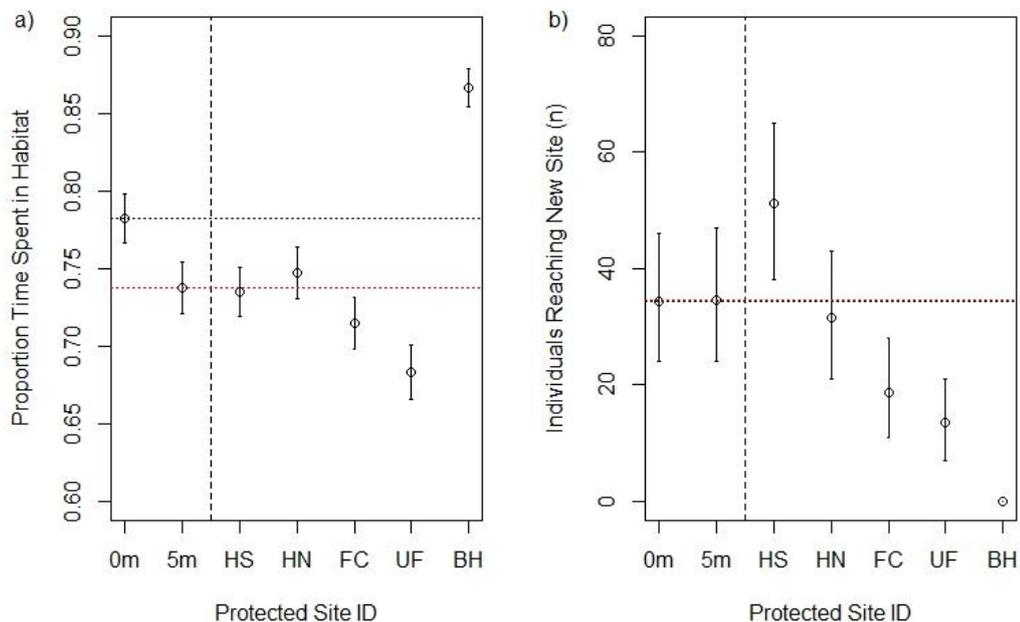


Figure 4.7 Means of simulated values of a) proportion of time spent in habitat (out of 100,788 second duration simulations), and b) number of *Pyrgus malvae* individuals reaching a different site from their starting locations, produced by long-scale simulations using landscapes where scrub cover area is equal to that of a 5 m scrub encroachment scenario, but each individual site (in ascending order of area) is protected from scrub. Protected site in each hypothetical landscape is denoted by letter code on the x-axis, alongside the 0 m and 5 m scenarios also shown in Figure 4.6. Dotted lines represent mean values from 0 m (black) and 5 m (red) scenarios. Error bars represent 95% confidence intervals.

We found that the greatest increase in time spent in grassland compared to a uniform scrub distribution scenario resulted from protecting the largest site, Bishops Hill (Figure 4.7.a). However, protection of the two next largest sites (Ufton Fields, and Fenny Compton) resulted in decreases in time in grassland compared to a uniform scrub distribution (Figure 4.7.a). This disparity suggests that beyond size, dimensions and shape of the site under protection are also likely to play a role. Protection of the two smallest sites, Harbury

Spoilbank North (HN) and South (HS), had little effect on time spent in grassland (Figure 4.7.a).

Protection of individual sites resulted in notably different numbers of individuals reaching a new site, compared to uniform scrub encroachment; whether the change was positive or negative depended on which site was protected. Only protection of the smallest site, Harbury Spoilbank South, resulted in an increase in connectivity compared to a uniform encroachment scenario (Figure 4.7.b). Protecting any site which did not have interchange of individuals (i.e. Ufton Field, Fenny Compton, Bishops Hill) resulted in a decrease in connectivity (Figure 4.7.b), due to resultant decreases in size of connected patches and populations by association. Connectivity decreases were greater when the unconnected sites being protected were larger. The greatest increases in connectivity appeared to result to a large extent from increases in area of the destination site for the highest number of individuals (Appendix 17).

4.4. Discussion

In this study, we aimed to quantitatively describe the flight patterns of *P. malvae* within grassland habitat, and the influence of boundaries between grassland and non-grassland on the butterfly's behaviour. We then used an Individual Based Model (Wilensky 1999) to estimate the effects of scrub encroachment at the boundaries of habitat patches on connectivity and landscape-level movement metrics.

We found that *P. malvae* showed edge avoidant responses and largely followed a Correlated Random Walk in line with our original hypothesis (Figure 4.2). However, while simulations appeared to produce movement in line with that observed, the findings from our encroachment simulations were not completely in accordance with our expectations. While on average, in simulations with greater encroachment, time spent within habitat did decrease as expected (Figure 4.6.a, Hyp 1), the number of individuals moving between sites did not increase overall (Figure 4.6.b, Hyp 2). On the contrary, at < 10 m encroachment, there appeared to be little difference in connectivity between encroachment scenarios, and a notable decrease in connectivity at 10 m encroachment (Figure 4.6.b). Also contradicting our original hypothesis (Hyp 3), we found that protecting one site at the expense of others could lead to positive or negative effects on both connectivity and average time spent in habitat (Figure 4.7) depending on site characteristics, which we explore in greater detail in section 4.4.3.

4.4.1. Features of *P. malvae* movement/behaviour

A correlated random walk ([CRW](#)) model of movement behaviour appeared to fit the movements of our observed individuals well and is well-established in other butterfly species (Crone and Schultz 2008). [CRW](#) has been used as the basis of diffusion and simulation models previously and produced realistic estimates of movement patterns (Codling et al. 2008, Evans et al. 2019b). We also found that that *P. malvae* had a higher probability of choosing grassland over scrub patches than expected from their availability ($C = 0.695$, $P = 0.018$). Similar edge avoidance responses, in which individuals modify their behaviour to avoid crossing structural habitat transitions, have been observed in many species, including butterflies such as Fender's Blue (*Icaricia icarioides fenderi*) (Ries and Debinski 2001, Schultz et al. 2012). We chose to modify the likelihood of directions of movements to simulate the lower relative probability of selecting scrub over grassland habitat near habitat boundaries, but did not change step distances in the interest of limiting model complexity. We feel that this is a reasonable assumption, as prior studies of edge responses of butterflies have indicated that turning angles have differed more significantly in response to habitat boundaries than step distances (Ries and Debinski 2001).

We focused primarily on movements made in very close proximity to habitat boundaries as we assumed edge avoidant response behaviour was less likely to be masked by other environmental factors when the boundary was within typical 'step' distance. In reality, edge avoidant behaviour may occur at distances greater from habitat edges than typical movement steps, depending on the butterfly's sensory range (Grant et al. 2018), reducing the number of opportunities to encounter boundaries in the next step. If this were the case in *P. malvae*, it would help to explain the mismatch between simulated and observed rates of leaving habitat. It should also be noted that there were no observations of individuals re-entering the habitat, partially because individuals were unmarked and assumed lost if no longer within site. Some butterfly species have been known to make 'looping' flights and immediately re-enter habitat upon leaving (Crone and Schultz 2008), so rates of leaving a patch may be lower still than our estimates, but any possible occurrences of re-entry during our observations of *P. malvae* were rare.

However, movements further from habitat edges can be impacted by several other factors, including weather conditions and resource availability/density (Loertscher et al. 1995, Schneider et al. 2003, Evans et al. 2019b, 2020), so isolating the influence of edge response

in movement would be more difficult, particularly with the limited amount of data available. Therefore, to account for the effect of additional edge avoidant behaviour in long-term simulations, which we found to have notable impacts on movement metrics (Figure 4.5), we adjusted the edge response parameter (C) to produce more realistic estimates of likelihood of crossing habitat boundaries.

In addition, we found that our simulations tended to overestimate total distance and displacement of individuals at later time points compared to observed flight paths (Figure 4.3.). However, rather than being an inaccuracy in the model, this apparent discrepancy may reflect an artefact in observed data, as observed interval distances appear to decrease at later time points (Figure 4.3). Step distance decreases over time may result from observer effect, where the subject insect may accelerate when initially followed as a consequence of a ‘herding’ effect (Root and Kareiva 1984, Turchin et al. 1991) but soon become fatigued or return to non-evasive movements. In addition, slower individuals are likely easier to pursue for longer time periods, as indicated by the relatively low number of individuals recorded at later time points (Figure 4.3.).

It should be noted that our models did not capture individual variability in movements and behaviours, such as sex-specific flight patterns. We were unable to record individual sex or make repeated measures of single individuals as we did not have permissions or the time to capture and mark, or sex, individuals. Sex-specific behaviours have been shown to impact simulation outputs (Evans et al. 2020), and should be accounted for where possible, particularly for multi-generational studies where demography and reproduction are of key interest. Nonetheless, we feel our initial investigation of average edge responses in *P. malvae* provides valuable insights into short-term patch connectivity and behaviour.

4.4.2. Testing the Individual Based Model's Sensitivity

When running individual based models ([IBMs](#)), we were interested in the sensitivity of connectivity measures within simulations to the key parameters of edge responses and rates of movement within the matrix outside of grassland habitat patches.

Increasing the likelihood of selecting grassland habitat over scrub resulted in a generally linear decline in both the time spent out of habitat (Figure 4.5.b), and the proportion of individuals reaching a new site in their lifetime (Figure 4.5.a). Total time spent out of habitat and connectivity in particular notably decreased when increasing C (i.e. the grass preference intercept) values from 0.695 (i.e. the intercept determined from logistic

regression) to 4.8 (i.e. the value producing emigration rates in line with those observed), suggesting that varying \underline{C} does influence simulation outputs. Therefore, we ran all landscape scenario simulations with \underline{C} values of 0.6 and 4.8 for comparison, and outputs can be found in Appendix 14 and Appendix 15.

Our simulation results show that edge responses theoretically have important implications for metapopulation dynamics, in accordance with previous empirical and theoretical studies (Ries et al. 2004). Our results suggest that strong edge responses appear to reduce connectivity, with individuals on average having a lower likelihood of reaching new sites (Figure 4.5), potentially negatively impacting on the robustness of the population network to disturbance events, and increasing inbreeding effects (Baguette et al. 2013, Kool et al. 2013). However, individuals with stronger edge responses also appear to spend more time within habitat, potentially resulting in lower mortality likelihood associated with hostile environments (Nowicki et al. 2014).

As we were only able to observe movements of individuals in grassland habitats, and not areas of scrub or woodland, we had to make assumptions about movement within the matrix, which have been shown to differ from in-habitat movements in other butterfly species (Crone et al. 2019). Simulations of individuals with faster, straighter movements in the matrix, as previously seen in studies of empirical data (Schultz et al. 2017, Evans et al. 2020) resulted in increased total displacement and a higher connectivity (Appendix 16), in line with population theory (Lutscher and Musgrave 2017). However, proportion of time spent out of habitat was only slightly impacted by movement in the matrix, which suggests that accelerated movement outside of habitat would not necessarily impact on potential population growth. Despite this, it should be noted that mortality is likely to be higher in the matrix (Nowicki et al. 2014), particularly if encountering hostile environments, which was not accounted for in our simulations.

A previous study (Brereton 1997) explored *P. malvae* movements between and within habitats through Mark-Release-Recapture survey efforts, and reported mean movement distances over a number of days (Brereton 1997). Their estimates are roughly in line with simulated mean displacement for \underline{C} values of 0.6 (184.1 m) to 4.8 (120.4 m), assuming no acceleration outside of habitat (Appendix 18). However, Brereton (1997) predominantly recorded movements within sites, so there is less confidence on movement within the matrix, and these surveys were conducted in southern England several decades ago in the early-mid 1990s. Dispersal capacity of *P. malvae* may differ in more northern or more

recent landscapes, given established effects of environmental conditions (e.g. climate, habitat resources) on movement behaviour in other butterfly species (Schneider et al. 2003, Cormont et al. 2011, Schultz et al. 2012, Delattre et al. 2013, Evans et al. 2019b).

4.4.3. Impact of Habitat Change on *P. malvae*

The level of scrub encroachment had impacts on both the proportion of individuals that reach a new site in their lifetime (Figure 4.6.b), and the proportion of time spent in grassland (Figure 4.6.a). Even in more severe succession scenarios of 10 m of encroachment, individuals spend only approximately 10% less of their lifetime in grassland (Figure 4.6.a) and so are likely to have largely the same opportunity to feed and reproduce under short-term encroachment. However, this assumption does not account for additional degradation of habitat suitability for *P. malvae* likely to occur within sites under continued succession (Chapter 3) (Brereton et al. 1998). Meanwhile, in contradiction to our hypothesis (Hyp 2), connectivity appears to decrease markedly with increasing scrub (Figure 4.6 b.), and this relationship could be even stronger if edge avoidant responses were weaker ($\underline{C} = 0.6$ vs. $\underline{C} = 4.8$) (Appendix 14).

Two processes were likely driving effects of encroachment in effective connectivity; the likelihood of leaving a site (i.e. emigration), and the likelihood of encountering and entering another site (i.e. immigration). Scrub encroachment is likely to increase the likelihood of emigration by potentially increasing the boundary-length-to-area ratio and decreasing the average distance of individuals to the edge of habitat. Simultaneously, encroachment could also decrease the likelihood of encountering new sites once in the matrix (Baguette et al. 2000, Kindvall and Petersson 2000, Englund and Hambäck 2007).

If encroachment in a site increases the likelihood of encountering a boundary while within habitat, a stronger edge avoidant response (e.g. from a higher structural contrast at boundaries (Prevedello and Vieira 2010)) could mitigate the positive effect of encroachment on likelihood of emigration, at least at lower levels of scrub extent (i.e. < 10 m). In this case, encroachment would primarily negatively affect connectivity by decreasing the likelihood of encountering sites once in the matrix.

However, we take our findings on the effects of encroachment on connectivity with great caution as it is based on only one landscape configuration, and proximity and arrangement of patches is a very important component of connectivity (Dover and Settele 2009). We are particularly aware of the impact of proximity, given that in the simulations which explored

scrub encroachment, only two of the five sites (Harbury Spoilbank North and Harbury Spoilbank South) were reported to be close enough for movements between sites (Appendix 16).

The importance of habitat spatial arrangement in our simulations was further reinforced by our finding that protection of one site from encroachment at the expense of others could have either positive or negative effects on both connectivity and time spent in habitat (Figure 4.7). Protecting the smallest, and connected site, Harbury Spoilbank South, resulted in the greatest increase in connectivity but no change in time spent within habitat (Figure 4.7). Meanwhile, protecting the largest, and unconnected site, Bishops Hill, resulted in the complete loss of connectivity, but the greatest increase in time within habitat (Figure 4.7). The complete loss of interchange of individuals in the latter scenario resulted from the loss of the two connected Harbury Spoilbank sites (HN and HS) to encroachment when Bishops Hill was protected.

The very different outcomes of individual site protection highlight different considerations when planning for management; protecting larger sites could maintain cornerstone populations with high density and population growth, but come at the cost of smaller sites and network connectivity if those smaller sites are well-connected, potentially leaving populations isolated, vulnerable to stochastic extinctions (Lande 1993), and unable to track their climate envelope (Travers et al. 2021). On the other hand, protecting smaller sites comes at little expense to others and could increase the resilience of the population network. However, those sites are likely to contain small populations which are vulnerable to stochastic variation and local extinction, so may be less valuable to the overall population network in terms of source-sink dynamics (Guo et al. 2005).

Our simulations did also reveal outcomes which appeared to be detrimental to both connectivity and population growth. Protection of sites, Ufton Fields and Fenny Compton, as medium sized but unconnected sites, resulted in fewer individuals moving between habitats and less time spent within habitat on average than under uniform encroachment (Figure 4.7). Our findings highlight the risks of prioritising resources at sites which may be expensive to maintain but are not heavily involved in the population network. It should also be noted that while aggregation of sites is important for connectivity, north-south connectivity is also relevant in a changing climate (Travers et al. 2021), so less connected sites closer to cool range edges may still also offer unique value for conservation planning. The positioning of a habitat patch should also be considered in relation to future

conservation plans, and whether they are strategically important as a stepping stone to areas that may become suitable for colonisation under climate change, or land-use change.

It is important to consider that the connectedness of sites in this network in our simulations was based on average movements and likely does not account for rare long-distance dispersal events which are notoriously difficult to estimate (Bennie et al. 2013). Additionally, our simulation does not include all possible habitat patches or populations in Warwickshire, and so should not be used as a guide for actual connectedness in that area. The simulated matrix also does not account for areas with hostile features, such as predators, or barriers to movement, such as dense woodland stands, which could introduce further complexity if located between connected sites.

Protecting sites which were not connected at the expense of site with individuals moving reduced overall proportion of individuals reaching new sites, and subsequently connectivity. Meanwhile, protecting a 'connected' site in a simulated landscape with encroachment in fact increased overall connectivity compared to a scenario of no-encroachment (Figure 4.7.a). This could suggest that strategic management of sites in scrub encroachment scenarios could lead to improved overall connectivity. However, it should be noted that our simulations assumed the size of the starting populations at each site was in proportion to the area of the site.

Population size in reality is not necessarily proportional to total possible habitat area, which is a blunter measure than resource-based area for example (Turlure et al. 2010). Distributing individuals between sites based on site area also complicates inferences about the effect of encroachment on connectivity and theoretically population site through time spent within habitat because even uniform encroachment resulted in different rates of area loss between sites. The unequal habitat loss under encroachment was likely based on the boundary-length-to-area ratio, with more irregular shapes being more impacted by encroachment.

However, for the purposes of our simulation, we assumed that habitat quality was largely consistent between sites, given that we pre-selected our sites on the basis of recent records and high likelihood of encountering individuals. We also assume in our simulation that area of the site correlated with functional area of habitat and roughly translates to population sizes at carrying capacity after reaching equilibrium after landscape change.

One factor not included in simulations was the influence of edge effects (Ewers and Didham 2006) with potentially adverse impacts of *P. malvae* at edges of habitat as opposed to the core, which are likely more common in irregular habitat patches. If *P. malvae* density is lower towards patch edges, it is likely that population growth could be even lower in smaller and more irregular sites than expected from time spent within habitat alone.

4.4.4. Conclusion

Our observations of *P. malvae*'s flight behaviour suggest the species does show edge responses, and highlight the importance of patch size, shape and spatial configuration, all of which are impacted by scrub encroachment, an already established threat to habitat quality (Bell et al. 2021). Our simulations indicated that scrub encroachment at habitat boundaries could reduce time spent within habitat and population growth by association (Cantrell and Cosner 1999). At greater extents of encroachment, movement of individuals between sites are also reduced. It appears that in our simulated network, potentially higher rates of emigration were negated by lower rates of immigration once in the matrix due to lower likelihood of encountering smaller sites.

However, effects of encroachment were greatly mediated by the size, shape and spatial arrangement of sites. Our simulations indicate that protecting small connected sites can increase connectivity, possibly due to increased area of destination sites associated with higher immigration. Further research could look into different configurations of site connectedness and size to determine the point of encroachment at which higher emigration becomes outweighed by lower immigration. There is also evidence to suggest that edge responses are mediated by structural contrast at habitat boundaries (Prevedello and Vieira 2010, Schultz et al. 2012), and that connectivity between sites can be increased through the creation or protection of corridors or stepping stones between sites (Dover and Settele 2009). Both of these could be incorporated into our simulations to explore strategies to mitigate impacts of encroachment on landscape scale connectivity.

Aside from connectivity within the species' current range, scrub management could be of particular importance towards the edge of *P. malvae*'s range, where populations are likely to be more vulnerable to local extinction (Antonovics et al. 2006), and dependent on source-sink dynamics (Holt et al. 2005); but see (Sagarin et al. 2006). The role of connectivity may be even more important for conservation of *P. malvae* given impending risks from continued climate change. Climate change is likely to not only shift *P. malvae*'s

theoretical climate envelope north (Settele et al. 2008), but also result in more frequent extreme weather events, such as extreme precipitation, or warm winters, both of which we have previously shown to negatively impact *P. malvae* (Bell et al. 2021). In a future where conservation funds are likely to be increasingly competitive (Gerber et al. 2018), land-use pressures are likely to increase (Foley et al. 2011), and the climate is changing (Masson-Delmotte et al. 2021), there is an increasingly urgent need to prioritise our resources for the best chance of conserving threatened species in fragmented landscapes. Our simulations highlight the significance of selecting sites for protection, the choice of which could mitigate, or exacerbate, the effects of habitat loss on connectivity and population growth.

CHAPTER 5

General Discussion

In this thesis, I aimed to better understand the threats and opportunities for the Grizzled Skipper (*Pyrgus malvae*), as one of many species threatened by fragmentation and loss of its semi-natural habitat while simultaneously responding to a changing climate (Brereton et al. 1998, Oliver et al. 2015, Hayhow et al. 2016).

I posed a number of core research questions with the aim of improving our understanding of the complex interactions of climate and land-use change for this threatened species. I specifically explore the role of climate in driving long-term trends, predictors of habitat suitability and impacts of land-use change scenarios on metapopulation dynamics. In this chapter, I will summarise my answers in response to these questions, and subsequently suggest evidence-based recommendations for conservation planning going forward.

- i. What are the long term trends of *P. malvae*, particularly in the north where climate-driven range expansions are expected? How much of these trends are driven by climate effects?
- ii. Which habitat features are significant predictors of Grizzled Skipper occupancy and abundance? Do the habitat requirements of *P. malvae* differ geographically, and between habitat types?
- iii. What is the flight behaviour of *P. malvae*, and do they show edge avoidance responses to wooded boundaries of habitat patches? How does scrub encroachment impact on connectivity metrics between patches in a network?

5.1. Findings and Conclusions

Although no northern expansion has yet been observed (Hayhow et al. 2016), I hypothesised that if expansion was imminent, abundance trends would be more positive towards the north of the species' UK range than the south. I also expected that climate effects would explain some of the variation in long term trends (Settele et al. 2008). Our results instead indicated long term abundance declines (Figure 2.3), which were steeper in the north and west, and not driven by climate effects (Figure 2.2). Of climate's impacts, negative effects of both summer rainfall and winter temperature were the most significant (**Error! Reference source not found.**).

Steeper northern declines suggest that climate-driven northern expansion is currently unlikely, and that other factors, most likely linked to habitat loss, remain dominant drivers of trends (Brereton et al. 1998). Indeed, climate change could have negative effects on habitat quality and connectivity for *P. malvae* by exacerbating the effects of abandonment under scenarios of lengthening growing seasons and reduced vegetation dieback (Wallisdeevries and Van Swaay 2006). Our findings highlight the risks of using spatial-only data to predict future climate niches in a non-equilibrium system which is being acted on by multiple, interacting pressures.

As climate appears to have a limited direct impact on *P. malvae* abundance, the threat to the species by the trailing warm range edge shifting northwards and trapping the species seems low at present. The primary concern appears to be habitat degradation (Brereton et al. 1998), and the long-term need to maintain networks of sites for a sustainable metapopulation. We will need to sustainably create early successional habitats and protect existing patches, both conventional (e.g. lowland grassland) and novel (e.g. industrial brownfield), perhaps more in the north. Scrub and rank vegetation management will likely require increasing resources given possible exacerbating factors of climate and nutrient deposition.

There have been several studies into the particular habitat requirements of *P. malvae* in the UK and central Europe (Brereton 1997, Krämer et al. 2012, Streitberger and Fartmann 2013, de Schaetzen et al. 2018), but little is known about whether requirements differ geographically, or between the two most dominant habitat types in the UK. Knowledge of this topic is particularly relevant in light of our findings of *P. malvae* steeper declines in the north and west of its UK range, independent of climate drivers.

We found negative effects of sward height on presence likelihood, and shade on both presence likelihood and abundance (Table 3.3). Additionally, higher nectar diversity, and a higher ratio of dead vegetation to bare ground, had positive effects on abundance (Table 3.3). No interaction effects seemed to suggest stricter habitat requirements or selection for warmer microclimates in the north and west (Thomas et al. 1999). I did, however, find positive effects of non-live cover on both presence and abundance which became negative in woodier areas (Table 3.3; Figure 3.4).

The habitat effects on presence and abundance which were most frequently retained in the final models were generally related to warmer microclimate. It seems that less-shaded areas with short sward and high non-live vegetation cover, assuming the area has low

wood cover, were generally more suitable for *P. malvae* (Table 3.3), largely in agreement with previous studies (Brereton 1997, de Schaetzen et al. 2018). Notably, habitat requirements did not appear to differ with latitude or longitude (Table 3.3), indicating that features of 'suitable' habitat are consistent geographically, although could differ at the very range edge limits (Oliver et al. 2012a). Less is known about specific hostplant requirements; hostplant cover was not retained in any of the low-AIC models, but hostplant related features (e.g. plant height, leaf size) have been reported as having significant effects on abundance in other studies (Krämer et al. 2012, de Schaetzen et al. 2018).

Our results corroborate existing habitat recommendations for short-swards, limited shade and high cover of bare ground and dead vegetation (Brereton et al. 1998), and highlight some potential evidence-based indicators of suitable habitat when assessing a site. Furthermore, our findings suggest that habitat creation techniques will be similarly effective across *P. malvae*'s UK range (Table 3.3), but that factors such as increasing nectar diversity or grazing pressure may be more beneficial in habitats in more wooded locations.

Having identified impacts of succession on habitat quality of *P. malvae* (Table 3.3), I was interested in whether succession in the form of scrub encroachment also affects adult movement, with implications for metapopulation dynamics. I found a statistically significant tendency to avoid leaving grassland (Chapter 4; Figure 4.4), and that higher encroachment in our simulations decreased both connectivity and time spent within habitat (Figure 4.6). Protection of small but well-connected sites led to higher connectivity, but less time within habitat on average (Figure 4.7). Meanwhile, protection of large unconnected sites caused the loss of the small well-connected sites, decreasing connectivity, but increasing time within habitat (Figure 4.7). Protecting unconnected, medium-sized sites reduced both connectivity and time within habitat (Figure 4.7).

Encroachment appeared to decrease connectivity in our simulations (Figure 4.6), against our initial hypotheses, indicating that greater levels of succession will not only have negative implications for habitat quality (Chapter 3; Table 3.3) but could also interfere with source-sink dynamics, and *P. malvae*'s potential for reaching and colonising newly suitable habitat patches. In the simulated landscape, connectivity appeared to be most affected by the area of the destination site (Appendix 17), suggesting that encroachment reduced connectivity because the likelihood of individuals encountering smaller sites is lower.

While prioritising unconnected sites always decreased connectivity (Figure 4.7), protecting the largest unconnected site increased average time spent in habitat (Figure 4.7), which could produce higher population density or population growth. Meanwhile, protecting isolated medium-sized sites reduced both connectivity and time spent within sites (Figure 4.7), so their prioritisation may only be useful if their location is strategically important (e.g. for range expansion) (Saura et al. 2014).

Our findings suggest that continued succession at the landscape level could reduce individuals' time within habitat and likelihood of reaching another site in their lifetime. In a landscape where management resources are limited, and succession rates are likely to increase with further nutrient deposition and lengthening growing seasons (Smart et al. 2004, Masson-Delmotte et al. 2021), decisions to prioritise scrub management at particular sites could have considerable impacts on metapopulation dynamics. Choice of sites to protect should consider whether it is more important to increase connectivity (i.e. prioritising connected sites) or population growth (i.e. prioritising large sites), and be aware of the risk of prioritising a medium-sized, unconnected site which could reduce both of these metrics in the network overall.

5.2. Implications for conservation and suggested key performance indicators

My findings highlight ongoing pressures for *P. malvae*, despite numerous conservation efforts, and hold potential value for informing conservation planning. In the interest of contextualising my findings against the backdrop of UK environmental policy and conservation, I here briefly review the progression of conservation in the UK, and protections for *P. malvae*. I then discuss the current status of *P. malvae* conservation efforts, and the need for a more standardised approach in order to reduce the risk of further local extinctions. I subsequently provide a possible set of indicators which could be adopted by a leading organisation in the species' conservation, Butterfly Conservation, and which could be of use for other target species.

5.2.1. Conservation Policy

5.2.1.1. UK Conservation

Environmental protections within the UK are complex and long-running. Legislation began in 1949, with the National Park and Access to the Countryside ([NPAC](#)) Act (British Parliament 1949). Since then, the [NPAC](#) Act has been succeeded, and added to, by new legislation (UK Government 1994, British Parliament 2006, Lawton et al. 2010), resulting in

several statutory designations for various priority habitats and species (Adams 1984, UK Government 1994). Environmental protections come from both within the UK (e.g. Natural Environment and Rural Communities ([NERC](#)) Act (Section 41)) (British Parliament 2006), and the EU (Council Directive 1992). The most recent iteration of internal UK environmental protections are at the country level (JNCC et al. 2012), having devolved from the previous UK-wide UK Biodiversity Action Plan ([BAP](#)). These acts use the [BAP](#) list of priority species and habitats as a reference for statutory designations (Lawton et al. 2010). The numerous transitions between schemes and stewardships, the most recent of which being the Local Nature Recovery Strategies (Local Nature Recovery 2021), can make it difficult to track for landowners and tracking progress towards targets.

The current UK government have released several plans for environmental protections since 2019, including the 25 Year Plan for the Environment, Local Nature Recovery Strategies, and the Nature Recovery Network (Defra 2018). However, these plans and reports of success have come under some criticism (Natural Capital Committee 2020), including possible misrepresentation of target-meeting, and inflated portrayals of levels of protection. For example, there are a number of protections and schemes for sites, but these are often disparate and have different purposes. Designations can be primarily conservation-oriented, or conservation can be a sub-component of protections, and can be loosely grouped into three tiers of purpose and conservation proximity (Lawton et al. 2010). These tiers correspond to the level of protection afforded to sites across several schemes; Tier 1 sites receiving the highest level of protection, Tier 2 sites being recognised for high biodiversity value and receiving partial protection, and Tier 3 sites having wildlife designations as only part of their statutory purpose (Lawton et al. 2010). The conflation of these 'tiers' for the purposes of conservation assessment or targets can therefore be misleading to stakeholders and the public.

5.2.1.2. Grizzled Skipper Protections

P. malvae's decline has been noted since the late 20th century (Brereton 1997). In response, Butterfly Conservation released a Species Action Plan (1998) (Brereton et al. 1998), but the species did not receive statutory protection in the UK until 2006, when it was added to the UK Biodiversity Action Plan during a review (Biodiversity Reporting and Information Group 2007). Prescribed actions for the species in England ([NERC](#)) include implementation of Agri-Environment Schemes ([AES](#)) to preserve grassland habitat, English Woodland Grant Schemes ([EWGS](#)) to maintain wide glades and rides in regular rotations, and greenfield

measures to create sites in urban areas (e.g. topsoil stripping, adding low nutrient substrate) (British Parliament 2006). *P. malvae* is not currently listed as a ‘threatened’ European Species (Council Directive 1992), given that trends in central Europe may be less severe, though still likely occurring, particularly in northern Europe (Maes and Van Dyck 2001, Streitberger and Fartmann 2013, de Schaetzen et al. 2018), so the species may be added to the list in coming years.

Plans for conserving *P. malvae* do not appear to be centralised or have clear legal mandates, and instead rely primarily on the participation of private landholders within schemes, and efforts of Non-Government Organisations (NGOs) and local wildlife groups. *P. malvae* is likely to also be protected in Sites of Special Scientific Interest (SSSIs), and other Tier 1 sites (Lawton et al. 2010). However, it is unclear to what extent habitats can be managed to ensure sufficient habitat in the required structure for this particular butterfly, given needs of other target species at those sites (Davies et al. 2007) and increasing pressures from nutrient deposition and longer growing seasons (Menzel and Fabian 1999, WallisdeVries and Van Swaay 2006). Furthermore, goals for increasing woodland cover (Defra 2018) have driven conversion of some grasslands to woodlands and could jeopardise some sites with potential for recolonization (UKCEH 2020).

5.2.2. Grizzled Skipper Conservation Actions and Efforts

Conservation work for *P. malvae* tends to be done on the county level (e.g. Derbyshire, Newark) (Butterfly Conservation 2018, Churcher 2021b), led by a few select individuals leading volunteer work parties. This reliance on local ‘biodiversity groups’ (Winch et al. 2021) tends to result in variable levels of activity and management between groups, depending on expertise, accessibility, (Oxford 2013) and funding (Winch et al. 2021). There can also be rapid turnover in key voluntary roles (Winch et al. 2021), impacting management continuity and expertise.

Because *P. malvae* is found in a range of different habitats (Brereton et al. 1998), from heathland, to grassland, to brownfield sites, to woodlands, there are a number of management techniques for creating and maintaining *P. malvae* suitable habitat (Brereton et al. 1998), which are usually decided at the site level. The majority of habitat creation is oriented around halting succession and replicating the outcomes of historical, economically non-viable techniques (Fuller and Warren 1993, Poschlod and WallisDeVries 2002, Merckx and Pereira 2015), and cultivating suitable microclimates.

Modern management for conservation takes a somewhat unprecedented approach given that historically habitats were grazed and coppiced in a more landscape-scale rotational approach (Fuller and Warren 1993, Poschlod and WallisDeVries 2002). Traditional approaches produced a mosaic of habitats, so there were generally always patches for individuals to move to once a habitat was disturbed or lost to succession. In the current landscape, remnant populations, particularly small ones (Lande 1993), are thought to be vulnerable to extreme disturbance events (e.g. overgrazing, non-suitable weather) according to feedback from Butterfly Conservation staff. Their loss would then require additional habitat restoration, and/or reintroductions as the landscape is fragmented and *P. malvae* is largely sedentary with small populations (Brereton 1997, Thomas et al. 2001b), exacerbating strains on limited resources.

In grassland, habitat creation typically involves scrub management by cutting (and occasionally herbicide application), limiting grass growth through mowing (Walker et al. 2004), grazing (Brereton et al. 1998), and seeding yellow rattle (i.e. a parasitic plant which inhibits grass growth) (Field et al. 2005). Efforts to create areas of breeding habitat also include topsoil stripping, small controlled burns, cutting and removing grass (Walker et al. 2004), plug planting wild strawberry (or other *Rosacea* family plants), and adding ballast and tree stumps (Slater 2007). The creation of butterfly walls and mounds and ditches to create a range of topographies and microclimates has also been trialled with positive outcomes for *P. malvae* (Slater 2007). Habitat creation techniques in brownfields are similar, involving creating breeding patches across a range of slopes and aspects; for example, along railway lines, which could act as corridors in the landscape (e.g. Nottingham) (Nottinghamshire Biodiversity Action Group 2021a).

In woodland, meanwhile, rotational coppicing (Brereton 1997) is usually employed, replicating historical techniques as opposed to intensive productive coppicing (Fuller and Warren 1993). Creating wide rides and glades are also encouraged (Brereton 1997), and controlling deer's access to prevent selective grazing of plants and disruption of coppice rotations (Stewart 2001). In all habitats, practitioners can try to restrict entry at times of year from the public (e.g. dog walkers) to avoid risk of trampling and disturbance to larval stages and breeding patches (Brereton et al. 1998). In addition, because the traditional semi-natural sites where *P. malvae* are found tend to be protected (Lawton et al. 2010), there are often restrictions on the management that can be taken (e.g. burning, types of livestock permitted).

Centralised conservation efforts for *P. malvae* are likely to be hampered by limited up-to-date knowledge of the condition of its landscape level habitat network. [SSSI](#) condition status (e.g. 'recovering') is reported by Natural England staff, but at up to 6-year intervals, and for general condition of the overall site (Williams 2006), which is generally designated for a number of different species with individual requirements. Broad habitat condition reporting could obscure early indicators of declining habitat quality for *P. malvae*, and other early successional habitat specialists (Davies et al. 2007), resulting in more likely losses of vulnerable populations in areas with limited resources. The sites would likely then be deprioritised for management for that species' habitat, due to limited local resources (Winch et al. 2021) and could be functionally lost from the species' suitable habitat network.

Personal communication with land managers and practitioners gave an impression of a lack of information sharing between groups, despite clear enthusiasm for conserving species. *P. malvae* is just one species that may be falling through the gaps of national protection efforts, dependent on local level protections (Winch et al. 2021), which highlights the importance of conservation assessment (Sawhill and Williamson 2001). A more standardised, evidence-based approach to conservation measurement could help to create a more cohesive picture of priority species at the national level, and provide more timely early warnings for species at risk. Below I present a case study in producing indicators of conservation success tailored towards *P. malvae*, informed by previous work, and by the results of this study.

5.2.3. The Evolution of Conservation Assessment

Conservation has only relatively recently begun to be formally evaluated over the last four decades (Sawhill and Williamson 2001), following a model similar to the evolution of evidence-based healthcare (Pullin and Knight 2001). Previously outputs of conservation action were measured in simple metrics, such as area managed and money spent (Sawhill and Williamson 2001), but in order to improve conservation efficacy (e.g. adaptive management practices) (Salafsky et al. 2002) and provide accountability to the public and stakeholders (Sawhill and Williamson 2001), the field of conservation assessment emerged.

5.2.3.1. Key Performance Indicators

Key Performance Indicators ([KPIs](#)) are an increasingly widespread approach for measuring and communicating conservation actions and outcomes (Barros et al. 2017). [KPIs](#) are

quantifiable measures of various aspects of performance, which provide insights into activities, outputs, and overall progression towards a project or organisation-level goal. Their use originated in business to report on productivity and profits to stakeholders (Elwin and Hirst 2007), but more recently they have been employed within the conservation sector (Stem et al. 2005). However, its implementation in environmental protection can be more complicated than in business, where end goals ultimately focus on profits, with clear target audiences (e.g. customers, employees, shareholders), and are generally more quantifiable (Elwin and Hirst 2007).

Outcomes of conservation by contrast are often qualitative and highly diverse (Kapos et al. 2008), spanning across aspects of human well-being, species and habitat recovery, and ecosystems services. This can make developing quantitative indicators within the conservation sector difficult, and frequently incomparable between organisations and projects. The delivery mechanisms of conservation are equally varied; land management, public engagement, policy-making, species monitoring, and research are just some of the activities involved (Kapos et al. 2008). Furthermore, the most useful indicators are often data-intensive, requiring long-term monitoring and expertise (Kapos et al. 2009), often over wide geographic areas, which is particularly restricting in a field with limited and competitive funding (Gerber et al. 2018).

Despite difficulties in their implementation, [KPIs](#) have been used to good effect for communication and adapting management practices to improve efficiency (Salafsky and Margoluis 2003). They have been used by government bodies and local authorities to communicate progress towards goals for their constituents. For example, Natural England has used [KPIs](#) since 2014, incorporating them into their Annual Reports and Action Plans, and scoring them using the 'Red-Amber-Green' target assessment system (Natural England 2021). Similarly, the Jersey Government uses [KPIs](#) in their 2020 'Growth, Housing and Environment Plan' to communicate with their constituents. Also of note, the current government published an 'Outcome Indicator Framework' to accompany the 25 Year Environment Plan, containing indicators in 10 broad themes with the goal of communicating change and managing natural capital (Defra 2019).

Suggested [KPIs](#) have also been provided for use by business in regards to impacts on the environment, allowing private industry to measure and report on the progress to customers, shareholders, and be held accountable to regulatory groups. The Department for Environment, Food & Rural Affairs ([DEFRA](#)) released a report for small-to-medium

businesses recommending [KPIs](#) around ecosystem services to assist them in responding to reviews such as the 'EU Accounts Modernisation Directive' (Defra 2008). In this way, they are tools by which the public and stakeholders can hold authorities accountable for their pledges towards environmentally responsible actions, and be made more readily informed about when and why progress is falling behind schedule.

[KPIs](#) are increasingly used for a similar purpose by Non-Governmental Organisations [NGOs](#). [NGOs](#) are often reliant on voluntary contributions from the public, and can consequently wish to provide feedback to members and supporters to encourage continued engagement and provide evidence of a return on their investment (Sawhill and Williamson 2001). The Wildfowl and Wetlands Trust, for example, established a set of reserve-level [KPIs](#), which have been integrated into their Business Plan Review, and the trust has plans to create another [KPI](#) for use further along the impact chain (Wildfowl and Wetlands Trust 2019). Smaller organisations, such as the Bat Conservation Trust, have not necessarily employed [KPIs](#), but are orienting towards that approach with reports of metrics of conservation delivery (e.g. number of sites surveyed) (Bat Conservation Trust 2019). Such metrics have potential to be developed into [KPIs](#) with applications for evidence-based conservation assessment.

Although [KPIs](#)'s are often public-facing, they can be used internally to allow practitioners and conservation groups to assess the efficacy of their actions and progress towards targets (Salafsky and Margoluis 2003). The design and dissemination formats for [KPIs](#) should generally reflect their appropriate target audiences (Hammond et al. 1995); for example, the general public, landowners, government agencies, investors, and members. Indicators can signpost areas which may have been neglected and enable pre-emptive investment of resources and time, before long-term ecological consequences are felt. Similarly, careful selection of [KPIs](#) and linking actions to outcomes can provide vital insights into practices which are particularly effective (Salafsky and Margoluis 2003), and this information can be distributed between organisation branches, and amongst other organisations to improve efficacy. For example, through networks such as the Conservation Measures Partnership's Conservation Coaches Network and the Conservation Evidence publication (Redford et al. 2018).

However, while [KPIs](#) can be highly useful when designed, implemented and reported on carefully, their misapplication can have conversely negative outcomes. Key Performance Indicators are widely applicable and well understood, but their selection is deceptively

difficult; there is a trade-off between what is easy to measure, and what is useful to measure (Hammond et al. 1995). In an effort to aid practitioners and land owners in designing and implementing [KPIs](#), various groups globally have devised frameworks for creating [KPIs](#). Some frameworks that have emerged include:

- Pressure, State, Response (Hammond et al. 1995)
- Impact, Activity, Capacity (Sawhill and Williamson 2001)
- Cambridge Conservation Initiative (Kapos et al. 2008)

We present here some key stages common to most models that assess conservation management (those in bold are generally the focus for indicators).

- 1. Threats and Stresses (e.g. nutrient deposition)**
- 2. Human responses/conservation activities (e.g. topsoil stripping)**
- 3. Short-term outputs and outcomes (e.g. area of land managed)**
- 4. Long term environmental impacts (e.g. changes in plant communities)**
5. Evaluation and knowledge exchange
6. Adaptation of activities to improve effectiveness

There can therefore be a bias towards easy to measure indicators, particularly for simple metrics of input (e.g. money spent), and short term outputs (e.g. hectares managed) in Stages 2-3 (Sawhill and Williamson 2001, Mascia et al. 2014), as it is generally easier to measure activity and immediate consequences than to measure long-term impacts (i.e. Stage 4). However, long-term consequences for species and habitats are generally the most valuable for assessing effectiveness of action (Kapos et al. 2009).

An additional hazard of [KPI](#) usage is that metrics can be misleading if not provided with sufficient context, and can (intentionally, or otherwise) lead audiences to over- or underestimate the effectiveness of actions by an organisation. Either could result in lower public engagement, resources being invested inefficiently (Halpern et al. 2006), or public trust eventually being eroded when environmental conditions do not improve in the long term. Furthermore, the usefulness of an indicator can decrease over time as a result of increased focus on improvement of the metric itself, without necessarily improving the system it is meant to be representing (Newton 2011).

Good [KPIs](#) require the ability to implement targets; the [SMART](#) framework (Doran, 1981) for targets can be adapted for [KPI](#) selection, which I explore further in section 5.4.3.1. There is typically interest in the overall condition of the conservation target species or

habitat, regardless of the organisation's input. However, targets for [KPIs](#) should reflect specifically populations affected by the organisations involvement, while being clear that there are species level targets that the organisation can only partially contribute to. The latter requires extensive data to be collected on the area, duration, and quantity of activity undertaken in order to link the organisation's contribution to the outcome (Jones 2012).

Therefore, short-term target setting is more likely to be effective when undertaken by conservation practitioners familiar with organisation capacity. Long-term [KPIs](#) can be more general, with targets reflective of the species' requirements for sustainable conservation (Sutherland et al. 2008). [KPIs](#) of long-term trends or threats could theoretically be used by any group interested in the conservation or status of the species, even if they are not accompanied by specific and attainable targets. Additionally, targets for recovery can be suggested for the species, with appropriate context that they are not organisational level goals.

5.2.3.2. Suggested Grizzled Skipper KPIs

During a six month placement within Butterfly Conservation, I produced a report reviewing and suggesting Key Performance Indicator within the organisation, further details of which are available in Appendix 19. In the following section, I apply the KPI design principals outlined in the report to planning conservation planning for *Pyrgus malvae*.

P. malvae is one of Butterfly Conservation's 'Priority' Species in England and Wales, having been the subject of an action plan from the organisation in 1998 (Brereton et al. 1998). In light of recent research into this species, including within this thesis, I propose that our understanding of the drivers and requirements for *P. malvae* can provide a useful case study in devising metrics for assessing conservation strategies, both for an individual species in itself, and as a contribution towards Butterfly Conservation's broader goals. The organisational goals are outlined below:

5.2.3.2.1. Butterfly Conservation Goals and Initiatives

Taken from 2021-2026 Strategy (Butterfly Conservation 2020)

Goals

- G1. Halve the number of the UK's threatened species of butterflies and moths
- G2. Improve the condition of 100 of the most important landscapes for butterflies and moths
- G3. Transform 100,000 wild spaces in the UK for people, butterflies, and moths

Initiatives

- I1. Recover butterflies and moths
 - A. Increase our investment in species recovery actions by 65%
 - B. Increase the number of species with accurate trends in population/distribution from 60 to 100.
- I2. Connect nature to people
 - A. 50% of our engaged audiences are taking part in two or more activities run by the Charity
 - B. Monitor the diversity of our audiences across a range of measures, and improve this every year to 2026.
- I3. Unite for wildlife
 - A. Establish measures for stakeholder engagement across all key groups and set targets by March 2022.
 - B. Establish 100 engaged networks across the UK to actively meet the climate and biodiversity challenges.
- I4. Tackle threats to nature
 - A. Increase our investment in research by 80% to establish five habitat quality indicators.
 - B. Develop and launch campaigns across the five drivers of change and increase awareness among key stakeholders.
- I5. Manage land sustainably
 - A. Influence the management of 10,000 hectares of land through the land management hub.
 - B. Ensure 75% of land we give advice on is in favourable condition for butterflies and moths.

Therefore I propose a combination of individual and headline indicators, split by stage of the impact chain. Although I employed the 'Pressure-State-Response' model to suggest general KPIs for Butterfly Conservation (Appendix 19), for this exercise I focus on the 'State' and 'Response' measures. I chose these stages as they were more readily applicable for a single species, whereas broader 'Pressures' (i.e. drivers of decline) are more difficult to impact through conservation of a single species by one organisation.

In order to more directly attribute changes in target condition to Butterfly Conservation actions, I split measures along the chain of impact. I designated indicators as 'Input', 'Output' and 'Outcome', derived from the model posited by the Cambridge Conservation Forum (Kapos et al. 2008). 'Inputs' and 'outputs' tend to reflect short-term investment and efficacy of work completed, while 'outcomes' are more informative for the condition of the target species in the long-term.

Grizzled Skipper (Pyrgus malvae): Key Performance Indicators

For ‘Inputs’, ‘Outputs’, and ‘Outcomes’, I recommend *Headline Indicators* -- measures which should be communicable, widely understood, and of interest to the public and stakeholders – and *Species Level Indicators* – measures which should inform more specialist groups invested in the species or associated habitats, which are evidence-based and can be related to an impact chain for conservation of the species.

5.2.3.2.2. Inputs (Activity and Investment)

Headline Indicators: These measures should be easy to communicate and widely understandable by stakeholders, informing them on Butterfly Conservation actions, delivery mechanisms, their capacity/resources, and their division of resources.

Table 5.1 Suggested Headline Performance Indicators of Inputs for conservation of *Pyrgus malvae* for use within Butterfly Conservation, with associated links to organisation goals and initiatives

Indicator	Goal/Initiative
Sites (ha) advised on (1 st /2 nd species)	G3, I5A, I5B
Hectares under management (1 st /2 nd species)	G2, G3, I5A
Investment/man-hours (FTE) in research involving/listing <i>P. malvae</i> (total and trend)	I1A, 14A

Species Level Indicators: These measures should inform *P. malvae* stakeholders and practitioners on actions taken, and highlight potential issues where targets are not met. They should inform periodic refocusing of resources, but may require additional context (e.g. number of staff and volunteers, external drivers, etc).

Table 5.2 Suggested Species-level Performance Indicators of Inputs for conservation of *Pyrgus malvae* for use within Butterfly Conservation, with evidence and context for their recommendation

Indicator	Evidence
Number of man hours (staff, contractor, volunteer) (Percent of FTE) (1st/2nd species)	Established need for human intervention to create and maintain early successional habitats (Chapter 3) with suitable microclimates for breeding (Brereton et al. 1998), particularly in light of factors accelerating rates of succession (i.e. climate change and nutrient deposition) (Smart et al. 2004, Masson-Delmotte et al. 2021).
Number of grid squares managed in (1st/2nd species)	Evidence of regional declines (Bell et al. 2021), with implications for metapopulation robustness and capacity to track climate envelope (Settele et al. 2008). Findings of frequent local extinctions and intermediate population structure (i.e. between open and closed), with yearly movement between habitat patches (Brereton 1997).
Time spent on individual tasks; i.e. removing scrub, removing trees, grazing areas, planting yellow rattle, creating patches of bare ground/walls	Specific tasks employed by practitioners (Slater 2007)(Slater, Ben Coleman Pers. comm) to inhibit succession, and created breeding opportunities (Brereton 1997, Krämer et al. 2012, Streitberger and Fartmann 2013, de Schaetzen et al. 2018). Provides opportunities to quantify action efficacy, to be shared on conservation network (e.g. Conservation Evidence).

5.2.3.2.3. Outputs (Short term outcomes (e.g. for habitat) attributable to [BC](#))- Candidate [KPIs](#)..

Headline Indicators: These measures should be intuitively understood metrics with clear links to organisation goals and initiatives, and to inputs in relevant delivery mechanisms. They should ultimately provide context on short term consequences of the organisations efforts, and an early indication of the efficacy of their actions. Although public facing, they may require some additional context to avoid confusion (e.g. sites with intervention from [BC](#) are not necessarily representative of the landscape, some species are sedentary and there are lags in range expansion)

Table 5.3 Suggested Headline Performance Indicators of Outputs for conservation of [Pyrgus malvae](#) for use within Butterfly Conservation, with associated links to organisation goals and initiatives

Indicator	Goal/Initiative
Condition of managed/advised sites (percent of sites in each category (favourable), cover, spread)- before and after involvement. (1st/2nd species)	G2, G3, 15A, 15B
Presence of target species in all counties/grid squares	G2, G3, I3B, I5A
Number of research projects/articles/publications on GS	I1B, I4A

Species Level Indicators: These measures should relate to previous species-specific inputs, in order to give an earlier assessment of efficacy of techniques and approaches. They should be available to the organisation, and to local groups invested in the conservation of *P. malvae*. These could be disseminated in information exchange networks at regular intervals.

Table 5.4 Suggested Species-level Performance Indicators of Outputs for conservation of *Pyrgus malvae* for use within Butterfly Conservation, with evidence and context for their recommendation

Indicator	Evidence
Percent of sites advised/managed (>x years) with species	Evidence that species moves between patches between years (Brereton 1997), so depends on site size. Work not just carried out by BC, also through local biodiversity groups and AES, in need of advice. Indicator could also inform on conservation efficacy (e.g. Adaptive management) (Salafsky and Margoluis 2003), and establish causal link between intervention and outcome, and could compare to sites prior to intervention.
Number (or ha) of sites entered into agreements with species listed as a reason (total and trend)	Evidence that AES can deliver habitat conservation for <i>P. malvae</i> , and prevent land conversion under increased land-use pressure (Hayhow et al. 2016). Additionally greater numbers of habitat patches could improve metapopulation robustness to stochastic extinction observed in <i>P. malvae</i> (Lande 1993, Brereton 1997).
Average functional habitat area for each known population, and distance to nearest known	Evidence that site size can impact on carrying capacity (Brereton 1997) and migration between patches (Chapter 4), influencing metapopulation persistence. Impacts of greening and eutrophication could lead to smaller, fragmented patches (Lawton et al. 2010), and be combatted by BC intervention (Slater 2007,

population	Butterfly Conservation 2018).
No of landscapes with GS (% in landscapes suitable and ever had records of GS)	Evidence of regional declines (Bell et al. 2021) and loss of individual populations (Pers. Obs), which makes meta-populations more vulnerable (Chapter 4). Presence and persistence of <i>P. malvae</i> across its previous range can facilitate genetic diversity and tracking of shifting climate niche (Lande 1988, Settele et al. 2008). Also reflective of BC branch intervention efforts.
Habitat metrics (across sites): i.e. Sward height, canopy cover, bare ground cover in open areas	These are measures that have been found to be positive predictors of <i>P. malvae</i> occupancy or abundance (Chapter 3) ((Brereton 1997, Krämer et al. 2012, Streitberger and Fartmann 2013, de Schaetzen et al. 2018)), particularly those related to warmer microclimates, so could inform on short term habitat condition changes, particularly following intervention from BC.

5.2.3.2.4. Outcomes (Longer term effects for target species):

Headline Indicators: Measures should be clear and easy to understand by wider public, but accompanied by context, as these will often be the furthest removed from Butterfly Conservation’s involvement. Their primary use may be to inform the public on state of habitats and species.

Table 5.5 Suggested Headline Performance Indicators of Outcomes for conservation of *Pyrgus malvae* for use within Butterfly Conservation, with associated links to organisation goals and initiatives

Indicator	Goal/Initiative
Still on priority list (eventually aim to be removed) (internal threatened list)	G1

Species Level Indicators: These measures should be of general interest to Butterfly Conservation, and practitioners, particular in different branches. However, these will again require a great deal of context, and could be best used to highlight when *P. malvae* is particularly threatened. However, proper implementation of inputs and outputs along the impact chain may allow for attribution of outcomes to Butterfly Conservation itself, and inform long-term conservation assessment.

Table 5.6 Suggested Species-level Performance Indicators of Outcomes for conservation of *Pyraus malvae* for use within Butterfly Conservation, with evidence and context for their recommendation

Indicator	Evidence
Long term trends (trajectory) (10 year window)- regional county level	Although short term trends can be of interest for practitioners, long terms trends are less influenced by stochastic variation between years (Didham et al. 2020). Evidence of regional declines (Bell et al. 2021) suggest that early identification of continued trends could adapt management and signpost areas in need of further intervention.
One of species no longer declining (BC aims)	In long term decline, most likely driven by habitat loss, similar to other specialists (Fox et al. 2015, Thomas et al. 2015, Bell et al. 2021). Indicator reflects efficacy of conservation actions and habitat conditions, with potential information on state of drivers with further context.
Stage in (Butterfly Conservation) recovery curve	Higher resolution measure of progress towards target, guiding recommended actions to reach next stage, and encourage identification of sustainable management (combatting drivers of habitat loss, balancing land-use needs and financing actions) (Sutherland et al. 2008).
Population trends reversing/improving in the north	Evidence of long-term declines steeper in the north (Bell et al. 2021), suggesting that climate change is not negating other drivers of decline, and that species likely unable to track climate change (Settele et al.

2008). With further context on regional inputs and outputs, could highlight effects of continued climate change or conservation action.

Further information on scoring of each indicator against a [‘SMART’](#) based framework, and possible data sources within Butterfly Conservation, can be found in Appendix 20.

5.3. Final Conclusions and Recommendations

Overall, my investigation of *P. malvae* produced some novel findings with potential applications for the conservation planning for the species, and contributed more generally to the field of research in unexpected effects of interactions between major drivers of biodiversity decline. In this study, I attempted to answer three main questions pertaining to the circumstances of *P. malvae*.

1. Are population size trends of *P. malvae* more positive in the north compared to the south, indicating early signs of northern expansion, and how much of the long-term trends are explained by climate?

We found declines of $-0.18 \log(\text{abundance})$ per year (Bell et al. 2021), which were exacerbated in the north and west, likely driven by habitat loss and degradation (Brereton 1997). Winter temperature and summer rainfall have negative impacts on population size (Pollard and Yates 1993, Bell et al. 2021), possibly due to their role in accelerating succession, and cooling microclimates (Wallisdevries and Van Swaay 2006).

2. What are predictors of habitat suitability for *P. malvae* in the UK, and do they vary with geographical location or habitat type?

We identified a few robust predictors of habitat suitability (Chapter 3), generally related to habitat structure associated with warmer microclimates (Chapter 3) (Stoutjesdijk and Barkman 1992). However, we found only isolated interaction terms between geography and habitat features with significant effects on presence or abundance (Chapter 3), so habitat requirements appear to be consistent across the species' range in England.

3. Do *P. malvae* exhibit edge avoidant responses to boundaries of grassland and scrub/woodland, and does scrub encroachment at the borders of habitat patches impact on connectivity and landscape scale movement?

The results of our investigation using individual based models indicate that under scrub encroachment, *P. malvae* individuals spend a lower proportion of their lifetime within habitat (Chapter 4), and when encroachment is more severe, fewer individuals travel between sites (Chapter 4). Encroachment appears to generally increase the rate at which individuals leave habitat (Chapter 4), but decrease the likelihood of encountering new sites once in the matrix (Chapter 4). In addition, protection of individual sites at the expense of others could increase or reduce both connectivity and time spent in habitat compared to

uniform encroachment (Chapter 4), depending on which site was protected. Our findings suggest that encroachment poses a risk not just to habitat suitability (Thomas et al. 2015), but also to short-term connectivity within a population network (Chapter 4), the effects of which can be exacerbated or mitigated by site prioritisation (Chapter 4).

Furthermore, protecting larger sites could result in fewer, larger sites (Chapter 4) and increased time spent in habitat (Chapter 4), while protecting better connected sites could increase rates of interchange of individuals between sites (Chapter 4). Meanwhile, protecting mid-sized unconnected sites reduced both time spent in habitat and connectivity (Chapter 4), due to a resultant increase in number of habitat patches, a decrease in average patch size, and connected patches becoming smaller, with fewer individuals.

Altogether, my results currently paint a bleak trajectory for the species, but also indicate that we do have the capacity to improve prospects. Measures to benefit the species will likely involve strategies to counter possibly escalating rates of succession (Menzel and Fabian 1999, Smart et al. 2005), in order to maintain suitable microclimates (Brereton 1997, Streitberger and Fartmann 2013). Hotter-than-ambient microclimates are largely required by for *P. malvae* under contemporary UK summer temperatures (Brereton 1997). Successful approaches in one area are likely to be applicable elsewhere as habitat requirements appear to be roughly similar (Chapter 3), and should prioritise providing suitable breeding habitats as has been the focus of recent conservation efforts in Warwickshire (e.g. Derbyshire, Newark, Nottingham) (Butterfly Conservation 2018, Churcher 2021b, Nottinghamshire Biodiversity Action Group 2021b).

5.3.1. Observed Conservation Approaches and Comments

Habitat networks for *P. malvae* and other early successional habitat specialists appear to be particularly vulnerable in modern landscapes. Although semi-natural grassland conservation management has had laudable success, at least more so than woodland recovery (Ridding et al. 2015, Defra 2021), many of the techniques employed seem to orient around keeping habitats ‘frozen in time’ (Merckx and Pereira 2015). Historically, populations occupied rotational mosaics of habitat successional stages, which likely provided buffers to extreme disturbance events and facilitated movements between patches between years (Bonari et al. 2017), as *P. malvae* has been seen to do. Modern conservation by contrast generally aims to preserve known populations and their habitats;

particularly for threatened sedentary species where populations are small and vulnerable and recolonisation is unlikely, as is the case for *P. malvae*.

Where rotational management is not possible, close monitoring and regular management by local groups (e.g. Biodiversity Groups, NGO branches) is often used to halt succession entirely. However, this approach can leave patch networks vulnerable. In some cases where there are insufficient local resources (Winch et al. 2021), sites can degrade rapidly due to lack of management, and be ultimately lost from the habitat network because their recovery would be too resource- and/or time-intensive (Pers. Obs). This issue may be compounding as increased rates of scrub encroachment have been reported at some sites (Ben Coleman, Pers. Comm., 2019), possibly due to atmospheric nitrogen deposition (Diekmann and Falkengren-Grerup 2002) as agricultural run-off was deemed unlikely. Higher soil nutrient-levels may also be increasing leaf size of *P. malvae* hostplants to the possible detriment of early instar stages, and further research into this process, and if necessary approaches to mitigate negative impacts for *P. malvae*, would be of interest.

We have received personal verbal reports from members of Butterfly Conservation of small populations which are flagging despite regular management actions across *P. malvae*'s range in England. This is seemingly more common in the more northern counties, in line with our own findings of steeper northern declines in abundance (Bell et al. 2021). The reports highlight vulnerability of individual populations, even those in managed patches, and could signpost need for greater investment in targeted habitat creation in the short term (e.g. breeding opportunity patches (Slater 2007)), depending on assessment of success in trial locations (e.g. Warwickshire), and in the long-term, increased connectivity to encourage rescue effects and recolonisations where individual populations are lost. Additionally, clear, accessible communication networks between conservation groups in different counties may be beneficial to ensure timely sharing of knowledge and conservation outcomes.

5.3.2. Summary of Advice and Perspectives

Long term conservation of the species will likely require adoption of less labour intensive techniques to create early successional habitat (Walker et al. 2004). Some approaches to remove nutrients from areas could slow succession and reduce dominance by tall nutrient tolerant species, such as topsoil stripping, winter cattle grazing, creating scrapes, planting parasitic species (e.g. yellow rattle) and trialling controlled burns. Additionally, plug planting hostplants, creating breeding opportunities using ballast, and building butterfly

banks (with sheltered south facing slopes) has been shown to be useful for bolstering local numbers (Slater 2007). Similar microhabitats occur naturally elsewhere (e.g. molehills, wild boar ground disturbance) with beneficial impacts on *P. malvae* (Streitberger and Fartmann 2013, de Schaetzen et al. 2018).

Further research into uses of corridors and stepping stones, and permeability of the landscape (Dover and Settele 2009) to movement may assist with rescuing small populations, tracking climate change, and taking advantage of ephemeral habitats (Suggitt et al. 2018). More emphasis on rotational management may be needed to create mosaics of habitat structures, to provide environmental heterogeneity and buffers from extreme climate events (e.g. temperatures, drought, high wind) (Suggitt et al. 2018).

Additionally, ensuring that land managers and practitioners involved in conservation work have channels for communication on effective and efficient management techniques may help to make the most of local pockets of specialist expertise around the country (e.g. website, newsletter, Conservation Evidence).

When prioritising areas for investment and conservation investment, it would likely be beneficial to choose clusters of sites with reliable numbers of volunteers to maintain numbers, and to allow for movement of populations between years, as small populations are easily lost in a year (Lande 1993). As it seems unlikely that climate change is about to change prospects in the north (Bell et al. 2021), and habitat loss is likely still the main driver of decline (Brereton 1997), it seems that there should be a focus on preventing loss of existing populations within the range for now. The loss of individual populations could eventually lead to a loss of genetic diversity, in addition to reintroductions often being resource-intensive, and possibly detrimental to already vulnerable populations from which individuals are taken for translocation.

The compounding issues of future land-use change from agricultural intensification, nutrient deposition, and climate change will require sustainable approaches to conservation, anticipating novel threats. I here suggested the types of metrics (i.e. Key Performance Indicators) that may help in assessing effectiveness of conservation efforts for a threatened species within the framework of an [NGO](#), linking stages of the impact chain, and progressing towards targets. My findings hold significance for species beyond *P. malvae*; early successional habitat specialists, and species reliant on semi-natural habitats in general, are likely to be facing the same threats, within the UK and potentially further abroad.

Table of Abbreviations

Term	Meaning
AES	Agri-Environment Scheme
AIC	Aikake Information Criterion
AN	Abundance, None'
BC	Butterfly Conservation
BNM	Butterflies for the New Millennium
C	Grass Preference Parameter
<i>CAP</i>	<i>Common Agricultural Policy</i>
CRW	Correlated Random Walk
CS	Countryside Stewardship
CSV	Comma Separated Values
DEFRA	Department for Environment, Food & Rural Affairs
EU	European Union
EWGS	English Woodland Grant Schemes
FTE	Full-Time Equivalent
G4 (EUNIS)	European Nature Information System
GHG	Green-House Gas
GLMM	Generalised Linear Mixed Model
GPS	Global Positioning Ssystem
HAP	Habitat Action Plans
IBM	Individual Based Model
IPCC	Intergovernmental Panel on Climate Change
KPI	Key Performance Indicator
LCM	Land Cover Map

LNRS	Local Nature Recovery Strategy
MAM	Minimum Adequate Model
NE	Natural England
NERC	Natural Environment and Rural Communities Act
NFI	National Forest Inventory
NGO	Non-Governmental Organisation
NPAC	National Parks and Access to the Countryside Act
NRN	Nature Recovery Network
Pg.	The observed probability of choosing grass (i.e. proportion of grass) (Chapter 4)
PN	Presence, None'
Pr.	The random probability of choosing grass (Chapter 4)
PSR	Pressure, State, Response
QGIS	Quantum Geographic Information System
ROI	Return on Investment
SARD	Site Advice Recording Database
SMART	Specific, Measurable, Attainable, Relevant, Timed
SMPE:PR	Sanguisorba minor & Potentilla erecta : Potentilla reptans
SSSI	Sites of Special Scientific Interest
UK	United Kingdom
UK BAP	United Kingdom Biodiversity Action Plan
UKBMS	UK Butterfly Monitoring Scheme
UKCEH	UK Centre for Ecology and Hydrology
WT	Wildlife Trust

Glossary

Term	Meaning
'Abundance, None'	Generalised Linear Model; Habitat predictors of abundance, with no interaction terms
Agriculture Act of 1947	An Act of Parliament to encourage high production through farming subsidies
Agri-Environment Scheme	Government-run programmes to direct land managers to take up environmentally sound practices
Aikake Information Criterion	A value to estimate model fit of data
Azimuth	The angle between two lines (e.g. angle from true north to a new direction)
United Kingdom Biodiversity Action Plan	A program begun in 1994 describing natural resources and setting out plans for conservation targets
Butterflies for the New Millennium	A recording scheme undertaken every five years producing a database of butterfly records across the UK
Butterfly Conservation	A registered UK charity aiming to conserve Lepidoptera and their habitats
Climate zones	Classifications of zones with similar weather patterns (see Köppen climate classifications)
Common Agricultural Policy	A European Union Policy (orig. 1962) subsidising farmers in member states to increase agricultural production
Correlated Random Walk	A series of movements where the direction of each movement is correlated with the previous direction taken
Countryside Stewardship	A UK scheme which financially incentivises land managers to improve their land for environmental benefit
Delta	Difference in a value (e.g. extent of change to AIC value)
Department for Environment, Food & Rural Affairs	A ministerial department in the UK government overseeing food production and land management
Edge response	A tendency in individuals to avoid crossing habitat boundaries
English Woodland Grant Schemes	An English Scheme (orig. 2005) providing grants to land owners to create, and improve existing woodland
Environment Act (Wales)	The Welsh successor to the UK Biodiversity Action Plan
Eutrophication	A build-up of nutrients and organic matter in an ecosystem,

	often leading to a homogenous habitat dominated by a small number of species
Full-Time Equivalent	A measure equivalent to the number of full time employees in a group, or working on a project
Gamma distribution	An exponential distribution of continuous positive variables
Generalised Linear Mixed Model	An extension of the generalised linear model (a linear model with a non-normal error distribution) including random effects (e.g. date, site number)
GPS survey points	Global Position System coordinates at the location of placed markers when following a butterfly individual
GPS tracking points	Global Position System coordinates automatically collected at timed intervals while walking transects
Grass Preference Parameter	A parameter used to change the likelihood of an individual crossing a habitat boundary when within a step's distance of it
Green-House Gas	A gas that can absorb and re-emit infrared radiation from the planet's surface (leading to increased temperatures)
Growing season	A period of time during the year when average temperatures remain above a given threshold, facilitating plant growth
Habitat Action Plans	Conservation plans within the UK Biodiversity Action Plan for each priority habitat
Individual Based Model	A simulation model based on the explicit activity and interactions of individuals within a population or community
Intergovernmental Panel on Climate Change	The United Nations body assessing climate change science, releasing periodic reports
Key Performance Indicators	Quantifiable measurements that gauge progress towards a goal and report performance
Land Cover Map	A map produced by the UK Centre for Ecology and Hydrology of land cover classes across the UK
Local Nature Recovery Strategy	A recent land management scheme following on from the Countryside Stewardship scheme to guide provision of habitat and provide grants for environmental improvement
Matrix	Areas of non-habitat within the landscape (for example, in an individual based model, cells outside of patches)
Metapopulations	A number of nearby populations forming a larger network
Minimum Adequate Model	The model with the best fit and fewest parameters possible when starting from a maximal model with all predictors of interest

National Forest Inventory	A UK survey programme which monitors forest and woodland area
National Parks and Access to the Countryside Act	An act of Parliament (orig. 1949) establishing ability to declare National Nature Reserves, and grant powers to the Nature Conservancy and local authorities to establish reserves
Natural England	A DEFRA-sponsored public body in the UK responsible for protecting and improving the natural environment
Natural Environment and Rural Communities Act	The parliament act (orig. 2006), and English successor to the Biodiversity Action Plan, which provisions for protecting and improving biodiversity
Nature Recovery Network	A network of wild spaces across the UK, managed by their respective local bodies
Normal distribution	A 'bell curve' distribution of values, where the probability distribution is symmetrical around the mean
'Presence, None'	Generalised Linear Model; Habitat predictors of likelihood of presence, with no interaction terms
Pressure, State, Response	A conceptual model for the impact chain of human activities on the environment, the state of the environment, the response of humans, and so on
Quantum Geographic Information System	Software facilitating mapping, editing and analysing of spatial information
Return on Investment	The ratio between inputs and outputs of an activity, traditionally meaning net income:investment
Seral stages	Phase in the successional development of a vegetation community, before a climax community is reached
Site Advice Recording Database	A database used by Butterfly Conservation to record site visits and advice provided
Sites of Special Scientific Interest	Sites with notifiable priority species, geology or habitat features, which are legally protected
Specialist species	Species with narrow requirements in at least one stage of its life (e.g. foods, plant, etc)
Species Action Plan	Conservation plans within the UK Biodiversity Action Plan for each priority species; also created by Butterfly Conservation to lay out advice for protecting priority lepidoptera species
Specific,	A set of recommended attributes to consider when

Measurable, Attainable, Relevant, Timed	designing objectives
Step	The movement made by an individual within one of our Individual Based Models, based on terminology within NetLogo
Tick	A time step within one of our Individual Based Models, based on terminology within NetLogo
Transhumance shepherding	The traditional grazing practice of moving herds of sheep between regions, including upland and lowland, dependent upon the time of year
UK Butterfly Monitoring Scheme	A long-running UK scheme with repeated weekly counts of butterflies along fixed transects between April and September, using a standard recording procedure
UK Centre for Ecology and Hydrology	A UK-based non-profit research institute focusing on environmental science

Supplementary Materials

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Appendix 1: Outputs of all models including only one singular fixed climate effects on *P. malvae* of either a) monthly mean temperature, b) total monthly rainfall on *P. malvae* index for all 12 months preceding the flight period, or c) the three-month average of monthly mean temperature and rainfall, beginning from June of the previous year. (Total of 32 models) (Methods Section ii.).

(a)

Month	(Intercept)	Coefficient	Standard Error	P value	family	df	logLik	AICc	delta
December (Prev)	0.92	-0.20	0.06	0.001	NB(1.1122,l)	6	-11980.4	23972.8	0
January (Current)	0.92	-0.10	0.05	0.044	NB(1.1119,l)	6	-11983.2	23978.4	5.6
November (Prev)	0.92	-0.11	0.06	0.083	NB(1.1121,l)	6	-11983.6	23979.3	6.48
May (Current)	0.92	-0.06	0.05	0.249	NB(1.112,l)	6	-11984.5	23981	8.18
October (Prev)	0.92	-0.07	0.07	0.307	NB(1.1128,l)	6	-11984.6	23981.2	8.41
June (Prev)	0.94	0.05	0.05	0.353	NB(1.1131,l)	6	-11984.7	23981.4	8.62
August (Prev)	0.94	0.04	0.06	0.455	NB(1.1119,l)	6	-11984.9	23981.7	8.95
July (Prev)	0.94	0.03	0.05	0.535	NB(1.1123,l)	6	-11984.9	23981.9	9.12
April (Current)	0.93	-0.03	0.06	0.625	NB(1.1122,l)	6	-11985	23982	9.26
March (Current)	0.93	0.01	0.06	0.916	NB(1.1121,l)	6	-11985.1	23982.3	9.49
September (Prev)	0.93	0.00	0.06	0.967	NB(1.1122,l)	6	-11985.1	23982.3	9.5
February (Current)	0.93	0.00	0.05	0.995	NB(1.1121,l)	6	-11985.1	23982.3	9.5

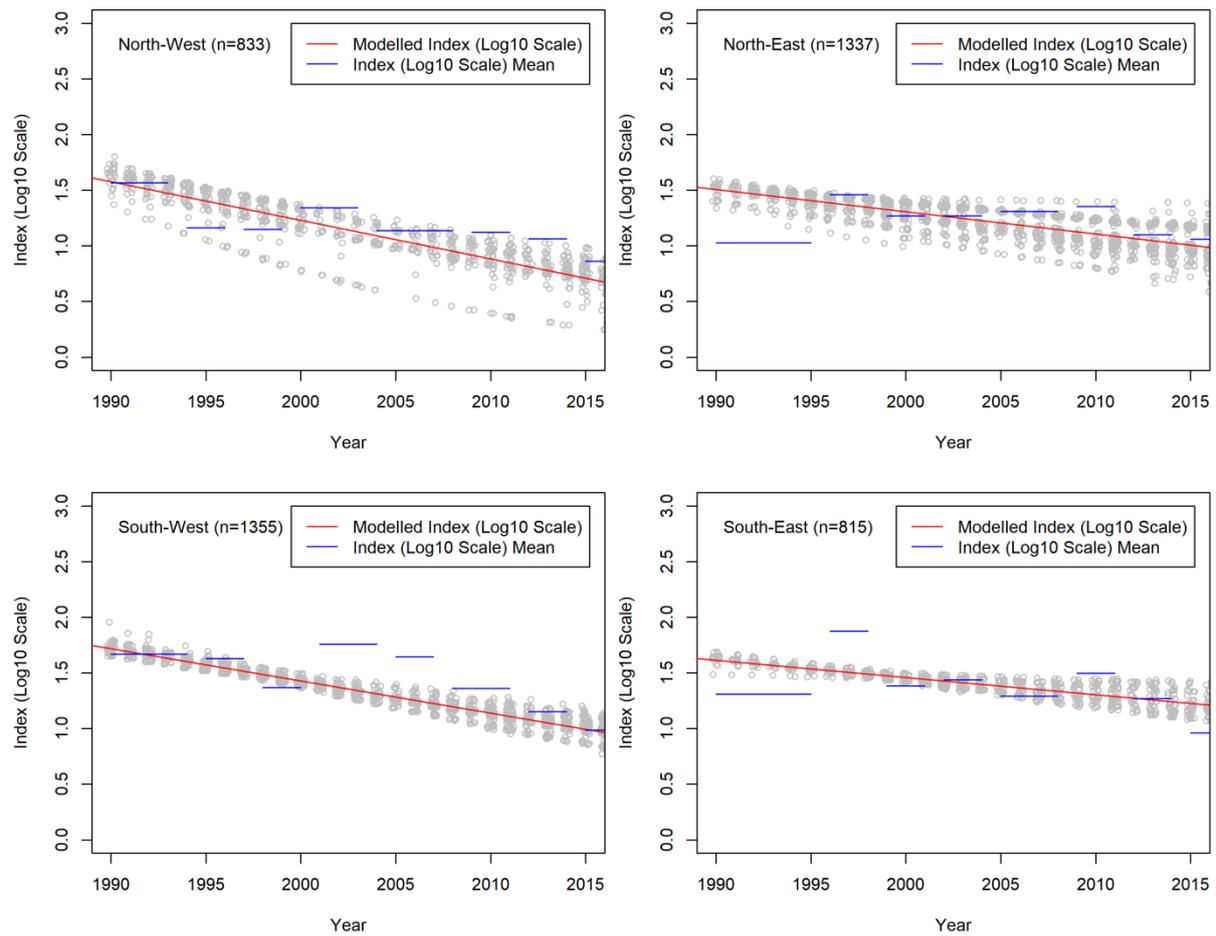
(b)

	(Intercept)	Coefficient	Standard Error	P value	family	df	logLik	AICc	delta	weight
December (Prev)	0.92	-0.20	0.06	0.001	NB(1.1122,l)	6	-11980.4	23972.8	0	0.831
January (Current)	0.92	-0.10	0.05	0.044	NB(1.1119,l)	6	-11983.2	23978.4	5.6	0.051
November (Prev)	0.92	-0.11	0.06	0.083	NB(1.1121,l)	6	-11983.6	23979.3	6.48	0.033
May (Current)	0.92	-0.06	0.05	0.249	NB(1.112,l)	6	-11984.5	23981	8.18	0.014
October (Prev)	0.92	-0.07	0.07	0.307	NB(1.1128,l)	6	-11984.6	23981.2	8.41	0.012
June (Prev)	0.94	0.05	0.05	0.353	NB(1.1131,l)	6	-11984.7	23981.4	8.62	0.011
August (Prev)	0.94	0.04	0.06	0.455	NB(1.1119,l)	6	-11984.9	23981.7	8.95	0.009
July (Prev)	0.94	0.03	0.05	0.535	NB(1.1123,l)	6	-11984.9	23981.9	9.12	0.009
April (Current)	0.93	-0.03	0.06	0.625	NB(1.1122,l)	6	-11985	23982	9.26	0.008
March (Current)	0.93	0.01	0.06	0.916	NB(1.1121,l)	6	-11985.1	23982.3	9.49	0.007
September (Prev)	0.93	0.00	0.06	0.967	NB(1.1122,l)	6	-11985.1	23982.3	9.5	0.007
February (Current)	0.93	0.00	0.05	0.995	NB(1.1121,l)	6	-11985.1	23982.3	9.5	0.007

(c)

Month	(Intercept)	Coefficient	Standard Error	P value	family	df	logLik	AICc	delta
June-August (Rain)	0.92	-0.16	0.04	<0.001	NB(1.1181,l)	6	-11975.3	23962.6	0
Dec-February (Temp)	0.91	-0.14	0.06	0.018	NB(1.1123,l)	6	-11982.4	23976.8	14.17
Sept-Nov (Rain)	0.92	-0.07	0.04	0.069	NB(1.1123,l)	6	-11983.5	23979	16.38
Dec-February (Rain)	0.94	0.07	0.05	0.124	NB(1.1156,l)	6	-11983.9	23979.9	17.23
Sept-Nov (Temp)	0.92	-0.09	0.07	0.167	NB(1.112,l)	6	-11984.2	23980.3	17.73
June-August (Temp)	0.94	0.06	0.05	0.304	NB(1.1125,l)	6	-11984.6	23981.8	18.61
March-May (Temp)	0.92	-0.04	0.06	0.507	NB(1.1122,l)	6	-11984.9	23981.8	19.21
March-May (Rain)	0.93	-0.01	0.05	0.789	NB(1.1118,l)	6	-11985.1	23982.2	19.59

(a)

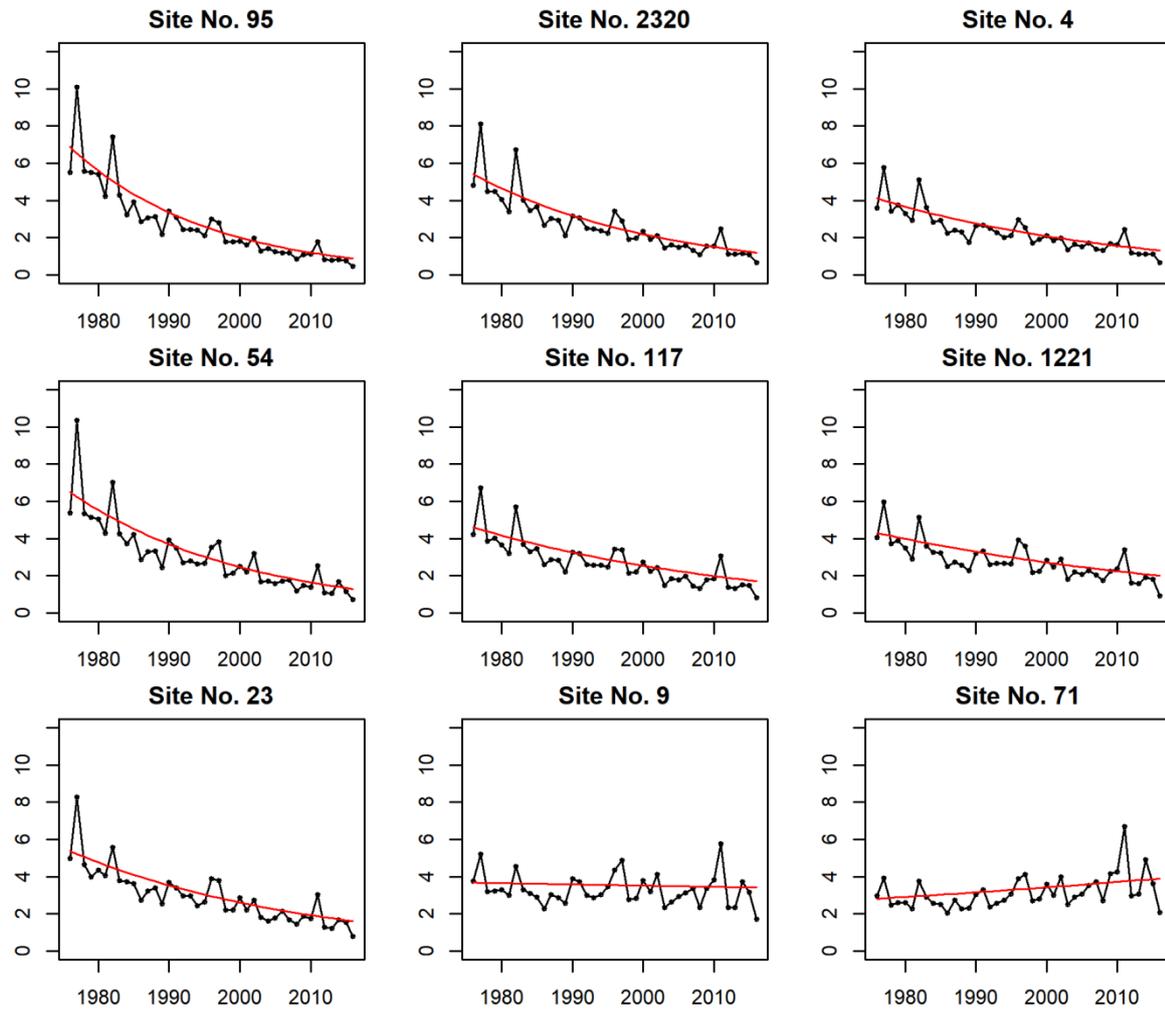


(b)

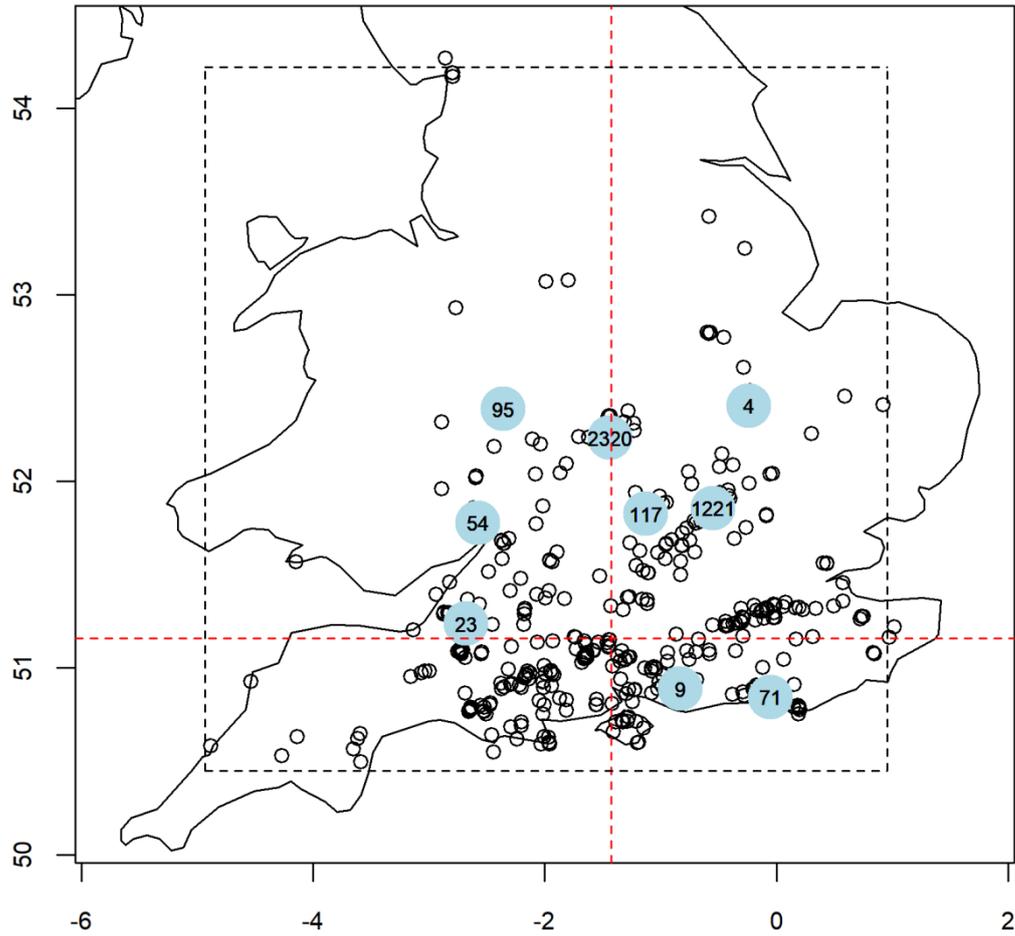
	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	0.98209	0.1585	6.196	5.79E-10
YEAR	-0.34499	0.07919	-4.357	1.32E-05
rX	0.05677	0.1178	0.482	0.6299
rY	-0.19493	0.11752	-1.659	0.0972
YEAR:rX	0.12657	0.0322	3.931	8.46E-05
YEAR:rY	-0.07895	0.03843	-2.054	0.0399

Appendix 2: (a) Modelled temporal trends of *P. malvae* index divided into North-West, North-East, South-West and South East regions by the median latitude (51.16) and longitude (-1.43) values of UKBMS sites with records, as shown in Figure 3. The model used to generate the values shown was MAM01 (non-climate effects only), but run with data from 1990 onwards, as opposed to the full dataset from 1976. (b) A table below shows the coefficients and p values of all predictors, which were qualitatively unchanged from those produced using the full data set.

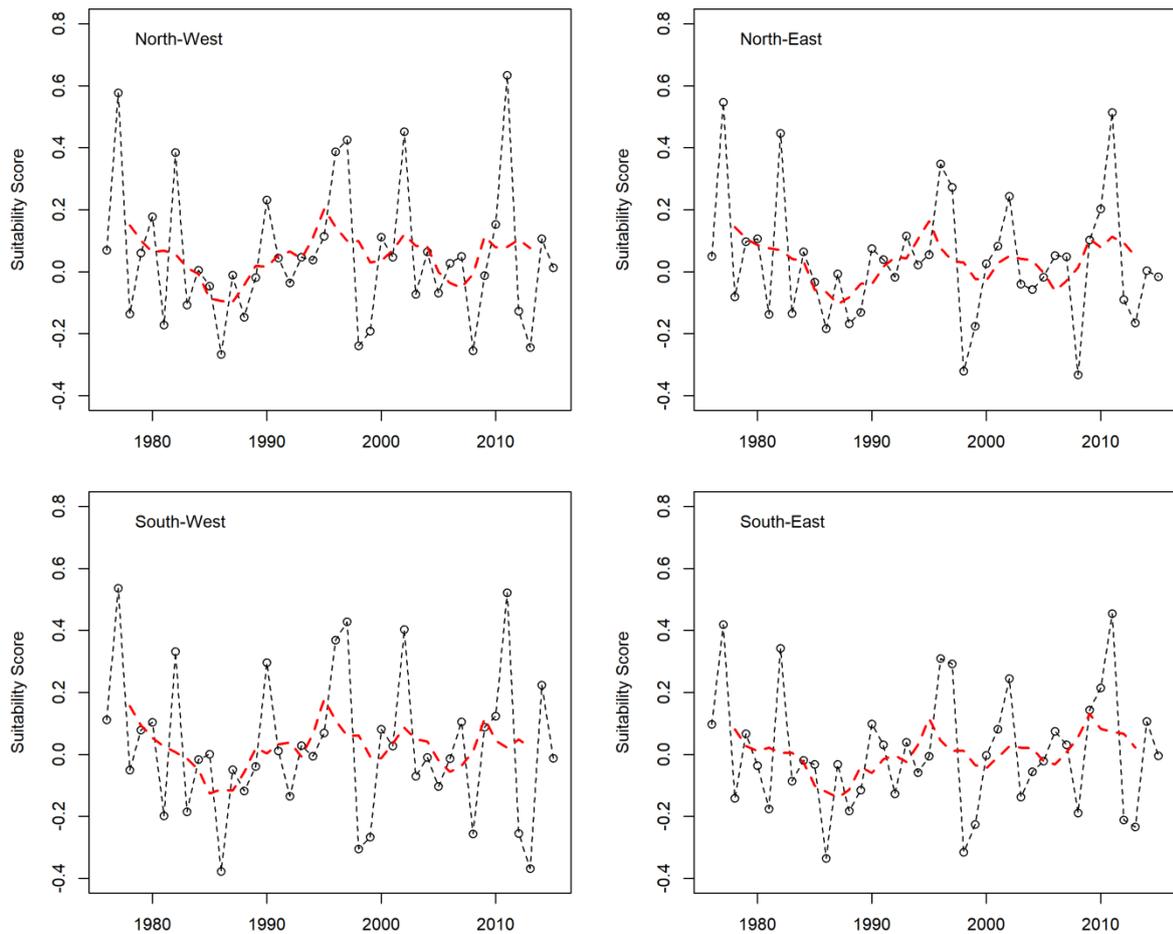
(a)



(b)



Appendix 3: (a) Temporal trends in modelled *P. malvae* UKBMS indices at a subset of UKBMS sites between 1976 and 2016 under scenarios of fixed and changing climate conditions. Indices are derived from the minimal adequate model of climate and non-climate effects (MAM03). Modelled index values when climate parameters are kept fixed at mean values from 1976-1980 are shown by the red line, while modelled index values when climate parameters represent actual climate data are shown by the black line. Geographic locations of the sites are shown (b) in the map of the UK below.



Appendix 4: Temporal trends in climate suitability, calculated using the yearly climate values for all climate effects in the best fitting model with climate and non-climate effects (MAM03), multiplied by the coefficients produced by the model. Each graph represents a geographical region of the UK range when divided into North-West, North-East, South-West and South East regions by the median latitude (51.16) and longitude (-1.43) values of UKBMS sites with records (shown in Figure 2.1). Black dashed lines represent the trend of the climate suitability, red dashed lines represent the 5-year moving average of the climate suitability. Values on the y-axis correspond to the total effect of all climate values (derived from climate coefficients from MAM03) for each year on log index.

A simple correlation test was run between the climate suitability score and year for each of the four sub-regions displayed above in order to assess whether climate suitability had significantly changed over time, and whether this was the case across the UK range. In all regions, the trend of climate suitability over time was consistently weak ($< \pm 0.2$), and non-significant.

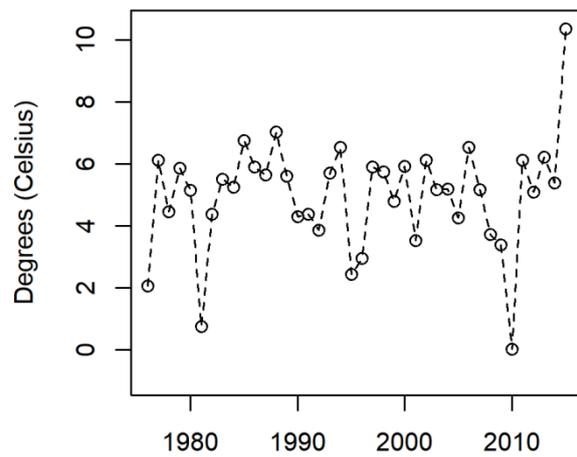
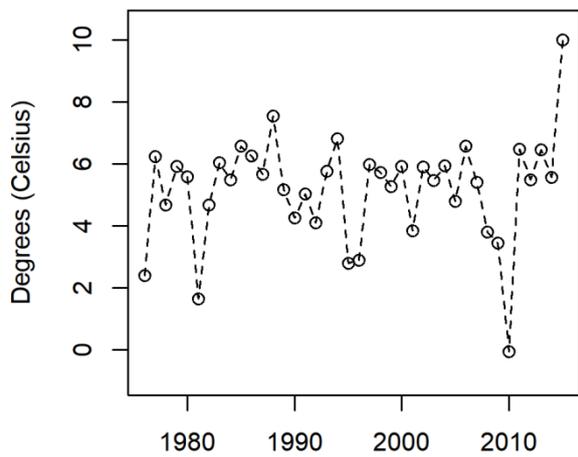
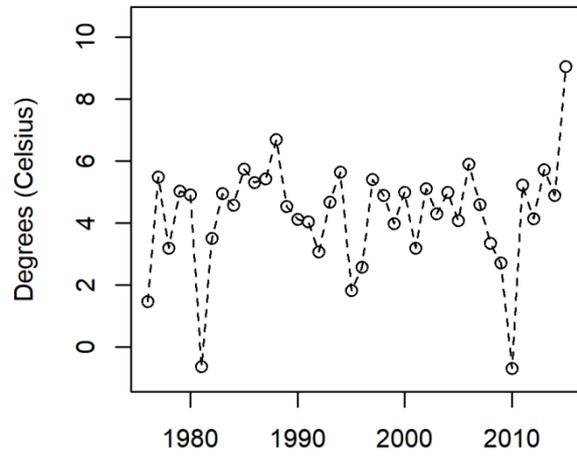
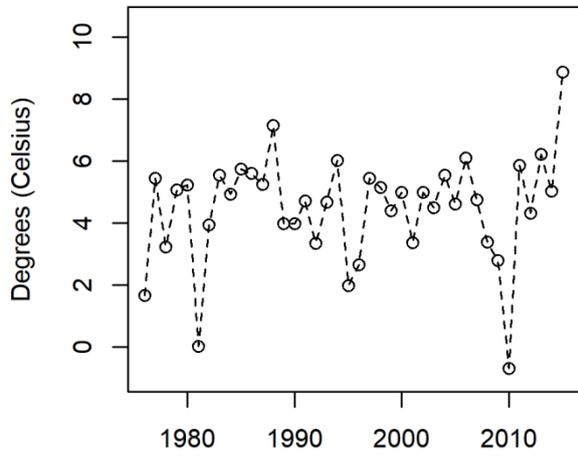
For the northwest region, the correlation coefficient was -0.072, with a p-value of 0.604.

For the northeast region, the correlation coefficient was -0.191, with a p-value of 0.167.

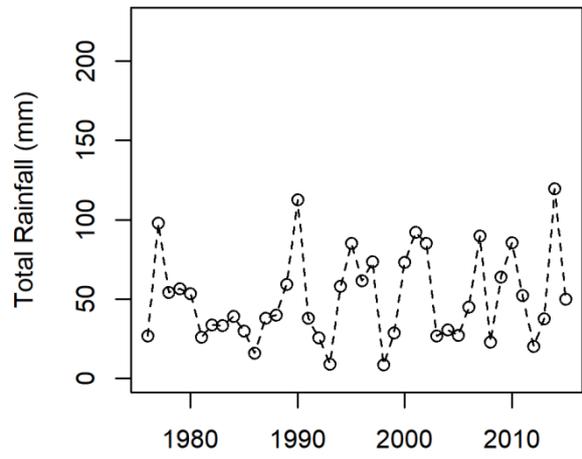
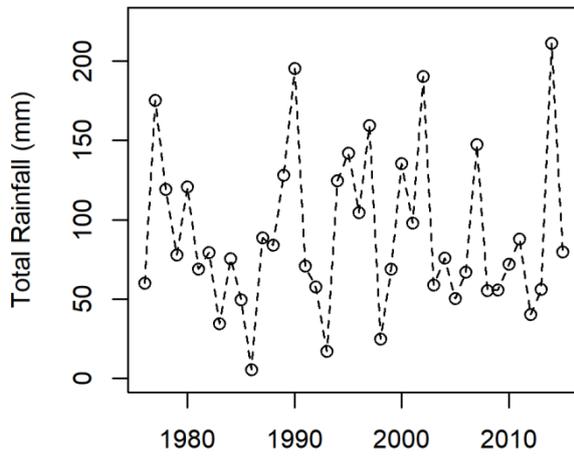
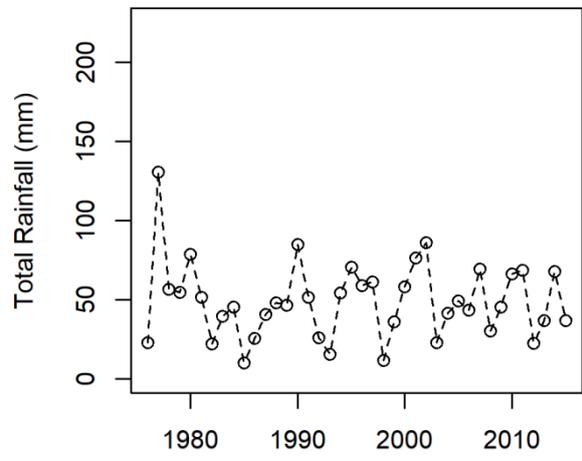
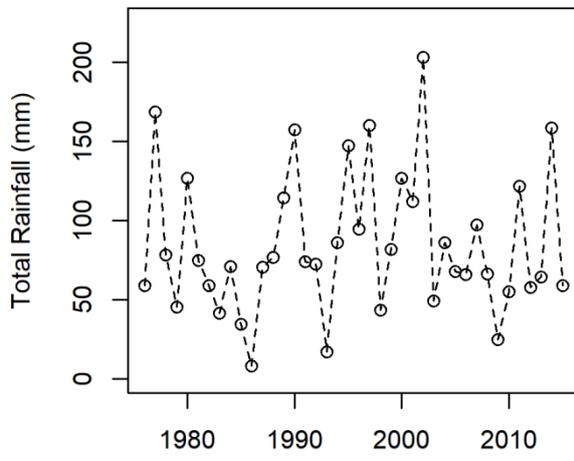
For the southwest region, the correlation coefficient was -0.076, with a p-value of 0.583.

For the southeast region, the correlation coefficient was -0.083, with a p-value of 0.553.

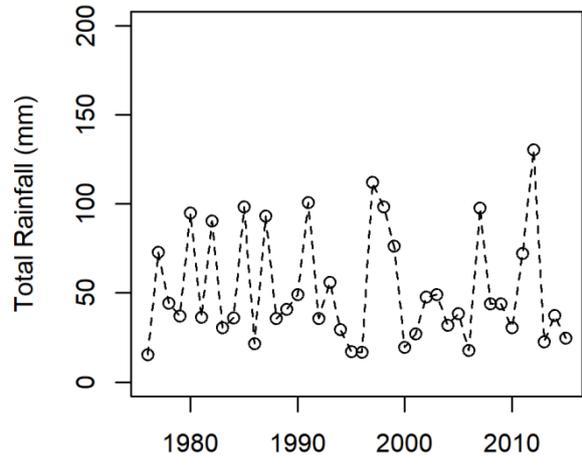
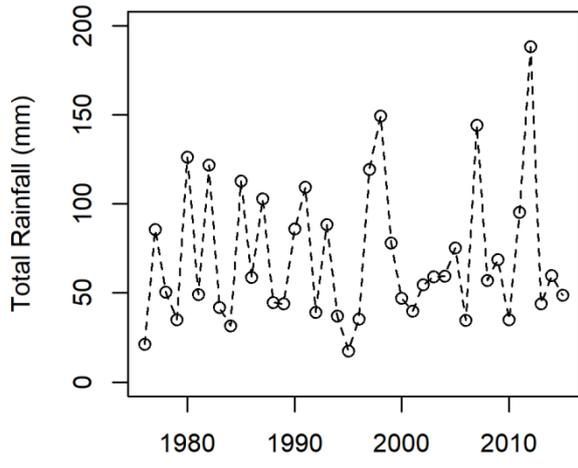
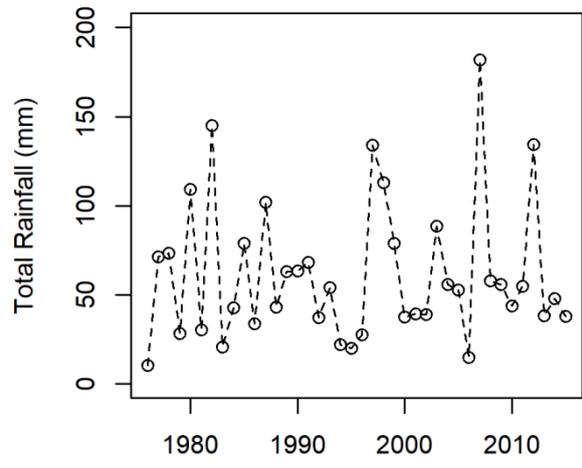
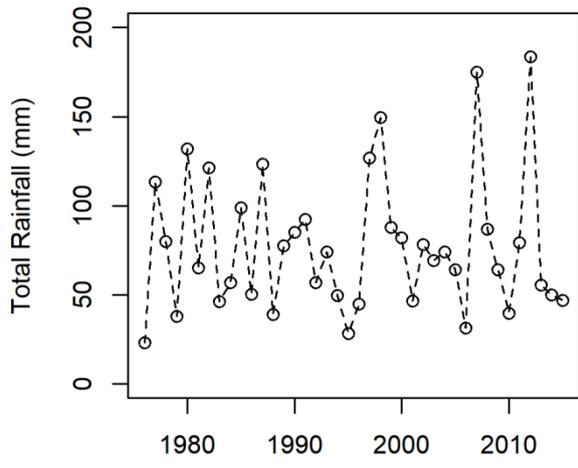
(a)



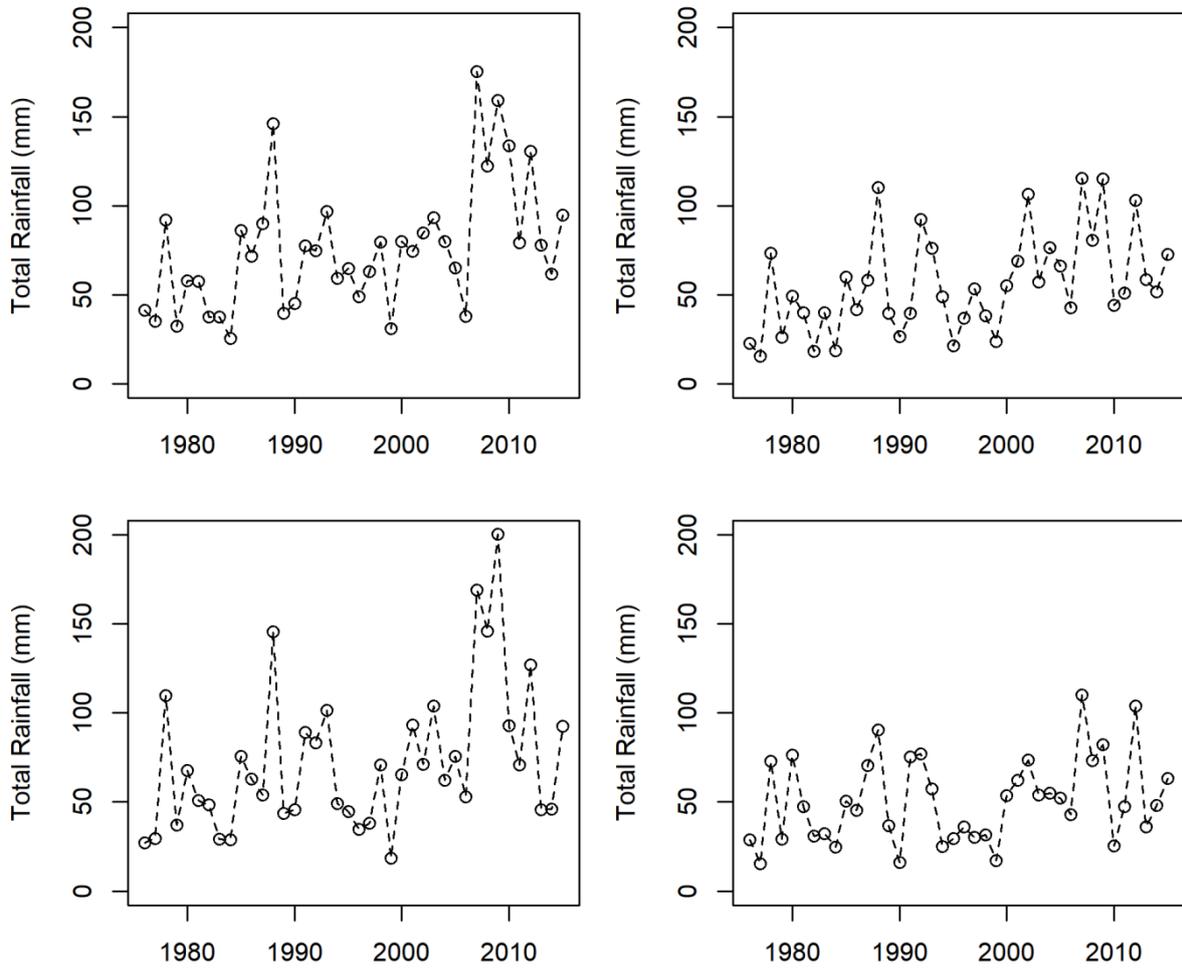
(b)



(c)

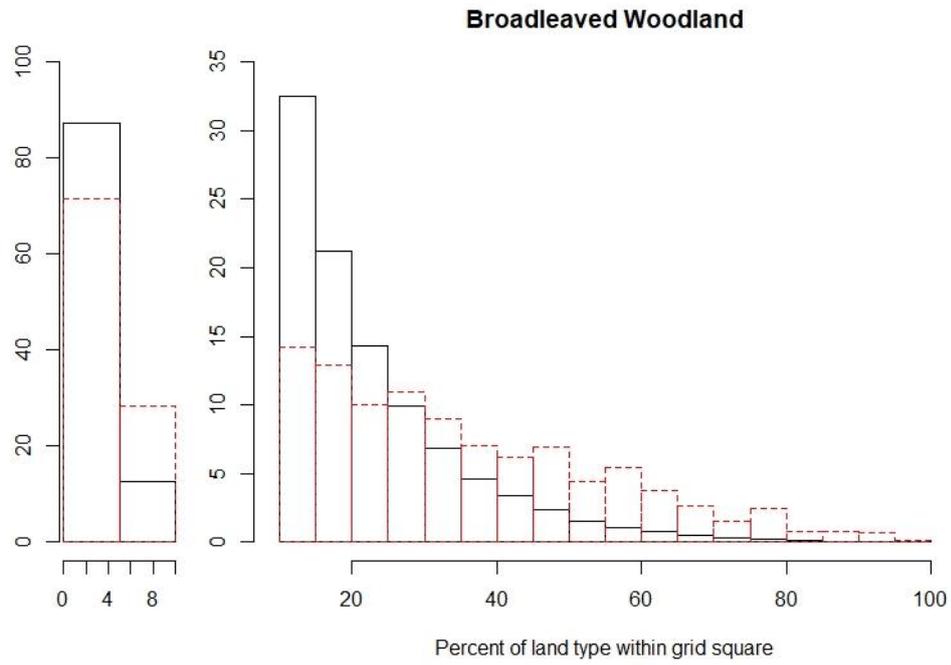


(d)

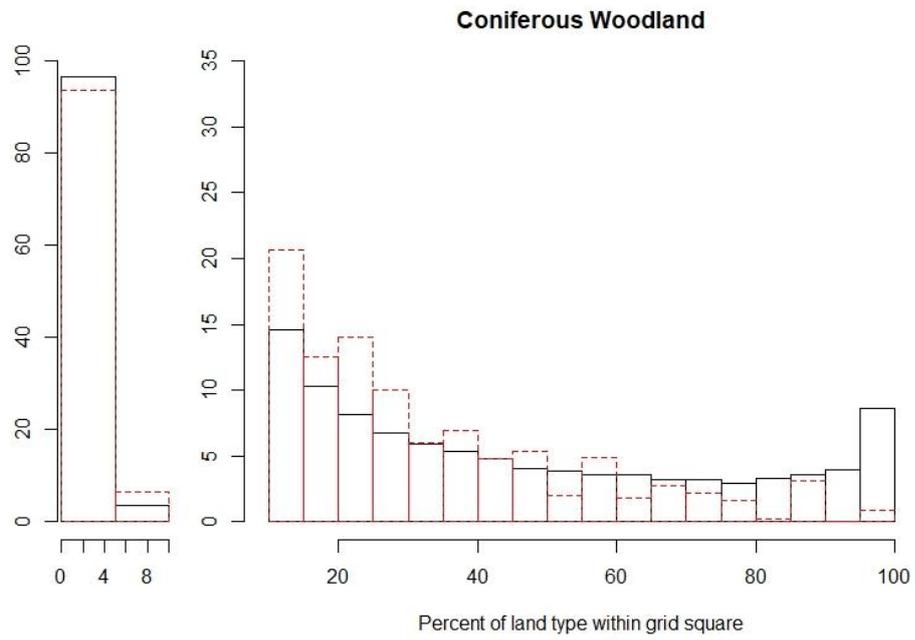


Appendix 5: Temporal trends in monthly UKCP09 climate measures within *P. malvae*'s UK range (1976-2016). Each panel represents a geographical region of the UK range when divided into North-West, North-East, South-West and South East regions by the median latitude (51.16) and longitude (-1.43) values of UKBMS sites with records (shown in Figure 2.1). Climate measures shown are a) December Temperature (Degrees Celsius), b) February Rainfall (mm/month), c) June Rainfall (mm/month), d) July Rainfall (mm/month).

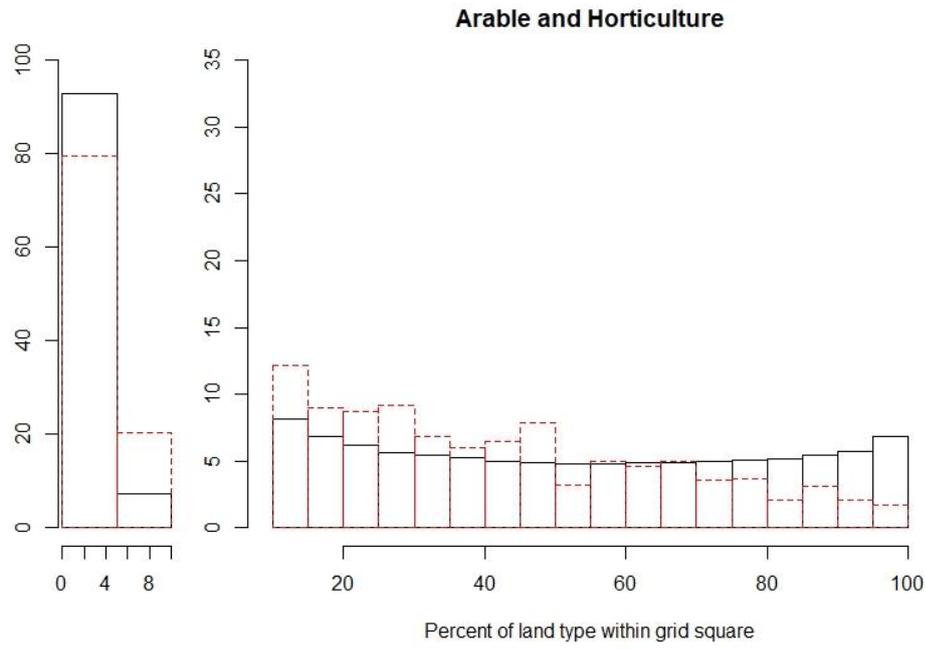
(a)



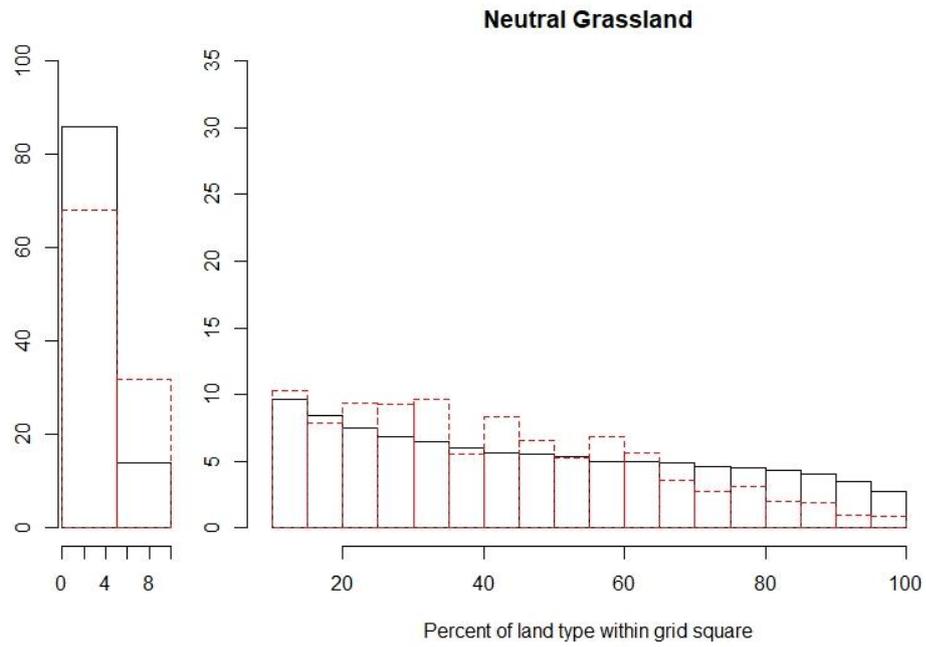
(b)



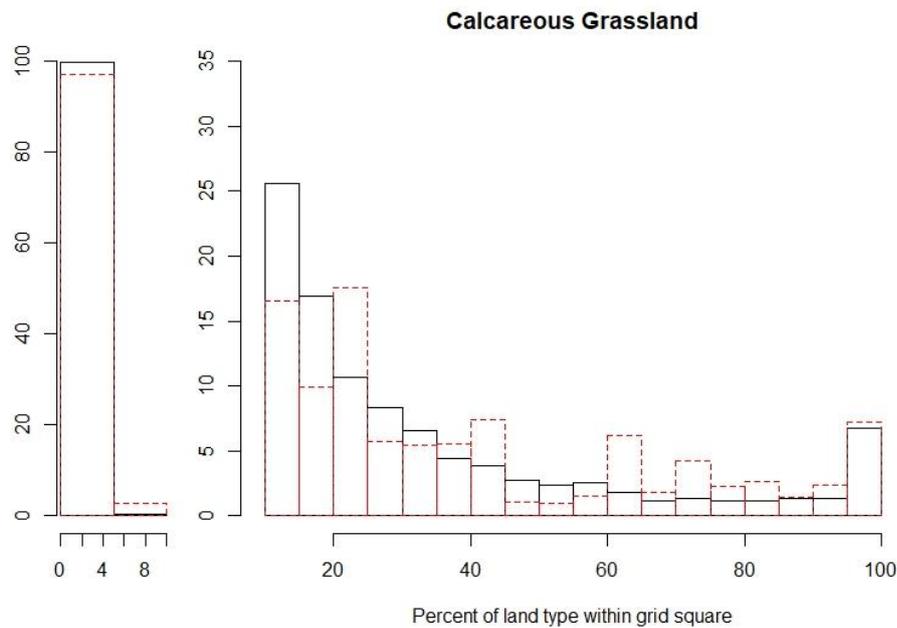
(c)



(d)



(e)



Appendix 6: The frequency of the range of land cover percentages for five target classes that are most overrepresented in grid-squares containing Grizzled Skipper (*Pyrgus malvae*) records in relation to all grid-squares across the UK. All *P. malvae* Sites (red dashed lines) represent each unique grid references in Butterflies for the New Millennium (BNM) records, accounting for multiple visits to sites between years.

In order to identify the dominant habitat types used by *P. malvae*, we obtained *P. malvae* records between 1904-2014 from the BNM, and data on habitat type from the UK Centre for Ecology and Hydrology (UKCEH) 'Landcover 1km Target Class Percentage Cover Map' (2015, downloaded as raster using Digimap repository), subsequently referred to as 'LCM'. The UKCEH Land Cover Map was loaded into RStudio as a raster stack ('raster' package), and cell values were extracted for each 1km x 1km grid square associated with at least one *P. malvae* BNM record.

The LCM contains 21 habitat target classes, and the frequency of the percentage cover within 1km grid-squares for each target class were determined for both grid-squares with *P. malvae* records, for and all grid-squares across the UK. The frequency of habitat percentage covers were compared between *P. malvae* grid squares, and total UK in order to explore which habitat types were potentially overrepresented at sites suitable for *P. malvae*. This revealed five main target classes of land-cover within the LCM that were identified as being overrepresented in 1km grid squares known to have contained *P. malvae* in comparison to 1km grid squares across the UK:

- Broadleaved Woodland (a)
- Coniferous Woodland (primarily in association with Broadleaved Woodland) (b)
- Arable and Horticulture (c)
- Neutral Grassland (d)
- Calcareous Grassland (e)

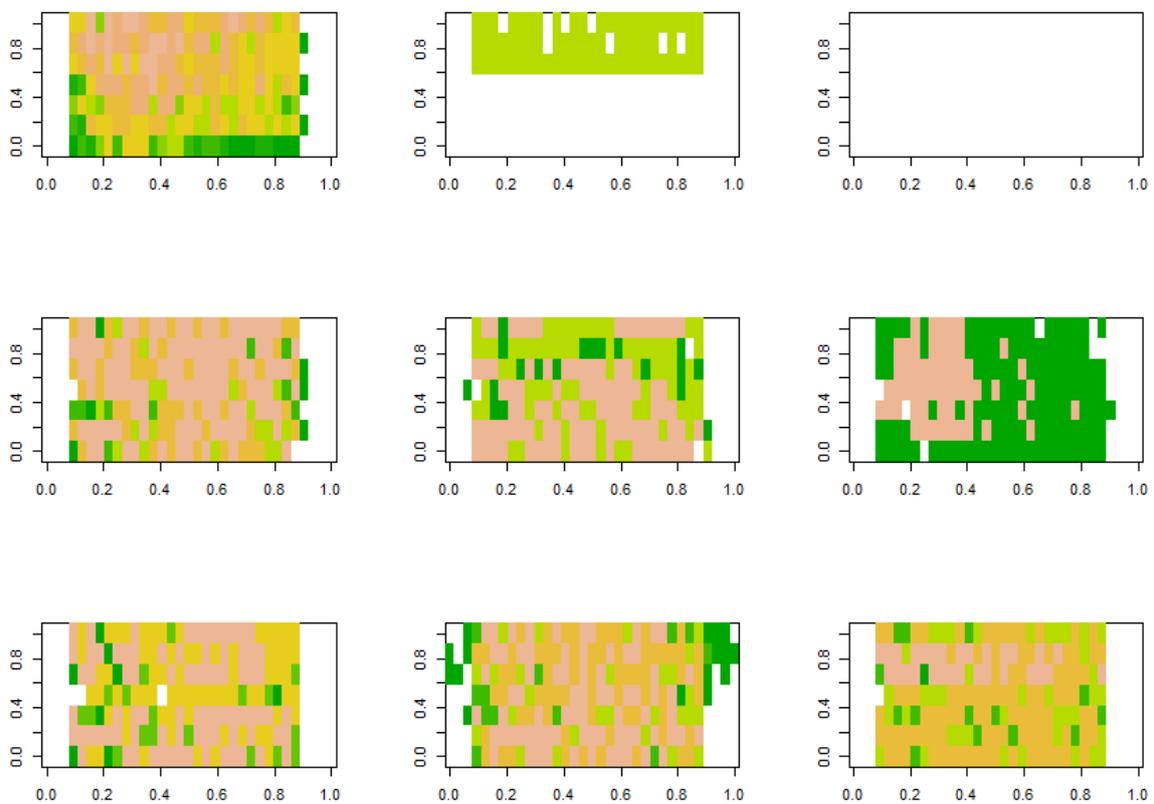
The above habitat types were then grouped into two main categories; woodland and grassland, particularly in light of limitations of the LCM to distinguish between types of grassland. Plots are split at <10 and >10% cover of a land class to increase visual resolution (note difference in Y axes).

Appendix 7: Summary of steps taken in data processing of butterfly tracking records (Chapter 3, App 2)

Available from doi.org/10.17638/datacat.liverpool.ac.uk/1764

Appendix 8: Code for dataframe creation for modelling work, including generating spatial autocovariates for presence and absence models (Chapter 3, App 3)

Available from doi.org/10.17638/datacat.liverpool.ac.uk/1764



Appendix 9: Survey efforts at UKBMS sites with *P. malvae* over time across the study area, represented by number of visits per week. Plots are arranged in geographical bands, with top left representing north west, and bottom right represent south east. X axis = Standardised week in survey period (April-September). Y axis = Standardised calendar year from 2009-2016. Colour of grid represent number of weekly visits (Green to pink in ascending order). Absence of grids represents absence of visits.

Appendix 10: Outputs of a) maximal presence model with no interaction terms and b) maximal abundance model with no interaction terms.

```
Call:
glm(formula = PRESENCE ~ NONLIVECOVER + BGDVRATIO + DROPPINGSMEAN +
     MEANSWH + HPCOVER + NECTARSPMEAN + SHADEMEAN + SMPetoPR +
     VisitMeter + AC_C + DAYS, family = "binomial", data = df.UKBMSec
```

```
Deviance Residuals:
    Min       1Q   Median       3Q      Max
-1.9321 -1.0406  0.6331  0.9086  1.9868
```

```
Coefficients:
            Estimate Std. Error z value Pr(>|z|)
(Intercept) -0.685322   0.600042  -1.142  0.25340
NONLIVECOVER  0.167351   0.218471   0.766  0.44367
BGDVRATIO    -0.272220   0.154650  -1.760  0.07837 .
DROPPINGSMEAN 0.019930   0.166143   0.120  0.90452
MEANSWH      -0.367845   0.170904  -2.152  0.03137 *
HPCOVER       0.083038   0.187651   0.443  0.65812
NECTARSPMEAN  0.261296   0.171259   1.526  0.12707
SHADEMEAN    -0.679482   0.209922  -3.237  0.00121 **
SMPetoPR      0.015364   0.172478   0.089  0.92902
VisitMeter    0.138016   0.155916   0.885  0.37605
AC_C          0.423779   0.337471   1.256  0.20921
DAYS          0.020750   0.009882   2.100  0.03575 *
```

```
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

(Dispersion parameter for binomial family taken to be 1)

```
Null deviance: 288.41 on 219 degrees of freedom
Residual deviance: 257.02 on 208 degrees of freedom
(28 observations deleted due to missingness)
AIC: 281.02
```

Number of Fisher Scoring iterations: 4

```
Call:
glm(formula = LOGCOUNTEFFORT ~ NONLIVECOVER + BGDVRATIO + DROPPINGSMEAN +
     MEANSWH + HPCOVER + NECTARSPMEAN + SHADEMEAN + SMPetoPR +
     DAYS + AC_CCOUNT, family = gaussian, data = df.UKBMSSectionCountsVisitHabitatFinalStand)
```

```
Deviance Residuals:
    Min       1Q   Median       3Q      Max
-3.4736 -1.1299 -0.1975  0.9101  4.7155
```

```
Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)  1.588757   0.435063   3.652  0.000329 ***
NONLIVECOVER  0.100532   0.158272   0.635  0.526003
BGDVRATIO    -0.347517   0.115851  -3.000  0.003031 **
DROPPINGSMEAN -0.035355   0.120841  -0.293  0.770135
MEANSWH      -0.021734   0.119077  -0.183  0.855353
HPCOVER       0.027228   0.134200   0.203  0.839415
NECTARSPMEAN  0.318143   0.122623   2.594  0.010144 *
SHADEMEAN    -0.441204   0.151720  -2.908  0.004030 **
SMPetoPR     -0.090879   0.119375  -0.761  0.447342
DAYS          0.001224   0.006895   0.178  0.859270
AC_CCOUNT     0.126339   0.038712   3.264  0.001285 **
```

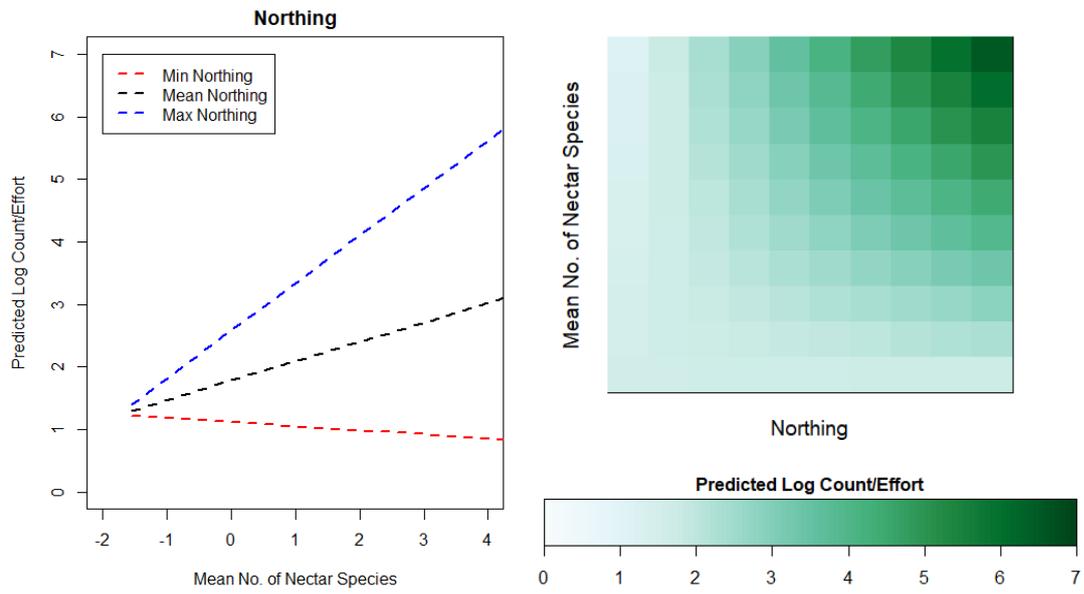
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```

(Dispersion parameter for gaussian family taken to be 2.708208)

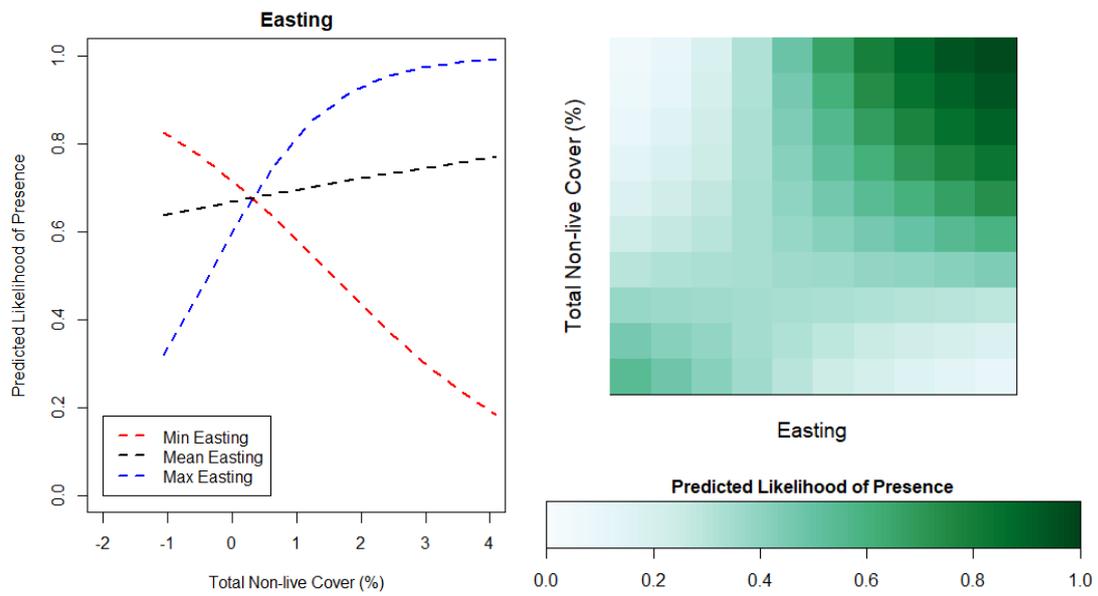
```
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Residual deviance: 566.02 on 209 degrees of freedom
(28 observations deleted due to missingness)
AIC: 856.23
```

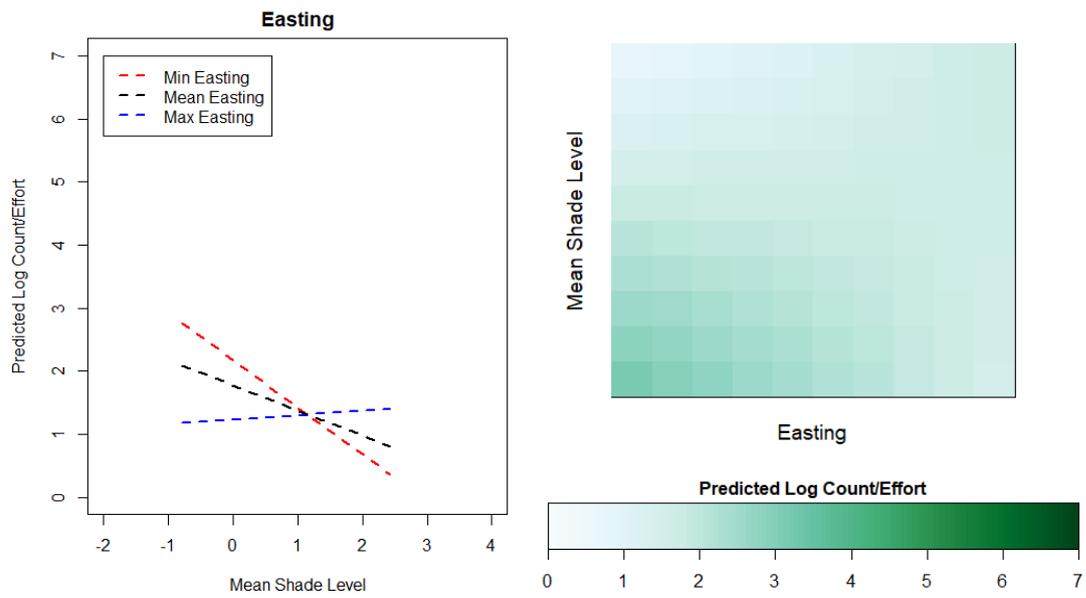
Number of Fisher Scoring iterations: 2

(i)

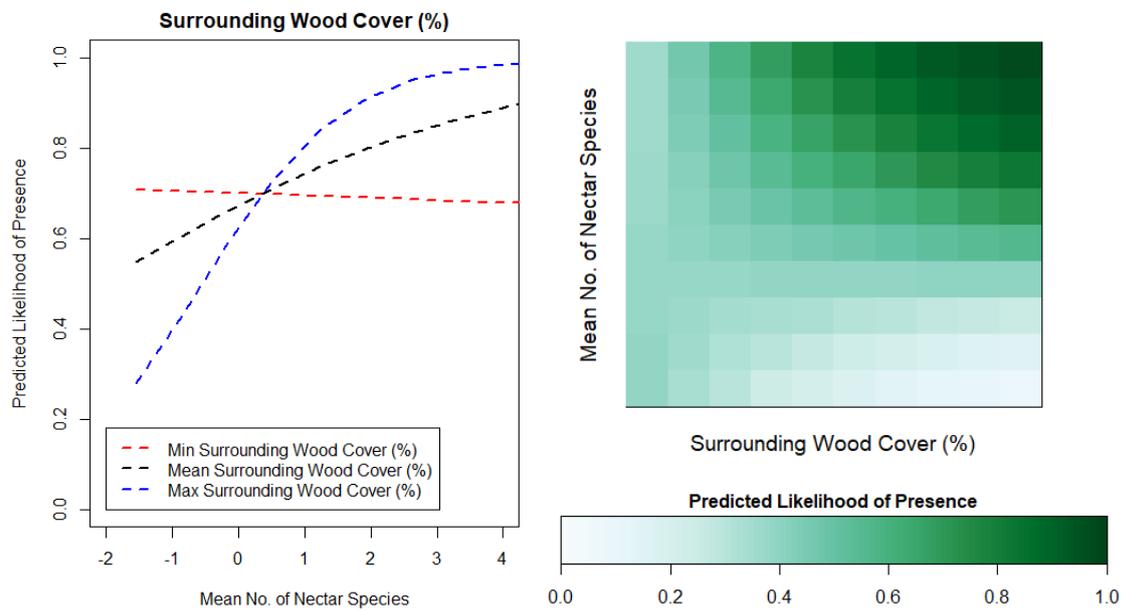


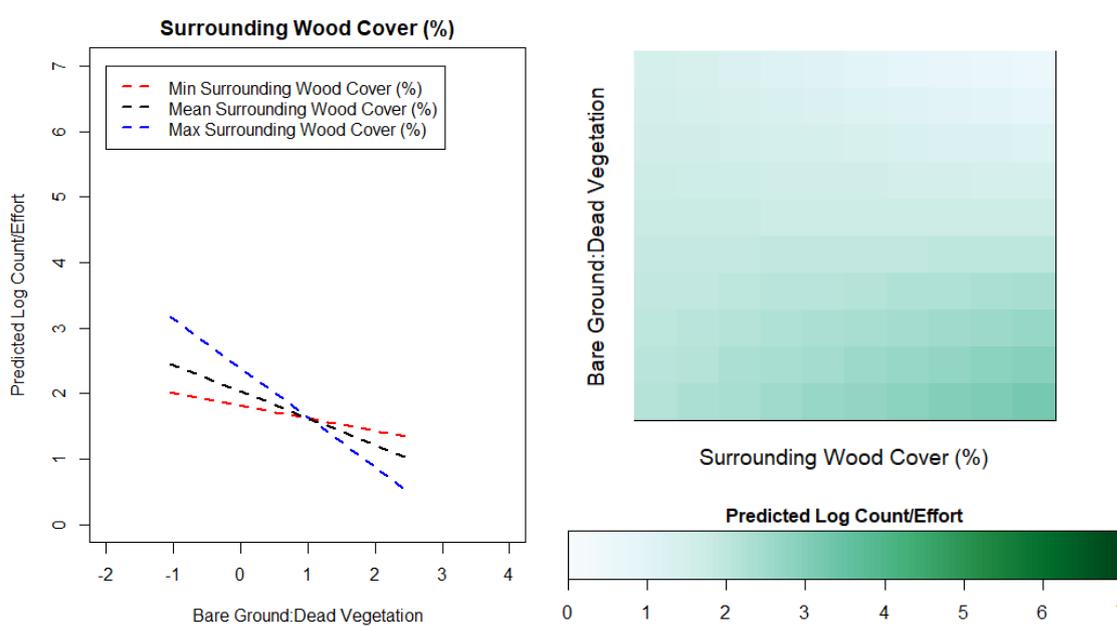
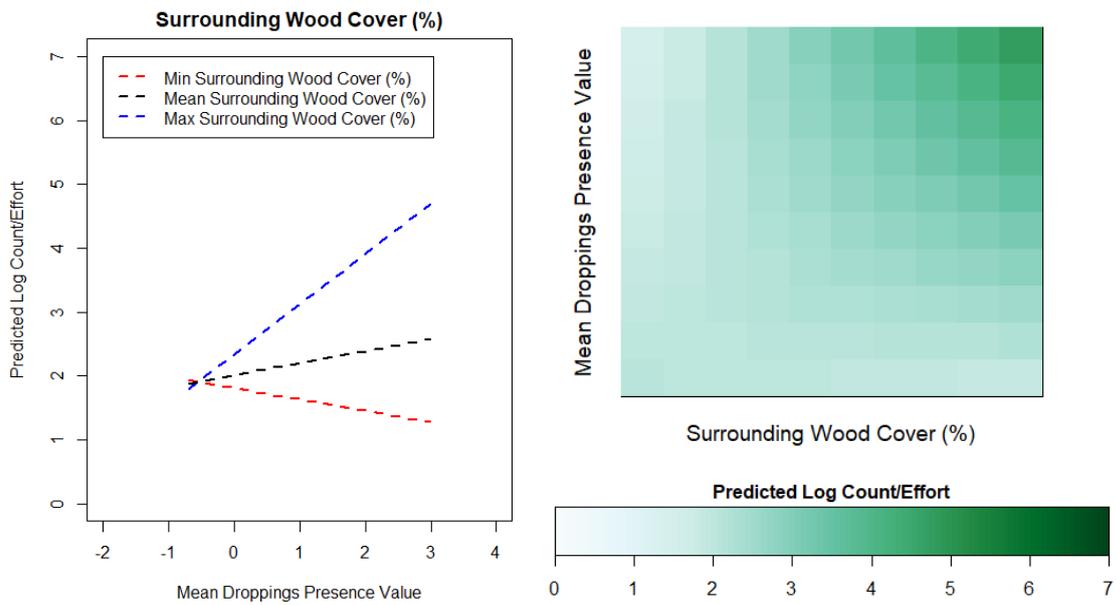
(ii)



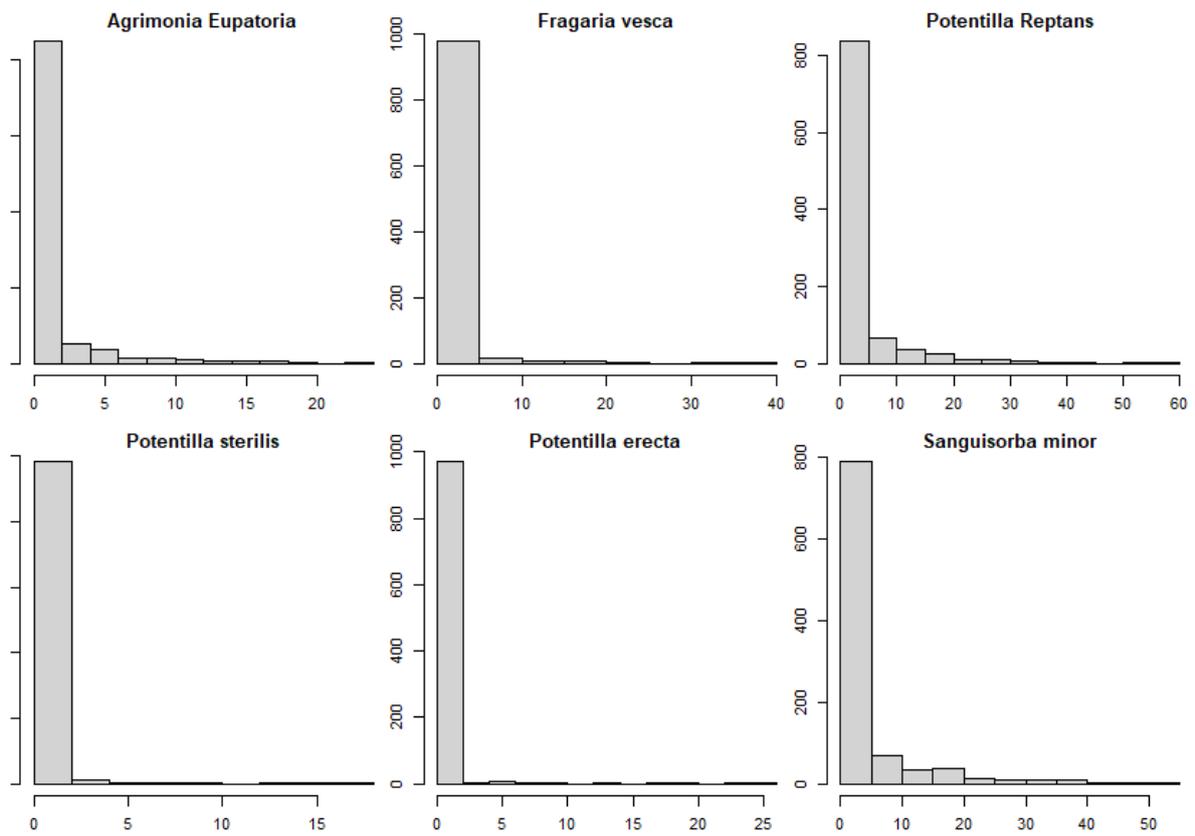


(iii)

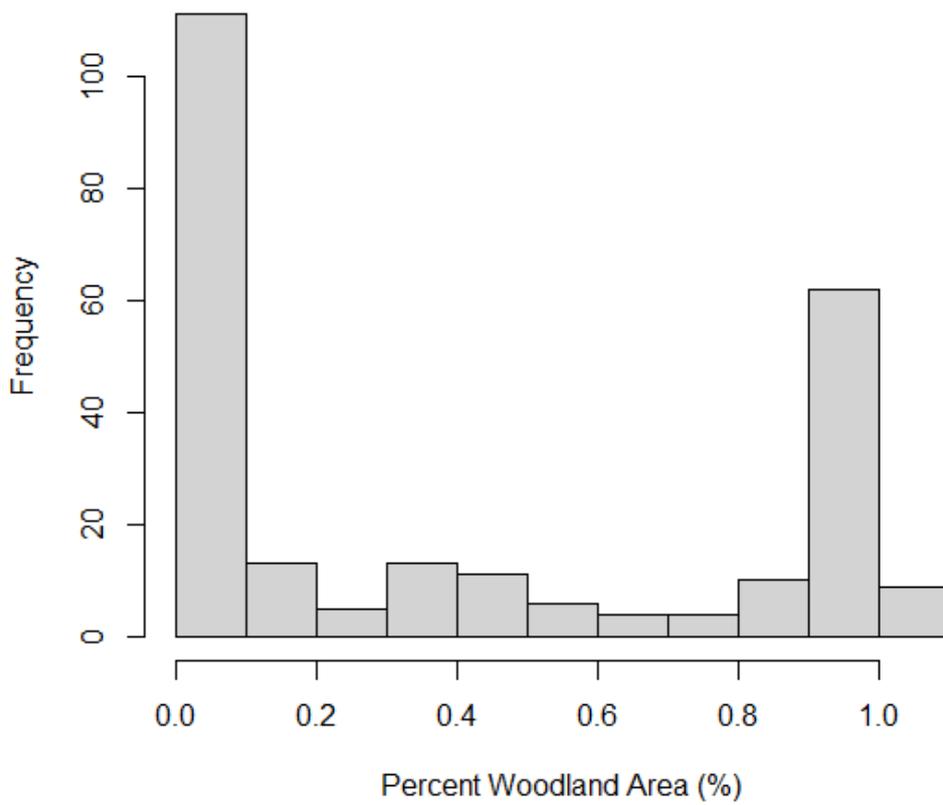




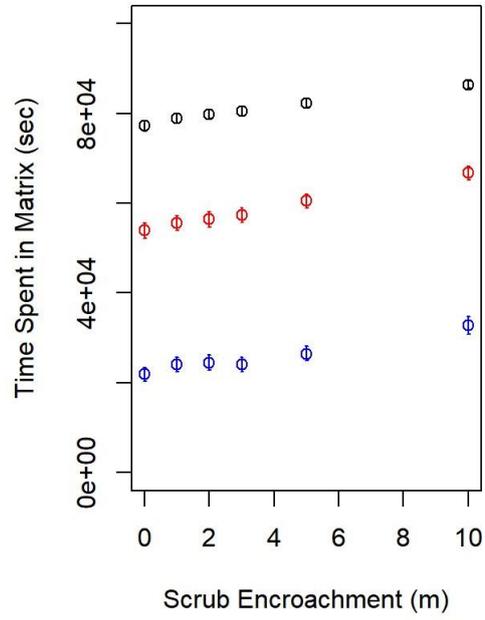
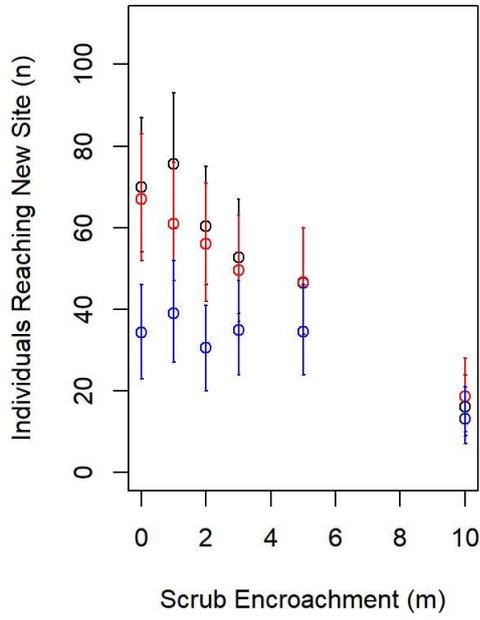
Appendix 11: Line graphs and accompanying heat maps showing the modelled effect of the interaction term between i) Latitude, ii) Longitude, iii) Woodland cover, and habitat effect s , on Presence and Abundance. Line graphs show the modelled (standardised) habitat effects at minimum, mean, and maximum geography and woodland cover values. In heat maps, effect size is shown at 100 combinations of the independent variables, with 10 values of each variable at regular intervals across their observed range from the empirical data.



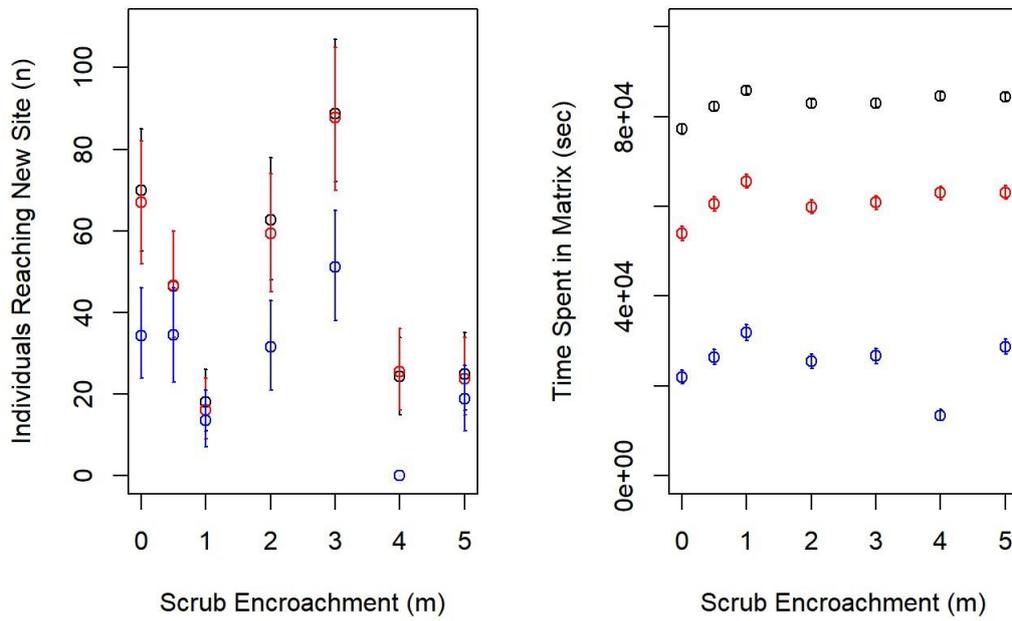
Appendix 12: Distribution of percentage cover values from all quadrats when surveying for *P. malvae* habitat features for each individual hostplant species.



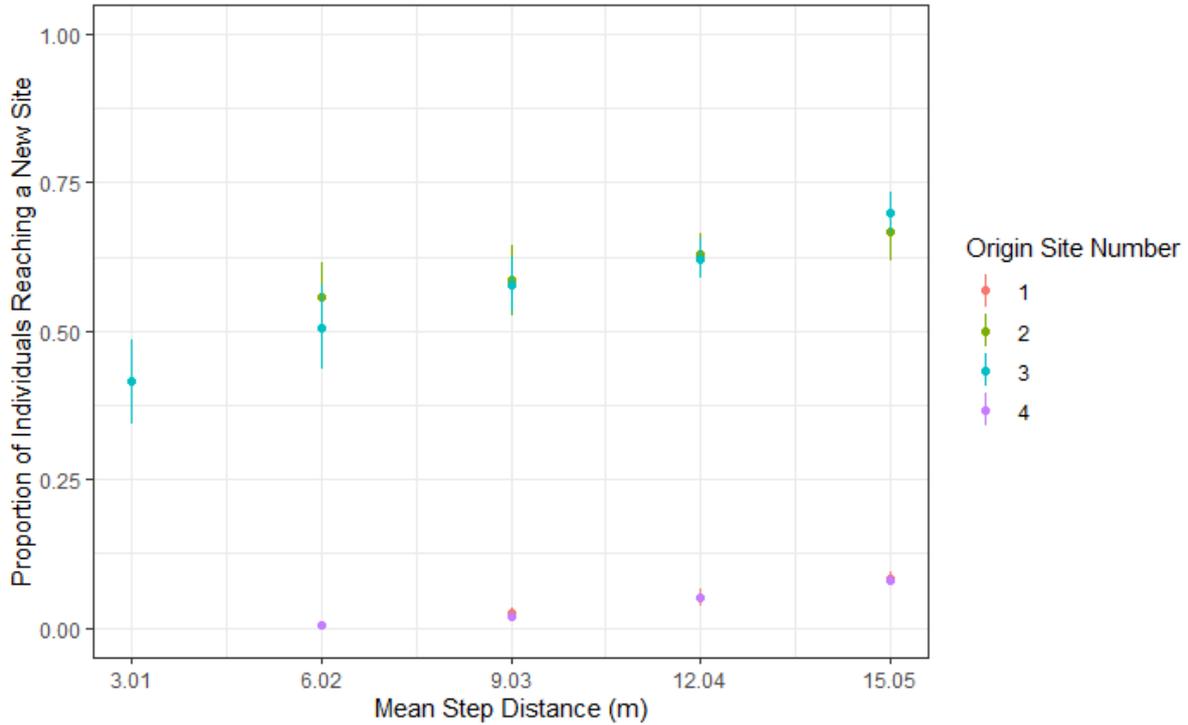
Appendix 13: Frequency distribution of nearby woodland percentage cover values across all UKBMS transect sections surveyed for habitat features for *P. malvae*. (Values over 1, are <1.0001, most likely attributable to rounding error during data processing.)



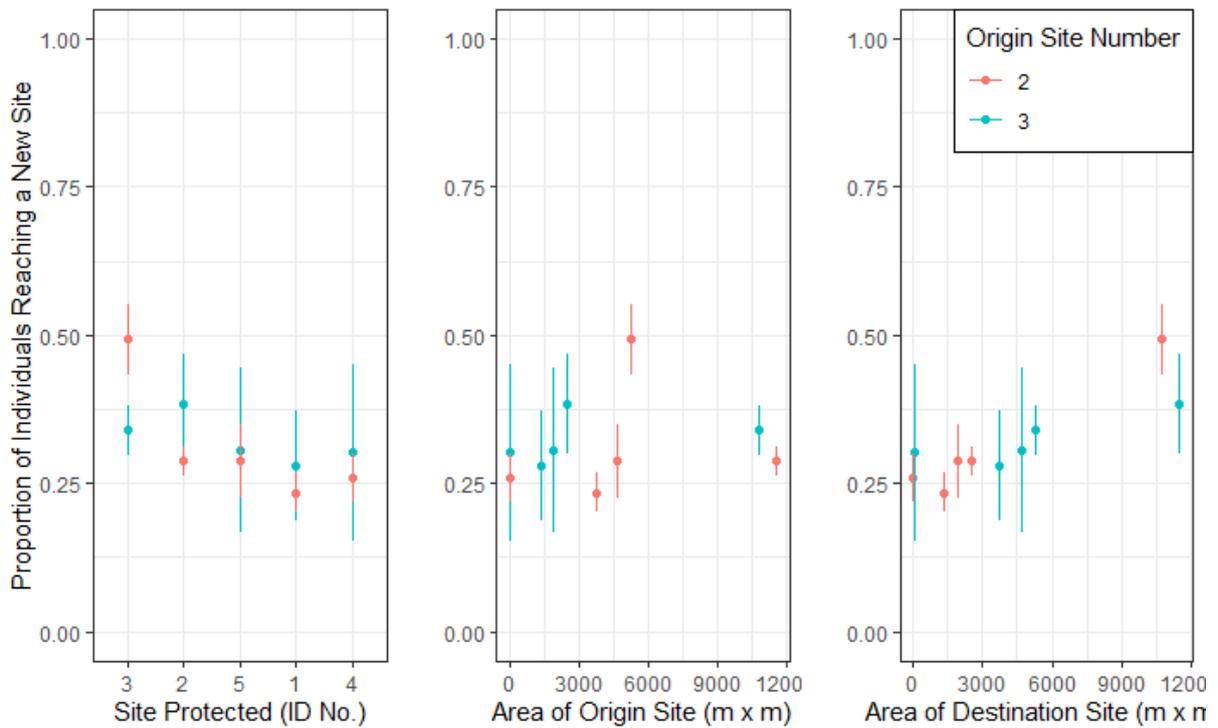
Appendix 14: Mean values of a) time spent out of habitat, and b) individuals reaching a new site, produced by models with varying levels of scrub encroachment, and at different grass parameter preference (C) values, as indicated by colour (Black; C = 0.695, Red; C = 2.4, Blue; C = 4.8). Error bars represent 95% confidence intervals.



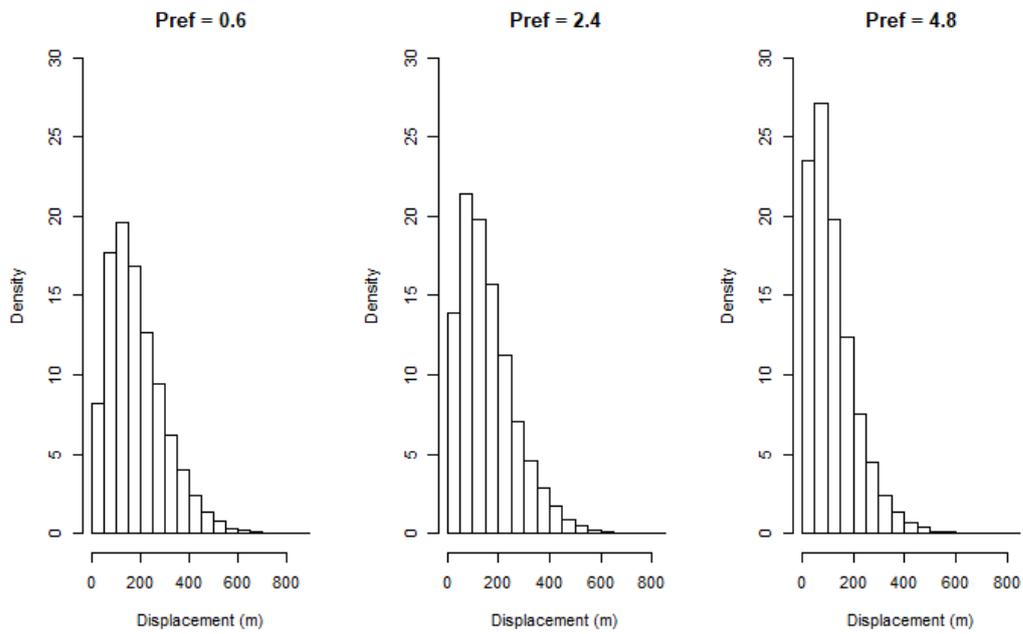
Appendix 15: Mean values of a) time spent out of habitat, and b) individuals reaching a new site, produced by models where scrub cover is equal to that in a 5 m scrub encroachment scenario, but different individual sites are protected from scrub. Colours indicate different grass parameter values (Black; $C = 0.695$, Red; $C = 2.4$, Blue; $C = 4.8$). Error bars represent 95% confidence intervals.



Appendix 16: Proportion of simulated individuals from each site having reached a new site by the end of a long-term simulation, under increasing mean step distances in the matrix (i.e. acceleration in the matrix). Origin site denoted by colour (see key).



Appendix 17: Proportion of simulated individuals from each site (2-3) having reached a new site by the end of a long-term simulation, under scenarios of 5 m scrub encroachment, and protection of each site ($n=5$). Origin site denoted by colour (see key).



Appendix 18: Frequency distributions of total displacement (i.e. Euclidian distance from flight origin point) at all time intervals from long-term simulation models with grass preference parameter (C) values of a) 0.6, b) 2.4, and c) 4.8.

During a 6-month placement with Butterfly Conservation, I undertook an investigation into the use of Key Performance Indicators within the organisation, and broadly across the conservation sector. We did this in order to propose a new framework for devising [KPIs](#) at project- and organisation-level to better report on progress to stakeholders and adapt management techniques. The following section samples parts of the report, modified for the interests of this study and *P. malvae* conservation.

We undertook an exploration of the use of standardised indicators by over 50 conservation organisations within the partnership authoring the State of Nature reports (Hayhow et al. 2016) and found that the number of organisations using [KPIs](#) has increased over time. Government and state bodies in particular are employing indicators; for example, the UK Government's Nature Recovery Network (Defra 2018), and Natural England strategy includes [KPIs](#) (Natural England 2021), with targets which are regularly measured. However, some indicators have been subject to criticism because their unattainability, or being misleading or irrelevant to the original purpose of the conservation action (Stem et al. 2005, Mascia et al. 2014, Thomsen and Caplow 2017).

Butterfly Conservation itself began formalising and standardising its approach to conservation in 1992, subsequently producing national and regional species action plans (Brereton et al. 1998) in response to the UK Biodiversity Action Plan. A '2020 Vision' followed after the dissolution of the UK [BAP](#), then a 10-year Flight Plan guiding document, accompanied by Conservation, Reserves, and Science strategies in 2017-2019. The charity primarily delivers conservation for identified priority species, as well as wider countryside species (i.e. habitat generalists widespread across the country (Lowe et al. 2020)), through a series of multi-objective projects on the ground, predominantly at the landscape scale with multiple delivery mechanisms (e.g. advice, management, recording).

An initial assessment of Butterfly Conservation's projects (n = 46) publicly available on the organisation's website (2020) revealed that the average project duration was ~4.5 years, that the vast majority of projects were delivered at the landscape level (40/46), and that most were focused on specialist species and habitats (33/46). The nature of these frequently landscape-level, short-term, and multi-objective projects presents difficulties in comparing project outcomes. Additionally, adequately capturing the scale of work done and subsequent impacts is complex, particularly with simple, country-level metrics.

One area in which the charity collects a great deal of information potentially informative for indicators is on site visits, and advice given through its Site Advice Recording Database (SARD), begun in 2002. This database collects details including date, location, activity, and focal species, with

the full list of details depending on iteration of the collection form at the time. The records collect could provide vital insights into the timing, duration, and nature of work on sites (i.e. monitoring, management or advice) with actions for priority species/habitats directly attributable to Butterfly Conservation, as opposed to partners. If appropriately selected, these data could be developed into Key Performance Indicators, which could provide valuable context for any outputs related to local species or habitat improvement, and inform adaptive management for the best outcomes (Salafsky and Margoluis 2003).

Butterfly Conservation, like many [NGOs](#), are frequently updating their strategies, priorities, and targets in line with the changing physical and legislative conservation landscape. Previously, there were a set of goals aimed at conserving specialists, Wider Countryside Species, engagement, and international work. However, these have been reworked, and the public facing strategies at present detail strategic goals, initiatives, enablers and values (Butterfly Conservation 2020).

Reviewing and Designing [KPIs](#) for Butterfly Conservation

During my placement with Butterfly Conservation, we reviewed existing conservation assessment approaches within the organisation, including use of [KPIs](#), and suggested a framework for [KPIs](#) design, and some potential [KPIs](#) going forward.

Butterfly Conservation has previously developed a number of targets, objectives, and indicators, in line with organisation-wide strategies and visions (Butterfly Conservation 2020). We aimed to evaluate some of these performance indicators against an existing framework (Doran, 1981), in order to make suggestions for standardised indicators. Below is our interpretation of the existing [SMART](#) structure for target setting, tailored to the requirements of Butterfly Conservation.

Supp. Table 1. Definitions of 'SMART' Key Performance Indicator attributes for use within Butterfly Conservation

Attribute	Definition
Specific	Has a clear definition and is related to a target
Measurable (Scientific)	Compilable, robust, data available
Attainable	Has a target been set? (If so, include)
	Can the target be met?
Relevant	Directly measures BC conservation effort
	Can inform BC decision making (in the context of conservation)
	Of concern to BC Members, Public, and/or Policy makers
Time-bound	Updateable annually

Butterfly Conservation has used [KPIs](#) for a long time in one form or another, but they have often been limited in their applicability. We found that the indicators given were generally measurable, used available data, and could be reported at regular (annual) intervals, with associated targets, and were relevant to the general public. The [KPIs](#) were, however, primarily useful for engagement purposes, and had limited potential for informing direct conservation guidance (e.g. management decisions, policy).

In addition, the majority of [KPIs](#) appeared to pertain to inputs and short-term outputs, and generally not to long-term outcomes, or to the status of priority species/habitats. Because of the nature of previous [KPIs](#) being contained within strategies, they tend to have been weighted towards evidence of activity and outputs, which is useful for justifying use of resources and building trust for stakeholders. The bias towards shorter term indicators (Ferraro and Pattanayak 2006) is also driven by the difficulty in obtaining reliable measures of outcomes, and proving a causal link with [BC](#) activities. Several of the key delivery mechanisms are not direct, being linked to advice, engagement, and policy information, in which it is difficult to trace long-term outcomes.

Less is known about long-term outcomes, for a number of reasons. It is difficult to obtain long-term funding for monitoring, and projects are often idiosyncratic with incomparable goals. Therefore, [KPIs](#) would often fail to capture outputs at the organisation level, as work is often done in collaboration with landowners and partners, muddying the contributions of Butterfly Conservation itself. Furthermore, the trends of Lepidoptera are being acted on by several pressures at once (Baillie et al. 2004, Fox et al. 2015, Hayhow et al. 2016), including land-use, development, pollution and climate, which are not abating but in fact worsening (Sutherland et al. 2008, United Nations Department of Economic and Social Affairs 2019, Masson-Delmotte et al. 2021) and interacting (Burns et al. 2016). Species trends are also notoriously hard to track for Lepidoptera, as weather can have dramatic impacts on yearly measures. Standardised monitoring schemes, such as the [UKBMS](#), can help to counteract this, but only to an extent.

Another approach that may assist in reporting on organisation level [KPIs](#) is the collection of data in [SARD](#) on specific inputs of Butterfly Conservation at a level that attempts to categorise particular activities, and total Full Time Equivalent ([FTE](#)) work. Such monitoring could enable reporting the organisation's influence on long-term trends, but will first require multiple years of records and will likely only be reported on at longer intervals (e.g. 5 - 10 years). None of the above is to say that Butterfly Conservation is not contributing to conservation of Lepidoptera, which is demonstrated in case studies of species such as the Large Blue (Warren 2012). However, such cases where outcomes are clearly attributable to Butterfly Conservation are rare. By comparison, activities such as advising

landowners on maintaining assemblages of non-charismatic moths within a priority landscape is harder to capture and less interesting to the public. Preventative measures, while often harder to report on, are arguably more cost-effective.

During the placement, we also suggested a new framework for designing/developing [KPIs](#) within the organisation (**Error! Reference source not found.**), in line with Butterfly Conservation’s delivery mechanisms, and measuring progress towards the organisation’s wider core aims (Butterfly Conservation 2020).

In our framework, we recommended that [KPIs](#) be devised for different stages of the impact chain (Kapos et al. 2008), primarily on outputs and activities measures, but eventually for impact measures when sufficient data is available. We considered which stages which [KPIs](#) should be relevant to, and used the Pressure, State, Response model (Hammond et al. 1995) as a basis.

Supp. Table 2. Recommended attributes of Key Performance Indicators to be completed during their design within a proposed framework for Butterfly Conservation, taken from placement.

Field	Example
BC Directorate/Team	Conservation
Cross-reference to theme, BC Overarching Strategy	Recover threatened butterflies and moths
Objectives	Improving the status of threatened species and their habitats
Themes	Site and landscape-scale conservation projects
KPIs	Annual number (and area) of funded BC volunteer led landscape-scale projects
Type of KPI	Response
Target	TBC
Units	Number of projects and area in HA
Audience	Internal
Type	Metric
Definition/Criteria	Weighted by number of man-houses, Disaggregated by Region in commentary
Data Sources	Senior Leadership Team, SARD
Availability	Can be developed now
Development Work Required	Discriminated between funded/BC volunteer-led and other lower impact projects in SARD

Separate [KPI](#) subsets may be more suitable for different audiences, likely requiring both external and internal reports. For this reason, it is worth having some [KPIs](#) which can be aggregated, or used to make an index for threatened species goals (Hammond et al. 1995), and some which are relevant to report progress on the conservation of each species itself for practitioners and stakeholders to safeguard against loss of lower profile species, such as some micro-moths which have only recently

been included in the National Moth Recording Scheme. [KPIs](#) can be developed for each of the recently updated core aims of the organisation (Butterfly Conservation 2020), including ‘improving the status of threatened species & their habitats’. With this in mind, we suggest the collection of annual indicators for each priority species, including some headline indicators common to all priority species to be reported at less regular intervals (e.g. 5 Year Intervals).

Appendix 20: Assessment of suggested KPIs in Chapter 5 against ‘SMART’ criteria , with accompanying Key of Criteria for ‘Red-Amber-Green’ categorisation.

See Supplementary Folder

Appendix 21: R Scripts in Chapter 2 for creating data-frames, running generalised linear mixed models, and plotting figures used in publication. Data archived on local hard-drive, available upon request.

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Appendix 22: R Scripts in Chapter 4 for describing P. malvae movements, modelling grass preference, and creating rasters for use in NetLogo , in addition to script for running Individual Based Models in NetLogo. Data archived on local hard drive, available upon request.

Available from doi.org/10.17638/datacat.liverpool.ac.uk/1764

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