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ORIGINAL PAPER

Optimising the reintroduction of a specialist peatland butterfly *Coenonympha tullia* onto peatland restoration sites

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Abstract
The two main goals of peatland restoration are habitat improvement and climate change mitigation by reducing greenhouse gas emissions from damaged peatlands and providing a net carbon sink. The biodiversity of specialist peatland species is threatened because of habitat destruction and the large heath butterfly *Coenonympha tullia* has become a flagship species for peatland ecosystem restoration, with a species reintroduction programme currently underway on a peatland restoration site within Chat Moss, Greater Manchester, UK. The aim of this study was to improve our quantitative understanding of *C. tullia* habitat resource requirements to optimise habitat restoration for further reintroduction attempts. We monitored butterfly micro-distribution and dispersal during the first three flight seasons (2020, 2021 and 2022) of the reintroduction using high-accuracy GPS, combined with a distance-bearing protocol. Analysis of butterfly flight points and rest points in relation to plant species distribution and abundance, identified the most important habitat resources. Using logistic regression, treatment-response curves were constructed, enabling us to identify critical thresholds for the abundance of these important habitat resources. The break of slope near the top of the logistic curve was identified using segmented regression, giving an estimate of the near-optimal abundance; fourteen *Eriophorum vaginatum* tussocks per 2 m quadrat and 13.4% *Erica tetralix cover.*
Implications for insect conservation During ecosystem restorations, prior to the reintroduction of species with specialist habitat requirements, it is necessary to have a clear understanding of the abundance of the important habitat resources that need to be provided. The quantitative approach we describe defines the most significant environmental factors and habitat resources, then uses segmented regression to estimate the near-optimal habitat resource requirements; increasing the likelihood of reintroduced populations thriving and reintroduction programmes achieving long-term success.

Keywords Conservation translocation · Peatland · Lowland raised bog · Habitat resources · Distance-bearing · Segmented regression

Introduction

The currently unfolding biodiversity crisis (Butchart et al. 2010; Potts et al. 2010; Ceballos et al. 2017; Hallmann et al. 2017; Goulson 2019) has been driven by multiple anthropogenic factors, most prominently land use change resulting in habitat loss (Bubová et al. 2015; Jaureguiberry et al. 2023). Climate change, already a significant factor, is predicted to accelerate over the coming decades (Parmesan et al. 2022).

Traditionally undervalued (Lindsay 1993), peatlands provide natural capital (Costanza 2003; Crump 2017; Ashby et al. 2021; Rouquette et al. 2021), multiple ecosystem services (Bonn et al. 2016) and are a UK Biodiversity Action Plan Priority Habitat (Maddock 2008). Peatlands have a unique flora and fauna (Rydin and Jeglum 2013) and over recent decades have gained international attention because of their potential to mitigate dangerous climate change by sequestering and storing globally significant quantities of atmospheric CO_2 into carbon-rich soils (Worrall et al. 2010; Yu 2011; Freeman et al. 2012; IUCN 2017; Hawken 2018; IUCN UK Peatland Programme 2021). The 6th International Panel on Climate Change report (Parmesan et al. 2022) highlights the role of peatland ecosystems in regulating the global carbon cycle.

When damaged by human activity, peatlands become net sources of greenhouse gasses (Evans et al. 2017), with about ten percent of global peatlands being drained or extracted

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(Leifeld and Menichetti 2018)and more than half of European peatlands lost (Andersen 2016); the protection and rewetting of peatlands has been identified as one of the most cost-effective (Moxey and Moran 2014; Office of National Statistics 2019) and practical methods for reducing emissions globally (Hawken 2018), moving to net zero with the objective of drawing down atmospheric CO_2 levels by mid-century (Drawdown.org, accessed 15/08/2023).

Coenonympha tullia (Müller 1764) (large heath butterfly) has a Holoarctic distribution with numerous local subspecies (Melling 1987) living in a diverse range of humid grassland environments. In continental Europe, calcareous fen and associated sedge species provide the richest habitat (Weking et al. 2013; Bernard et al. 2018) in contrast to the British populations which inhabit acidic grassland, wet heath and bog. *C. tullia* is listed on the IUCN Red List as 'Vulnerable and Decreasing in Europe' (van Swaay et al. 2010) and has been uplisted from vulnerable to endangered in the revised Red List of British Butterflies (Fox et al. 2022). *Coenonympha tullia ssp. davus* (Fabricius 1777), is a specialist peatland butterfly characteristic of good quality lowland raised bogs in the Northwest of England; it is the most threatened of the *C. tullia* subspecies in the British Isles (Bourn and Warren 1997) because of habitat destruction, with only 1.3% of lowland raised bogs in England remaining in good condition (Maddock 2008). Current efforts are restoring peatland sites across Europe (Andersen 2016), improving the condition of surviving bog, or returning farmland and peat extraction sites to semi-natural habitat with measurable improvements in biodiversity (Osborne et al. 2021) and carbon sequestration (Keightley et al. 2023).

Weking et al. (2013) investigated drivers of *C. tullia* population declines in southern Germany, where drying out of wetland habitat was found to be the main threat, the negative water balance being primarily due to agricultural intensification and drainage rather than the changing climate. Franco et al. (2006) studied populations of the four butterfly species that reached the southern limit of their ranges in Britain, concluding that habitat degradation rather than climate change was responsible for the extirpation of *C. tullia* at 52% of study sites; climate change was the main driver of extirpations and northward range shift in the other three species, with habitat degradation as a result of climate change likely to become more significant to *C. tullia* populations in future decades. Potential climate impacts on lowland raised bogs have been modelled (Berry and Butts 2002) with the likelihood of lower summer water tables under all scenarios by the 2050s—*C. tullia*'s range in Britain was predicted to move northward with more occupancy in northern Scotland and disappearing from southern Britain, northwest England becoming the southernmost limit of its range. Dennis and Eales (1999) found sites in Northumberland with large areas of good quality *C. tullia* habitat which appeared to be unoccupied due to high altitude and cold conditions, but which had the potential to become colonized as a result of a warming climate. A more recent study used species distribution modelling to predict the viability of planned species reintroductions onto the Manchester Mosslands concluding that predicted climate change scenarios would have a moderate impact on the viability of *C. tullia* by mid-century (Bellis et al. 2021).

The presence of *C. tullia* on the Manchester Mosslands is recorded by Lewin (1795); known at the time as the 'Manchester Argus', this was the first description of the species in Britain. Historical evidence documents the extent of Chat Moss, the largest of these peatlands, (Fig. 1) as a vast impenetrable wilderness (Defoe 1724-1727; Aiken 1795; Stephenson 1824). Over the following two centuries, all of the primaeval peatland habitat (Lindsay 1993) was drained, the peat cut away and the land converted to agriculture, industry, transport infrastructure and urban expansion, resulting in extirpation of the butterfly probably during the early 20th century although this loss was unrecorded. Modern-day surveying documents 27.9 km^2 of deep peat soils remaining on Chat Moss (Natural England et al. 2008; Natural England 2010) (Fig. 1) although the original Chat Moss was probably larger than this, with thin peat soil (now lost) and various wetland habitats (wet heath, lagg fen, reed bed, willow carr) forming a skirtland area (Hall et al. 1995).

Over the past 40 years, there have been determined efforts to restore areas of highly damaged Chat Moss peatland into functioning lowland raised bog, notably by the Lancashire Wildlife Trust (Osborne et al. 2021; Lancashire Wildlife Trust accessed 18/06/2023). These projects are now being funded and driven forward by the imperative to reduce greenhouse gas emissions (Natural England 2010; Worrall et al. 2010; Leifeld and Menichetti 2018; Smart et al. 2020; Evans et al. 2017) and optimise the natural capital of the area (Ashby et al. 2021).

The *C. tullia* species reintroduction in May 2020 (Weston 2020), now in its fourth year, was a significant milestone in the restoration work. The reintroduction population rapidly established a tight colony structure (Osborne and Coulthard 2022) with only occasional observations of wider dispersal across the reserve, in agreement with previous observations of the species' colonial nature (Wainwright 2005; Wainwright and Ellis, accessed 29/12/2021) and poor dispersal ability (Melling 1984; Wainwright 2005).

During the planning phase of this species reintroduction programme, potential reintroduction sites were developed by planting thousands of plug plants of specialist peatland plants. The plant species used by *C. tullia* in the British Isles have been identified by previous research; *Erica tetralix* (cross-leaved heather) is the main nectar source (Dennis and Eales 1997, 1999; Wainwright 2005). *Eriophorum vaginatum* (hare's-tail cotton sedge) is the main larval foodplant

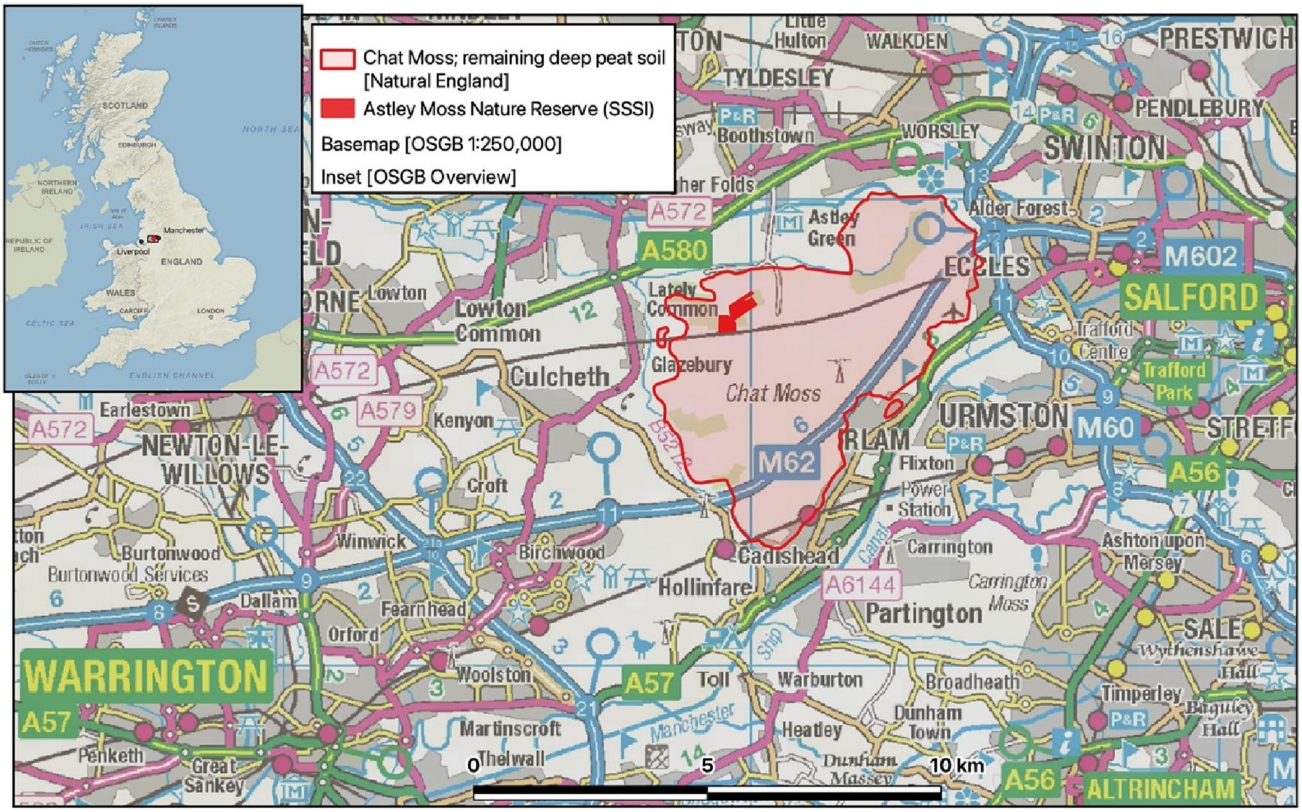


Fig. 1 Chat Moss, situated in the northwest of England on the outskirts of the Greater Manchester conurbation. The remaining 27.9 km^2 of deep peat soil is shown. Astley Moss Nature Reserve (SSSI) was selected as the best site for the 2020 large heath reintroduction

(Melling 1984, 1987; Dennis and Eales 1997, 1999), the dense tussocks being important habitat for ovipositioning (Joy 1991) and for overwintering larvae to survive seasonal flooding (Joy and Pullin 1997, 1999). *Eriophorum angustifolium* (common cotton sedge) has been proposed as a possible secondary larval food plant, based on a few observations (Melling 1984; Wainwright 2005); this is a potential problem on restoration sites where *E. angustifolium* readily colonises open water, but is not tussock forming, potentially creating an ecological sink (Hallmann et al. 2017) resulting in high larval mortality during winter flooding.

The IUCN Species Reintroduction Guidelines (IUCN 2013) emphasise the importance of having a clear understanding of the reintroduction species' abiotic and biotic habitat needs, success being unlikely without good quality habitat (Griffith et al. 1989). At best, only half of insect translocations are successful over the long term (Bellis et al. 2019) and the utility of more fundamental research to increase success rates has been underlined (Seddon et al. 2007; Armstrong and Seddon 2008). During the planning phase of this species reintroduction programme it became apparent that we did not have a quantitative understanding of the abundance of the critical habitat resources necessary to support the butterfly throughout its lifecycle (Dennis et al. 2003); at what stage in the decades-long restoration of very badly damaged sites to semi-natural habitat (Osborne et al. 2021) would there be sufficient habitat resources for a species reintroduction to have a reasonable chance of success? To address this question, a detailed environmental survey was conducted on peatland nature reserves across Northwest England where *C. tullia* was known to be present or absent (Osborne et al. 2022)—this defined the important environmental characteristics and habitat resources (E. *vaginatum* tussocks and *E. tetralix* percentage cover) necessary during the butterfly's life cycle and informed the final choice of reintroduction site. However, these estimates are deductions based on site-level presence-absence data, limiting our confidence in the conclusions.

This study's data collection was conducted as part of the post-release surveillance following a species reintroduction, with the release of approximately 60 adult large heath butterfly *Coenonympha tullia ssp. davus* onto Astley Moss SSSI (53.475, −2.457) (Fig. 1, Fig. 2), Greater Manchester, UK in May–June 2020 (Weston 2020; Osborne and Coulthard 2022). The population was augmented with a second release of 37 adult butterflies in July 2022 (Fig. 2), with future releases planned.

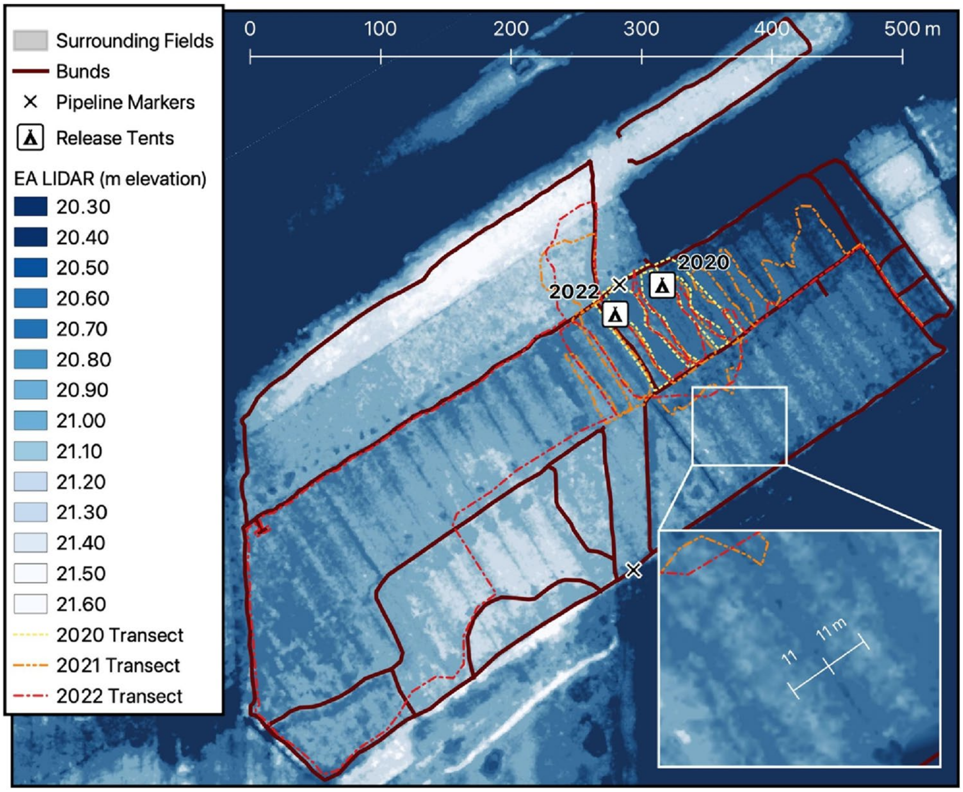


Fig. 2 Astley Moss site plan generated in QGIS using Environment Agency LIDAR imagery as a base layer with a 1 m horizontal and 10 cm vertical resolution. There is a prominent pattern of 30–50 cm deep troughs running north-west to southeast—evidence of traditional peat-cutting practice, based on a system of alternating 12-yard (11.0 m) wide trenches and intervening ridges, which took place up until the 1940s. Following this, the site was burned regularly to prevent scrub encroachment, before being managed as a nature reserve from the early 1980s. The 'bunds' are an extensive network of low peat dams constructed to retain rainwater on-site. The 2020, 2021 and much extended 2022 transects are shown

In the present study, we aim to increase the level of confidence in our estimates of habitat resource requirements through direct observations of butterfly behavior, relating fine-scale butterfly distribution from the first three butterfly flight seasons of the reintroduction to habitat data. This information will inform the planning of future *C. tullia* translocations onto neighboring sites in the Chat Moss area.

Research objectives:

1. To investigate the resources used by *C. tullia* for resting during flights, in order to detect any preference for specific plant species.
2. To investigate the relationship between the micro-distribution of *C. tullia* and the distribution of environmental factors within the release area.
3. Use breakpoint analysis to identify minimum and 'near-optimal' habitat resource levels.

Methods

Astley Moss Nature Reserve (SSSI) is based on 2 m depth of acidic Sphagnum peat. The reintroduction site's micro-topography consisted of alternating 30–50 cm deep troughs and ridges relating to previous peat cutting, visible in the LIDAR (Laser Imaging, Distance And Ranging) (Environment Agency 2020) elevations in Fig. 2. The troughs ('cotton-grass beds') (CGB) are shallowly flooded for much of the year, the vegetation cover consisting predominantly of *E. vaginatum* tussocks growing in shallow seasonal pools or on an uneven substrate of *Sphagnum hummocks and lawns*, with *E. angustifolium* in deeper pools. The dry ridges consist predominantly of dense *Molinia caerulea* (purple moor-grass) tussocks.

Field data collection

Coenonympha tullia flight monitoring

The micro-distribution of *C. tullia* adults in flight was monitored during the 2020, 2021 and 2022 flight seasons. A transect was devised, walking along the tough Molinia tussock on the edge of the cotton-grass beds, enabling visualisation of the release area (Osborne and Coulthard 2022) whilst avoiding repeatedly walking on and damaging the delicate regenerating peatland vegetation in the cotton-grass beds. This transect was extended during the 2022 flight season to document outliers/migrants from the release area (Fig. 2). A distance-bearing protocol (Osborne and Coulthard 2022; Růžičková and Elek 2021) was employed to accurately record Flight Point locations. A one-meter accurate position fix was obtained using a pole-mounted Bad Elf Surveyor BE-GPS-3300 GNSS receiver to establish a fixed reference point as close as possible to the initial observation. The estimated distance (m) and compass bearing (degrees) from the GPS were immediately recorded using the Epicollect5 mobile data-gathering platform (Aanensen et al. 2009; CGPS Team 2019–2022). As the butterfly moved, subsequent distance-bearing estimates were noted and the GPS relocated as necessary. Data were uploaded to the online Epicollect5 database.

The position of the start and end of documented flights, and rests during flights were recorded ('flight points'). Behaviours at flight points were recorded; *C. tullia* adults were noted to take frequent rests during flight ('rest points') and the plant species used for perching ('perching resource') (Dennis et al. 2003) was recorded at each rest point. In addition, behaviour on *E. tetralix* was noted—simply perching on the shrub or likely nectaring if the butterfly landed on an *E. tetralix* inflorescence.

Environmental assessment

All surveying took place during the winter or spring (December—May), outside of the main growing season, with a detailed environmental survey of the release area conducted during March 2021. A 12 × 12 grid of 144 survey points, spaced at 10 m intervals, was generated in QGIS, covering the whole of the 2020 dispersal polygon (Fig. 3), and dividing the release area into a regular grid of 10 m square 'compartments' (Post van der Burg et al. 2020; Pearce-Higgins and Yalden 2004; Anadon et al. 2018; Greenwood 2018). In the field, survey points were located with one-meter accuracy and used to centre a 2 m × 2 m open quadrat. Extra survey points and compartments were added to accommodate the butterfly's range expansion and correspondingly larger dispersal polygons; sixteen for 2021 and seven for 2022. It was assumed that the plant community

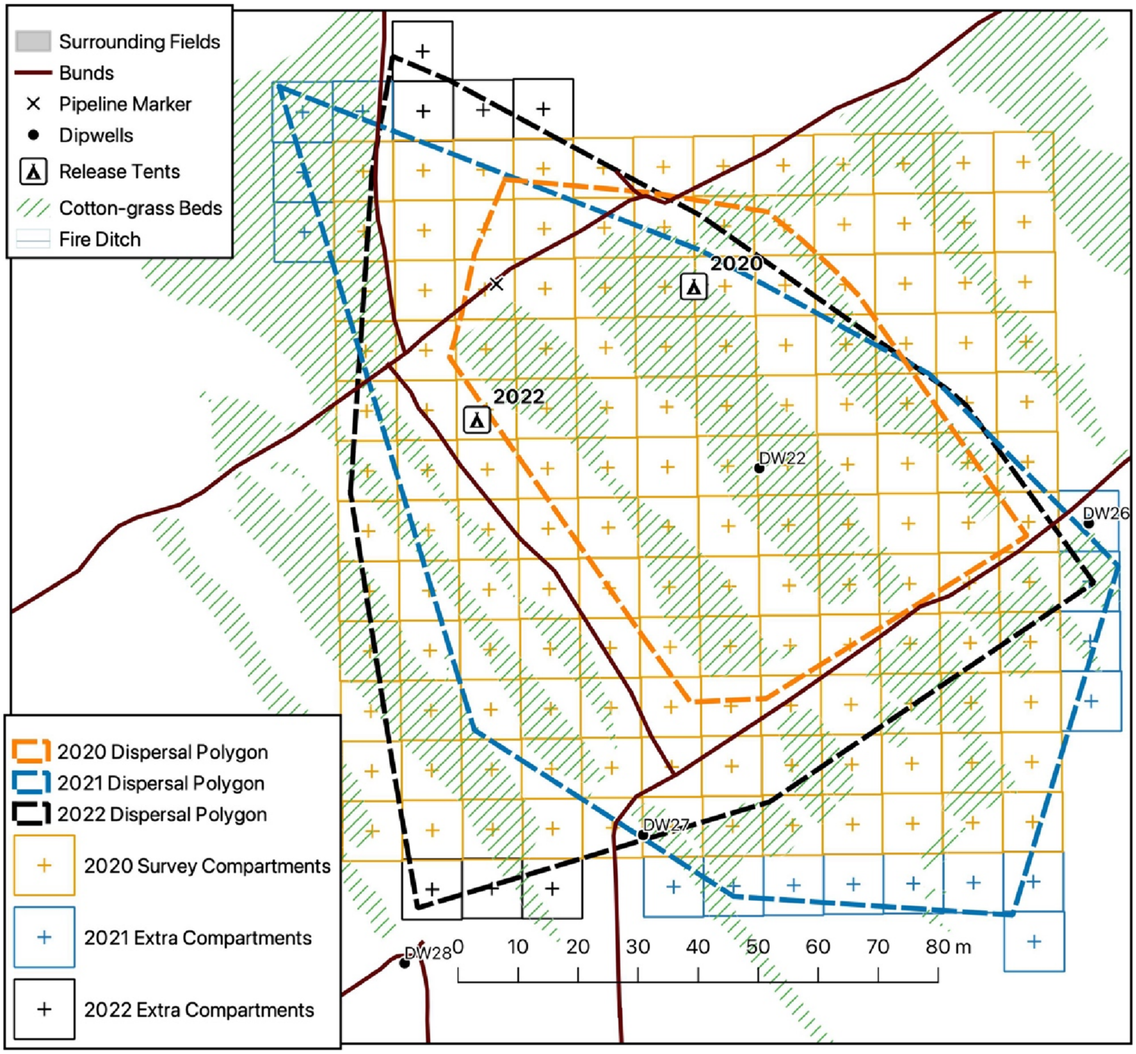


Fig. 3 The environmental survey of the release area. Showing the cotton-grass beds and the 167 survey points and compartments. The dipwells are plastic drainpipes installed in the peat to facilitate water table monitoring

would not change significantly between 2020 and 2022. *Eriophorum vaginatum* is a perennial, non-deciduous sedge and *E. tetralix* is a slow-growing evergreen shrub, creating a stable environment year on year. Overall, a total of 167 quadrats were surveyed.

Biotic and abiotic environmental factors were selected as indicated by the results of previous work (Osborne et al. 2022). At each survey point, percentage cover of *Erica tetralix*, *Eriophorum vaginatum*, *Eriophorum angustifolium*, *Molinia caerulea*, *Sphagnum* mosses (without attempting species level identification) ('Total Sphagnum'), *Calluna vulgaris* (ling heather) and mixed bryophyte carpet (mixed moss and liverwort carpet, excluding *Polytrichum ssp*. and *Sphagna)* ('Mixed Bryophytes') were recorded. The count of *E. vaginatum* tussocks was also recorded; *E. vaginatum* naturally forms a dense tussock with dry leaf litter at the base, an important ovipositioning and overwintering habitat resource. However, florid *Sphagnum* growth uses the tussock as a framework, growing up and amongst the tussock leaves to form a *Sphagnum* hummock and resulting in a 'lawn' of *E. vaginatum* leaves without any tussock structure—hence the utility of recording both *E. vaginatum* percentage cover and tussock count. The location of the quadrat within one of the cotton-grass beds (CGB 1/0) was recorded. Abiotic factors previously identified (Osborne et al. 2022) as discriminatory aspects of peat chemistry were also recorded; electrical conductivity (EC) using a Hanna Instruments low reading conductivity meter HI98311 and oxidation–reduction potential (ORP) using a Hanna Instruments HI98121 combo-meter.

Defining cotton-grass beds

Cotton-grass bed polygons were defined on the ground by walking GPS tracks—the configuration of the cotton-grass beds closely aligns with the microtopography resulting from previous peat cutting shown in Fig. 2. Working in QGIS the cotton-grass beds were overlayed on the grid of compartments (Fig. 3) and the percentage cover of cotton-grass bed ('CGB %') within each of the 167 compartments measured using the QGIS area measurement tool.

Graphical processing

Flight Point data were downloaded from the online Epicollect5 system as a.csv file. The data were cleaned and imported into QGIS (QGIS Development Team 2020) as new delimited text layer. Flight Point properties were set to show a vector field arrow, with the 'length attribute' corresponding to the distance measurement and the 'angle attribute' corresponding to the bearing measurement. Arrow tips could then be overplotted into a new Shapefile layer and coordinate attributes obtained. Flight points directly adjacent to the release tents were excluded from the analysis (Osborne and Coulthard 2022). The number of flight points and presence or absence of flight points in each compartment was noted. The dispersal polygon for each flight season was defined by the convex hull of the most peripheral flight points (Osborne and Coulthard 2022).

Statistical analysis

All data analysis was carried out in R (v.4.0.4) (R Core Team 2021), using R Studio (v.1.4.1106) (RStudio Team 2021).

Environmental assessment

An initial analysis of the biotic and abiotic environmental characteristics of the whole survey release area was undertaken. To investigate the variation in plant community composition between the cotton-grass beds and Molinia ridges, Permutational analysis of variance (PERMANOVA) (Anderson 2014) was performed using the 'adonis' function in the 'vegan' package with a Bray–Curtis dissimilarity distance matrix (Oksanen et al. 2013). Medians, interquartile ranges and maximum values across all 167 quadrats surveyed (Fig. 3) were calculated and differences in individual variables between the cotton-grass beds and Molinia ridges tested using the Wilcoxon rank sum test.

Perching resource preference

Outlier flight points, which lay outside of the combined dispersal polygon for the 2020, 2021 and 2022 flight seasons (Fig. 3, Appendix S1) were removed from the data.

Rests during flights ('rest points') from all three flight seasons were combined for this part of the analysis. Quadrats/compartments from the environmental survey, which lay outside of the combined dispersal polygon for the 2020, 2021 and 2022 flight seasons (Fig. 3) were removed from the data. The Chi-squared (χ^2) test was used to evaluate the statistical significance of the number of observed rest points on each plant species, in relation to the expected number of rest points based on the percentage area cover of plant species given by the environmental survey (Rouquette and Thompson 2007; Chang et al. 2020).

Models predicting *C.tullia* presence

As a preliminary investigation, we generated a density maps in QGIS to visually inspect the distribution of *C. tullia* flight points in relation to environmental factors. Flight Point density isolines representing the relative point density of all the individual flight points over the three years of the study were derived from a heatmap based on a 15 m radius, to combine data across groups of nine adjacent compartments.

These isolines were overlayed on heatmaps, based on a 15 m radius, generated from *Erica tetralix* and *Eriophorum vaginatum* percentage cover—habitat resources identified in previous studies (Dennis and Eales 1997, 1999). We also generated a heatmap from ORP data to differentiate waterlogged, anoxic, regions of the reintroduction area from regions with dryer more oxidised peat.

To examine the relationship between *C. tullia* occurrence within individual compartments and predictor plant species within their respective survey quadrats, generalised linear mixed-effects models (GLMMs) were constructed (Pearce-Higgins and Yalden 2004; Anadón et al. 2018; Greenwood 2018; Post van der Burg et al. 2020). Outlier flight points, which lay outside of the combined dispersal polygon for the 2020, 2021 and 2022 flight seasons (Fig. 3) were removed from the data. The 2020, 2021 and 2022 flight seasons were handled as distinct random variables (1|Flt_Season) to account for repeat sampling in successive years. Environmental predictors from compartments which were confluent with each respective flight season's dispersal polygon were used as fixed variables. Compartments, which lay outside of the dispersal polygons for each of the three flight seasons were removed from the analysis.

A series of GLMMs (Bolker et al. 2009; Harrison et al. 2018) were constructed using the 'glmer' function in the 'lme4' package (Bates et al. 2015), to test the hypothesis that *C. tullia* had a preference for flying over or close to the cotton-grass beds. We constructed four models using CGB 1/0 or CGB % as the fixed variable and either *C. tullia presence* or the number of *C. tullia* flight points as the dependent variable.

A second series of 26 GLMMs were constructed, employing a similar approach to our previous analysis (Osborne et al. 2022), to test the hypothesis that individual plant species predicted butterfly flight points. Because of the correlation between specialist bog plant species within the cotton-grass beds (Appendix S2) these predictors were test for colinearity by estimating the Variance Inflation Factor (VIF) using the 'check_colinearity' function in the 'performance' package (Lüdecke et al. 2021). The best models were selected based on their Akaike Information Criterion corrected for small samples (AICc) (Burnham and Anderson 2002) using the 'model.sel' function in the 'MuMIn' package (Bartoń 2020. The most influential of the fixed variables were determined from the sum of Akaike weights ($\sum \omega i$) using the 'importance' function in the 'MuMIn' package and the average and most significant *p*.values calculated. For the best-performing models we went on to estimate the R^2 attributable to the fixed (predictor) variables (theoretical R^2m) using the 'r.squareGLMM' function in package 'MuMIn'. To further clarify the relative contribution to the model's variation made by individual, highly correlated, predictors (Symonds and Moussalli 2010; Giam and Olden 2016; Lai et al 2022) we estimated the (theoretical) Individual Part R^2 values in the best performing models (IPR^2m) using the 'glmm.hp' function in the 'glmm.hp' package (Lai and Nimon 2023). Individual Part R^2 values were also estimated from the global model (IPR^2g) containing all predictors and interactions—the most accurate method for estimating Individual Part R^2 values for relatively small data sets with a high degree of corellation (Giam and Olden 2016).

Quantifying habitat resource thresholds

Using pooled data from the three flight seasons logistic regression models were constructed for fixed variables which had been identified as the most important habitat resources. We went on to identify inflection points on the curves which represented tipping points in the relationship between butterfly presence and habitat resource abundance.

Ecological thresholds resulting from non-linear population dynamics have been identified and modelled by previous authors (Fahrig 2001; Toms and Lesperance 2003; Ficetola and Denoël 2009; Betts et al. 2010; Toms and Villard 2015); we used logistic regression methods adopted from treatment-response studies (Adam et al. 1954; Haanstra et al. 1985; Dershwitz et al. 1998; Sharpe et al. 2016; Lappi and Luoranen 2018) to identify critical thresholds in the abundance of habitat resources necessary to support a population. The mid-inflection point of the 'lazy-S-shaped' logistic curve ('midpoint') (Goshu and Koya 2013) defined the tipping point between absence and presence, when the abundance of each habitat resource was sufficient to give a 50% probability of supporting a population. The midpoint was straightforward to identify but only gave an indication that the abundance of habitat resource was barely sufficient. We used segmented regression (Muggeo 2003; Toms and Lesperance 2003; Toms and Villard 2015) to identify the statistically and biologically significant break of slope, the inflection point at the top of the logistic curve ('breakpoint') (Passos et al. 2012). This gave an objective estimate of the 'near-optimal' (Gass and Harris 2001) abundance of habitat resource—investing more time and resources in increasing supply further would yield progressively less gain in the probability of maintaining a *C. tullia* population.

The 'segmented' function from the 'segmented' package (Muggeo and Muggeo 2017) was used to locate the breakpoint. Means and standard errors (SE) for habitat resources at the midpoint and breakpoint were calculated using the 'dose.p' function from the 'MASS' package (Ripley et al. 2013), the 95% confidence intervals (CI) at the breakpoint calculated as well as the odds ratios (OR) using the 'or_glm' function in the 'oddsratio' package (Schratz 2020).

Results

After collating the data, a total of 406 flight points, are included in the statistical analysis; 123 flight points across 70 compartments from 2020 (present = 42, absent = 28), 95 flight points across 131 compartments from 2021 (present = 40, absent = 91) and 187 flight points across 126 compartments in 2022 (present = 63, absent = 63). Pooled data across the three flight seasons, 154 compartments within the composite dispersal polygon (present = 82, absent = 72). Eight observations of migrants/outliers distant from this area (Appendix S1) are excluded from the statistical analysis. Additional flight point data is shown in Appendix S3.

Environmental Assessment

The PERMANOVA analysis demonstrates a significant difference in abiotic environmental factors and plant assemblages between the cotton-grass beds and intervening ridges ($R^2 = 0.265$, $p = 0.001$). Cotton-grass beds contain significantly more *E. angustifolium, E. vaginatum* tussocks, *Sphagnum* Cover and *E. tetralix,* and significantly less *M. caerulea* (Table 1). Additionally, the ridges have significantly higher EC and ORP consistent with higher nutrient levels and dryer, more oxidised peat. The wide interquartile ranges result from the heterogeneous nature of the site and the patchy distribution of the vegetation.

Perching resource preferences

In this analysis a total of 406 flight points are included in the analysis. 161 rest points are observed; *M. caerulea (78), E. tetralix (30), E. vaginatum (25), C. vulgaris(24) and E. angustifolium(4).* Of the 30 rest points on *E. tetralix* 14(47%) are on vegetative parts of the shrub, 16(53%) are on inflorescences, assumed to be evidence of nectaring ($\chi^2 = 0.00$, DF = 1, $p = 1.000$). In addition, no nectaring is observed on *Rubus fruticosus* (bramble) near the site boundary, adjacent to the 2020 release tent, and no rest points are observed on bare ground, on the moss layer, or on occasional areas of scrub or *Juncus effusus* (soft rush).

Based on the percentage area cover of the substrate, there are significantly more rest points on *E. tetralix* than expected ($\chi^2 = 26.21$, DF = 1, $p < 0.001$) and significantly more rest points on *E. vaginatum* than expected ($\chi^2 = 4.79$, DF = 1, $p = 0.029$) (Table 2). *Molinia caerulea* is the dominant ground cover plant species (60%) with the largest percentage of observed rest points (48%), however there are significantly fewer rest points on *M. caerulea* than expected ($\chi^2 = 3.84$, DF = 1, $p < 0.050$). There are significantly few rest points on *E. angustifolium* ($\chi^2 = 26.39$, DF = 1, $p = 0.001$).

Models predicting *C. tullia* presence

The density map (Fig. 4A) suggests a correlation between the number of flight points and the abundance of previously identified habitat resources (Appendix S2). This relationship is investigated further by constructing GLMMs. Figure 4B suggests a negative correlation between the number of flight points and dryer regions with a high ORP; in these regions the peat substrate is not waterlogged (and hence is more oxidised), which facilitates *M. caerulea* dominance and negatively correlates with specialist bog vegetation (Appendix S2).

In the first series of GLMMs, four models are constructed to test the hypothesis that *C. tullia* has a preference for flying over or close to the cotton-grass beds all achieve

Table 1 Median and interquartile ranges for environmental factors from 167 quadrats. There is a significant difference between plant assemblages, with the cotton-grass beds, containing significantly more *Erica tetralix, Eriophorum vaginatum, Eriophorum angustifolium* and *Sphagna*

Environmental factor	Within cotton-grass bed median(IQR); maximum	Outside cotton-grass bed Median(IQR); maximum	W statistic	*p*-value
E. tetralix (%)	0.0(0.0–0.5); 23.0	0.0(0.0–0.0); 15.0	2808.5	**$p = 0.002$**
E. vaginatum (%)	5.0(0.0–20.0); 80.0	0.0(0.0–0.0); 33.0	1513.5	**$p < 0.001$**
E.v tussock count	2.0(0.0–6.5); 22.0	0.0(0.0–0.0); 10.0	1673.0	**$p < 0.001$**
Mixed Bryophytes (%)	0.0(0.0–5.0); 68.0	2.0(0.0–5.0); 90.0	3887.5	$p = 0.102$
C. vulgaris (%)	6.0(1.5–14.0); 80.0	4.0(0.0–12.0); 46.0	2865.5	$p = 0.077$
E. angustifolium (%)	30.0(12.0–65.0); 97.0	1.0(0.0–10.0); 90.0	954.0	**$p < 0.001$**
Sphagnum Moss (%)	10.0(1.0–35.0); 100.0	0.0(0.0–0.3); 75.0	1544.5	**$p < 0.001$**
M. caerulea (%)	29.0(9.0–74.5); 100.0	88.5(63.8–96.0); 100.0	5353.0	**$p < 0.001$**
EC (µS/cm)	86.0(72.5–108.5); 210.0	96.0(81.8–129.0); 265.0	4192.0	**$p = 0.011$**
ORP (mV)	216.0(91.0–267.0); 421.0	290.5(169.0–356.5); 577.0	4425.0	**$p < 0.001$**
Number of Quadrats	71	96		

Statistically significant *p*-values highlighted in bold text

Interquartile range (IQR); electrical conductivity (EC); *E. vaginatum (E.v)*; oxidation–reduction potential (ORP); Wilcoxon rank sum test (W).

Table 2 Comparison of ‘observed’ rest points on each plant species with the ‘expected’ number of rest points, based on the percentage area cover of each plant species. Second column; the number of observed rest points on each plant species / the number of observed rest points not on the plant species, and the percentage of rests on each plant species. Third column; the number of expected rest points on each plant species / the number of expected rest points not on the plant species, and the percentage of rest points on each plant species

Substrate	Observe rests during flights	Expected rests based on plant Sp. area cover	χ^2	DF	*p*-value
Molinia caerulea	78 / 83 (48.45%)	96.51 / 64.49 (59.95%)	3.84	1	**$p=0.050$**
Erica tetralix	30 / 131 (18.63%)	1.65 / 159.35 (1.02%)	26.21	1	**$p<0.001$**
Eriophorum vaginatum	25 / 136 (15.53%)	11.54 / 149.46 (7.17%)	4.79	1	**$p=0.029$**
Calluna vulgaris	24 / 137 (14.91%)	16.18 / 144.82 (10.05%)	1.32	1	$p=0.250$
Eriophorum angustifolium	4 / 157 (2.48%)	35.12 / 125.88 (21.81%)	26.39	1	**$p<0.001$**

Statistically significant *p*-values highlighted in bold text

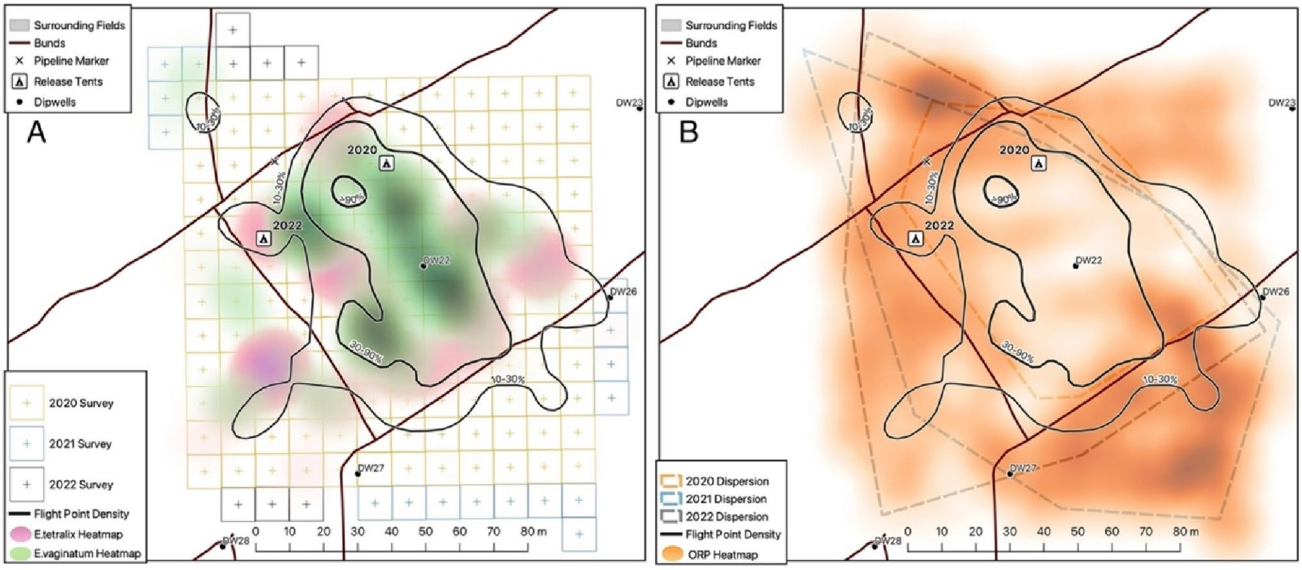
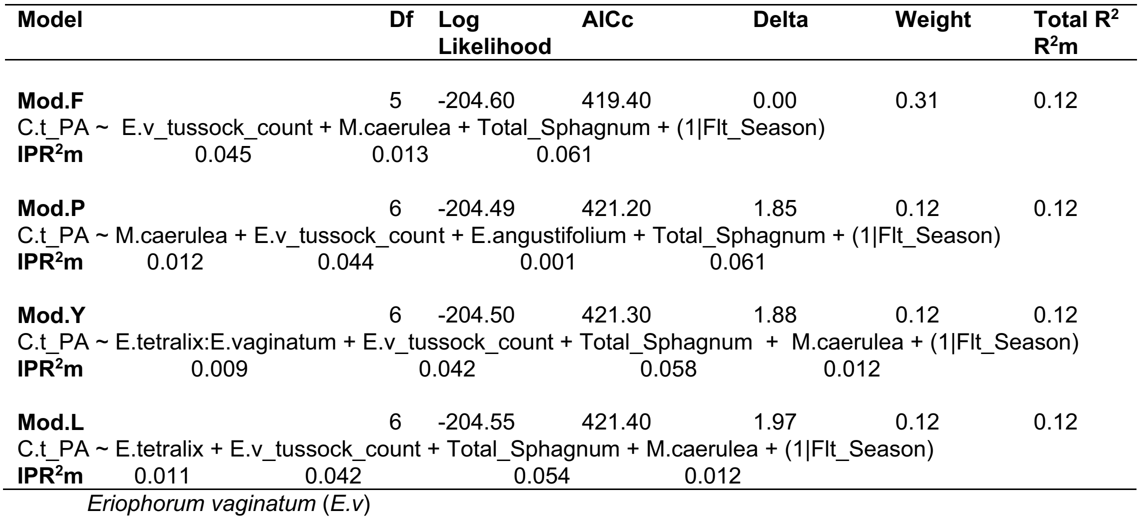


Fig. 4 Density maps generated in QGIS, showing the release area, survey points / compartments and dispersal polygons with the relationship between *Coenonympha tullia* flight points and habitat resources (**A**) and oxidation–reduction potential (**B**)

statistical significance. In the best-performing model, CGB % significantly predicts *C. tullia* presence (AIC = 430.4, df.resid = 324.0, $p < 0.001$).

In the investigation of specific environmental predictors, preliminary investigations showed that ‘binomial’ family models using *C. tullia* presence as the dependent variable were more reliable (converging consistently to yield good quality models, with lower AICc values) than Poisson family models using the count of *C. tullia* flight points. Hence binomial (logistic) models are used in subsequent stages of the analysis. In the second series of GLMMs, 26 models are constructed to test the hypothesis that individual plant species predict *C. tullia* presence. No problems with collinearity are identified from estimates of the VIF. The best four models, with the lowest corrected Akaike information criterion (AICc) all contain statistically significant predictor variables (Table 3). The multimodel inference approach identifies the most important predictor variables associated with *C. tullia* presence (Table 4). Total *Sphagnum* ($\sum \omega i = 0.98$), *E. vaginatum* tussock count ($\sum \omega i = 0.90$), *E. tetralix* ($\sum \omega i = 0.28$), *E. vaginatum* ($\sum \omega i = 0.13$) and the interaction of *E.tetralix:E.vaginatum* ($\sum \omega i = 0.22$), all showing significant *p*.values in the best models. The four best performing models have similar R^2m values attributable to their fixed predictor variables and Individual Part R^2 (IPR^2m) values for predictors in these models are shown in Table 3. *M. caerulea* ($\sum \omega i = 0.67$) is identified as an important negative predictor, appearing in all four of the best models, but not attaining statistical significance in any model. *M. caerulea*’s strength is inconsistent, having a much lower Individual Part R^2 (IPR^2g = 7.52%) (Table 4.) than would be expected from its high Sum of Weights—this probably reflects its role in supporting models and other predictors, without in itself predicting *C. tullia* presence. *E. angustifolium* ($\sum \mathrm{\omega i} = 0.13$)

Table 3 The best four models, having the lowest Akaike Information Criterion corrected for small samples (AICc) scores, predicting the presence of *Coenonympha tullia* from the multimodel inference approach and the Total R^2 (R^{2}m) and Individual Part R^2 (IPR^{2}m) for each model



Model	Df	Log Likelihood	AICc	Delta	Weight	Total R^2 R^{2}m
Mod.F	5	-204.60	419.40	0.00	0.31	0.12
C.t_PA ~ E.v_tussock_count + M.caerulea + Total_Sphagnum + (1|Flt_Season)						
IPR^{2}m 0.045 0.013 0.061						
Mod.P	6	-204.49	421.20	1.85	0.12	0.12
C.t_PA ~ M.caerulea + E.v_tussock_count + E.angustifolium + Total_Sphagnum + (1|Flt_Season)						
IPR^{2}m 0.012 0.044 0.001 0.061						
Mod.Y	6	-204.50	421.30	1.88	0.12	0.12
C.t_PA ~ E.tetralix:E.vaginatum + E.v_tussock_count + Total_Sphagnum + M.caerulea + (1|Flt_Season)						
IPR^{2}m 0.009 0.042 0.058 0.012						
Mod.L	6	-204.55	421.40	1.97	0.12	0.12
C.t_PA ~ E.tetralix + E.v_tussock_count + Total_Sphagnum + M.caerulea + (1|Flt_Season)						
IPR^{2}m 0.011 0.042 0.054 0.012						

Eriophorum vaginatum (*E.v*)

Table 4 The predictors of *Coenonympha tullia* presence, ordered by descending sum of weights ($\sum \omega i$)

Fixed effect	Sum of Weights ($\sum \omega i$)	Number of Models	Average *p*-value	Most significant *p*-value	Individual % part R^2 (IPR^{2}g) (%)
Total *Sphagnum*	0.98	11	**$p=0.005$**	**$p<0.001$**	35.29
E.v tussock count	0.90	11	**$p=0.023$**	**$p<0.001$**	18.42
M. caerulea	0.67	7	$p=0.310$	$p=0.091$	7.51
E. tetralix	0.28	11	$p=0.386$	**$p=0.025$**	6.27
E.tetralix:E.vaginatum	0.22	5	$p=0.506$	**$p=0.014$**	4.02
E. vaginatum	0.13	9	$p=0.096$	**$p=0.003$**	11.15
E. angustifolium	0.12	9	$p=0.651$	$p=0.426$	0.85
C. vulgaris	0.03	6	$p=0.365$	$p=0.312$	3.25
E.vaginatum:E.v tussock count	0.02	5	**$p=0.038$**	**$p=0.002$**	8.59
Mixed Bryophytes	<0.01	5	$p=0.851$	$p=0.666$	0.46
E.tetralix:E.v tussock count	<0.01	5	$p=0.298$	**$p=0.014$**	4.18

Statistically significant *p*-values highlighted in bold text

has a low level of importance, does not achieve statistical significance in any models and has an Individual Part R^2 under 1% (IPR^{2}g = 0.85%). The Individual Part R^2 values of other predictors broadly agree with the estimates of predictor strength; Total *Sphagnum* (IPR^{2}g = 35.29%) is the strongest predictor, *E.vaginatum* tussock count (IPR^{2}g = 18.42%) is a stronger predictor that *E. vaginatum* (IPR^{2}g = 11.15%) and *E. tetralix* (IPR^{2}g = 6.27%). Of the interaction terms *E.vaginatum:E.v* _tussock_count (IPR^{2}g = 8.59%) is the strongest by this method.

Models quantifying the response to habitat resource thresholds

Logistic regression models for the most important habitat resources are shown in Fig. 5A and C; *E. vaginatum* tussock count significantly predicts *C. tullia* presence (AIC = 434.60, $p<0.001$), OR = 3.79, CI = 2.03–7.52 and *E. tetralix* percentage cover significantly predicts *C. tullia* presence (AIC = 444.65, $p=0.007$), OR = 3.80, CI = 1.52–10.64. The odds ratios at the breakpoint of 3.79 for *E. vaginatum* tussock count and 3.80 for *E. tetralix* percentage cover quantifies the distinction in habitat resource abundance between compartments with *C. tullia* presence or absence—*C. tullia* presence is associated with almost four times the abundance of important habitat resources.

Segmented regression identifies statistically and biologically significant inflection points in the relationship between habitat resource and the probability of *C. tullia* population presence in Fig. 5B and D.

The results of the breakpoint analysis (Table 5) give quantitative estimates for the resource abundance at the midpoint

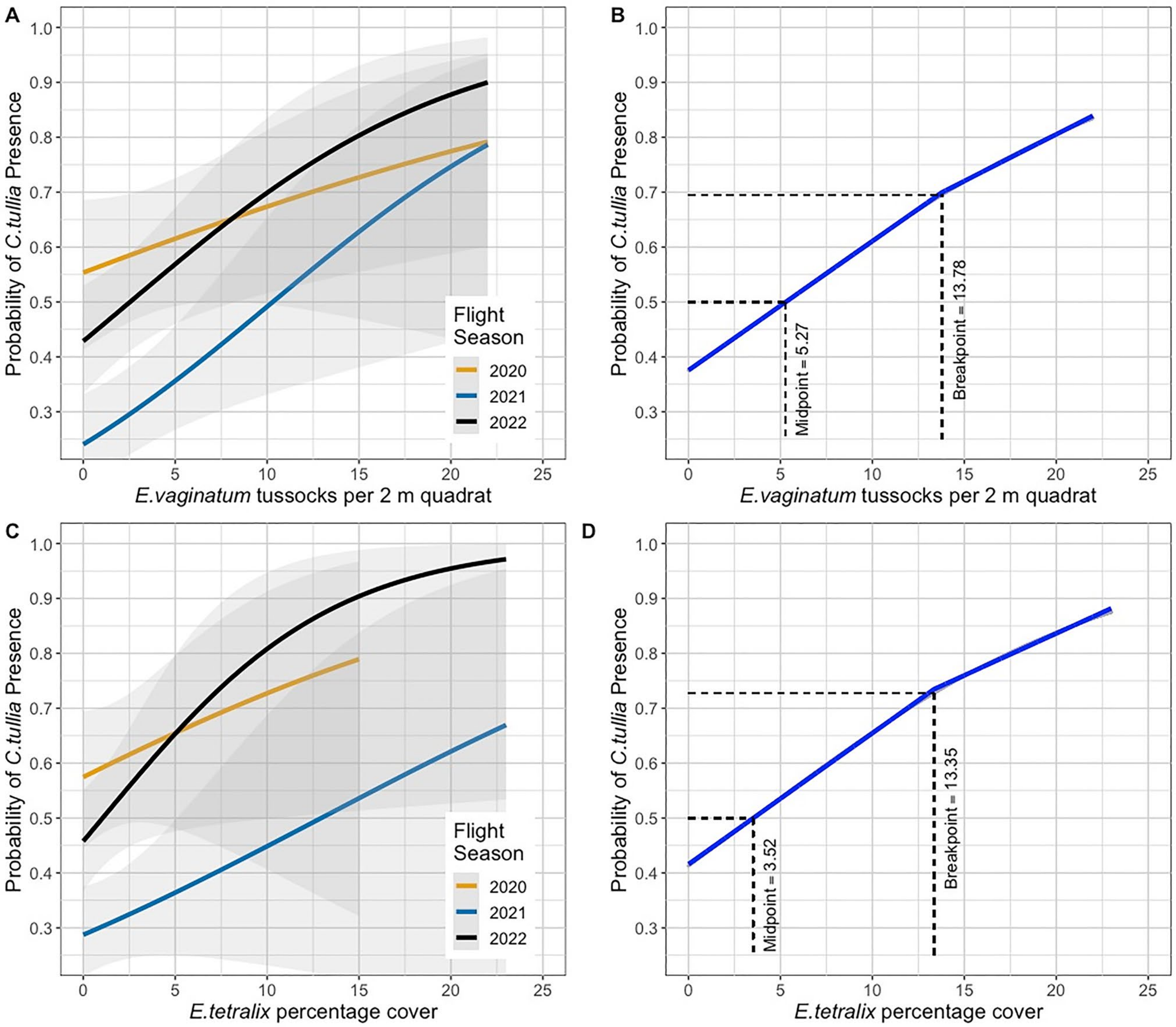


Fig. 5 Logistic curves for each season (**A**, **C**) and segmented regression lines (**B**, **D**; pooled data for all three seasons) represent the probability of *C. tullia* presence as a function of the amount of the two main habitat resources (*Eriophorum vaginatum* tussock count, *Erica tetralix* percentage cover). The midpoint defines the abundance of both plant species that is sufficient for a 50% probability of *C. tullia* occurrence. The breakpoint determines the optimal abundance of both resources

Table 5 Calculated values for the most important habitat resources predicting *Coenonympha tullia* presence at the midpoint and breakpoint

Habitat resource	Midpoint ± SE	Breakpoint ± SE	95% CI of breakpoint
E.v tussock count (per 2 m quadrat)	5.27 ± 1.35	13.78 ± 3.01	7.87–19.69
E. tetralix (% cover)	3.52 ± 1.43	13.35 ± 4.64	4.25–22.88

SE standard error; *CI* confidence interval; *E.v Eriophorum vaginatum*

and breakpoint of the logistic curves; *E. vaginatum* tussock count of 5 and 14 (95% CI 8–20) tussocks per 2 m × 2 m quadrat, and 3.52% and 13.35% (95% CI 4.25–22.88) *E. tetralix* cover.

Discussion

This study reports the fine-scale habitat use of a colonial butterfly during the first three years of a species reintroduction programme onto Astley Moss (SSSI), a peatland restoration site within Chat Moss, Greater Manchester UK. *C. tullia* displayed a strong preference for *E. vaginatum* tussocks and *E. tetralix.* By adopting statistical methods developed for analysing treatment-response relationships we were able to make quantitative estimates of the near-optimal abundance of these critical habitat resources.

We have defined the abiotic and biotic environmental characteristics of the release area confirming statistically significant differences in the plant assemblages within and outside of the 'cotton-grass beds'—the shallow troughs resulting from previous peat cutting. The peat chemistry is more favourable to bog plants in the cotton-grass beds, being less oxidised and having lower nutrient levels; there is significantly more *Sphagnum*, less *M. caerulea* (a marker of poor conditions of bog restoration) (Thomas 2015) and significantly more *Eriophorum sp.* and *E. tetralix*—the semi-natural, restored habitat resembling an 'M18 *Erica tetralix—Sphagnum papillosum* raised and blanket mire community' (Rodwell et al. 2000).

When moving about their habitat *C. tullia* are significantly associated with *E. vaginatum* and *E. tetralix.* There was a greater association with regions that contain discernable *E. vaginatum* tussock than regions with lawns of *E. vaginatum*, probably reflecting the importance of tussocks for ovipositioning and larval overwintering, in addition to being the larval food plant. The analysis of R^2m values for best-performing models and Individual Part R^2 for predictors was a useful addition to our analysis, providing an independent method for evaluating the strength of mixed models beyond AICc, Sum of Weights and their p values, whilst dealing with the problem of correlated predictor variables (Symonds and Moussalli 2010; Giam and Olden 2016; Lai et al 2022). Additionally, the calculation of IPR^2g is based on the global modal, hence eliminating any subjective bias in model selection. Even for the best performing models the R^2m is only 0.12, indicating that a large part of the variation in the model is accounted for by additional factors. Flight points may be related to exploratory or patrolling behaviors, not closely correlated with habitat resources—short flights were observed moving away from the main part of the reintroduction area, then rapidly returning to the more populated central area (Appendix S3). The hotspot in butterfly numbers shown in Fig. 4a suggests that colonial behavior itself may be a predictor of butterfly flight point numbers—this would explain the poor performance of models using the number of *C. tullia* flight points as the response variable. Pheromones have a role in coordinating lepidopteran social behavior and sex pheromone receptors have been identified in 10 lepidopteran families, including in the Nymphalidae (Yang et al 2022), suggesting a plausible explanation for this observation.

Sphagnum moss cover is also a strong predictor of *C. tullia* presence; whilst not a direct habitat resource *Sphagna* are the peatland's keystone species (van Breemen 1995) and form a large part of the ground cover, controlling the local environment, with specialist bog plants *E. vaginatum* and *E. tetralix* co-existing with *Sphagnum* within the 'M18' community (Rodwell et al. 2000). As noted by previous authors (Čelik 2018) microtopography is relevant to *C.tullia* habitat quality, with *M. caerulea* forming a dense sward in raised, dryer areas (Fig. 4b) which inhibit the growth of specialist bog plant species. *Molinia* tussock is a marker of poor water table management and nutrient enrichment (Anderson 2015; Thomas 2015); ongoing work building low peat dams (bunds) is improving the water tightness of the site and raising water levels, hummocks of *Sphagnum* moss (mean cover 4.8%) within the *Molina* dominated area confirming gradual paludification. *Coenonympha tullia* was not associated with *E. angustifolium,* which suggests that areas of open water with *E. angustifolium* resembling 'M3 *E. angustifolium* bog pool community' (Rodwell et al. 2000) are not likely to be utilised for ovipositioning, with consequent high levels of mortality to exposed overwintering larvae.

The *C. tullia* reintroduction population continued to maintain a tight colony structure, over the three years of this study in agreement with previous authors (Wainwright 2005; Wainwright and Ellis, accessed 29/12/2021). In common with other colony-forming butterflies (Anthes et al. 2003; Thomas 2016) this behavior is likely to be driven by the close association with the specialist habitat niche containing the ovipositioning and larval food plant resource, *E. vaginatum* tussocks, as well as the major nectar resource, *E. tetralix* (Fig. 4). These habitat resources are themselves located within the wide cotton-grass beds that form the main part of the reintroduction area and result from the microtopography of the nature reserve (Fig. 2). This heterogeneous microtopography facilitated our study by producing a field of clearly differentiated, alternating, strips of rich habitat and poor-quality matrix across which butterfly movements could be measured and compared. Outside of the reintroduction area there is a marked deterioration in habitat quality as cotton-grass beds give way to Molinia dominated matrix with occasional, isolated habitat resource plants. This is probably containing the colony expansion (Appendix S3), although there is potential to extend the colony's current limits westward across the fire ditch and northward into a newly restored region (Figs. 3 and 4). However, there are other reasonable habitat patches at a few hundred meters distance from the current reintroduction area, within the footprint of the outlier flight points (Appendix S1).

There have been very few observations quantifying *C. tullia*'s migration potential (Melling 1984; Wainwright 2005), however a total of eight flights extending several hundred meters beyond the colony's home range are noted—a surprisingly large number of observations considering the relatively large area involved (Appendix S1), and consequent dilution of surveying effort compared with the release area. The ability to change movement pattern from sedentary within habitat patch to more active movement, crossing large distances of inhospitable matrix (Schultz 1998; Schtickzelle et al. 2007) should facilitate the establishment of a metapopulation structure across the reserve in future years.

Breakpoint analysis of the logistic curves yields estimates of the near-optimal abundance of the most important habitat resources. Fourteen *E. vaginatum* tussocks per 2 m quadrat was associated with a 69% chance of C. tullia presence and 13.4% *E. tetralix* cover was associated with a 73% chance of *C. tullia* presence. The confidence intervals are relatively wide, however the estimate gives a practical indication of the aspirational abundance of these habitat resources during the ecosystem restoration—ongoing data gathering during future years of the programme will increase the level of precision of these estimates. Our analysis of logistic curves is based on the well-established use of treatment-response curves (Adam et al. 1954); critical points on the curve have traditionally been defined arbitrarily with 'ED50' (Dershwitz et al. 1998) or 'ED90' (Sharpe et al. 2016). The use of segmented regression defines a statistically and biologically significant upper inflection point (Passos et al. 2012) on the logistic curve, which represents an objective estimate of the near-optimal requirement for habitat resource provision—this is an improvement on the traditional approach of arbitrarily choosing a 90% cutoff, which results in an overestimate of the habitat resource requirement. This analysis is straightforward to conduct within the R environment and would assist practitioners in ensuring adequate habitat resource provision, prior to species translocations (Example R code; https://doi.org/10.23634/MMU.00633943) (Osborne et al. 2024).

This study's results are guiding ongoing habitat restoration on Astley Moss and other potential reintroduction sites within the Chat Moss restoration area; helping to balance time, logistical and financial constraints by advising at what stage nature reserves are suitable for a *C. tullia* reintroduction attempt. In suitable areas *E. vaginatum* forms dense lawns with the potential to create habitat islands and metapopulations, sitting well with *C. tullia*'s colonial nature. *E. tetralix* plug plants establish reliably when planted into *Sphagnum* hummocks within *E. vaginatum* patches, although access to these boggy areas can be challenging. Within the current reintroduction area, there is ongoing inter-planting with additional *E. tetralix* in order to optimize the nectar supply. *Calluna vulgaris* flowers from July to September (Miller 1979), too late in the season to provide a nectar source for *C. tullia*. However, *Narthecium ossifragum* (bog asphodel) has been identified as a secondary nectar source (Wainwright 2005), with recent plant translocations onto Astley Moss (Osborne 2022) and nearby Little Woolden Moss (Hartley 2023).

This study is based on observation of flight points, whilst avoiding disturbing the butterfly's behavior as much as possible—*C. tullia* has proved to be highly avoidant of being approached. Additionally, we avoided repeatedly walking across the delicate regenerating bog vegetation in the cotton-grass beds, damaging this protected site—hence the transect is restricted to bunds and tough *Molinia* tussock. Adult butterfly numbers have remained low throughout the three years of this study, possibly reflecting the limited area of high-quality habitat, or lack of genetic fitness. Because of these constraints close observations of butterfly behavior and sex were therefore limited. The underlying assumption of the study is that flight points indicate a preference for a specific environmental niche or habitat resource, our analysis supports this view at the spatial scales of the cotton-grass beds, regions within the cotton-grass beds containing greater abundance of relevant plant species and individual plants used for perching. This is in agreement with previous research which has identified resource quality as the most important variable in *C. tullia* patch occupancy (Dennis and Eales 1997, 1999; Dennis et al. 2006).

Other factors which are also likely to be relevant and need to be investigated in future work include the functional relationship between the two important plant species, which are related to distinct life-cycle stages, suggested by the moderate strength and statistical significance of interaction terms in the multimodel analysis. The relevance of the patchy distribution of *E. tetralix* (Table 1) which results from varying patterns of planting, survival and growth of plug plants merits further investigation. It would also be useful to monitor butterfly behaviour at rest points more closely; observations of nectaring, ovipositioning, eggs and larvae would confirm that areas of preference (present) are also areas of high performance and habitat value (Gaillard et al. 2010).

The historical context of *C. tullia*'s local extinction and this species reintroduction programme is significant. The onset of the industrial revolution in south Lancashire 300 years ago and the destruction of the vast wilderness area which lay on the outskirts of Manchester until the early part of the nineteenth century; subsequently, over the past 40 years, the determined efforts to restore lowland raised bog on Chat Moss. The return of the Manchester Argus was a significant milestone in this decades long ecosystem restoration, attracting national media attention (Weston 2020). Future climate change is a threat to peatlands and increased evaporative water loss is an obvious threat during warmer summers (Berry and Butts 2002), although increased seasonal rainfall should mitigate this problem. Good quality restoration work to prevent the outflow of groundwater from the peatland is vital, in order to engineer a stable microclimate (Osborne et al. 2021) and refugia for bog species. Both *C. tullia* and *Narthecium ossifragum* were assessed to be safe translocation candidates by Bellis et al. (2021).

Peatland sequesters and stores nationally (Office of National Statistics 2019; IUCN UK Peatland Programme 2021) and internationally (Yu 2011; Crump 2017; Parmesan et al. 2022) important quantities of atmospheric CO_2 making conservation of the natural capital of this unique habitat an increasingly high priority. Other species benefit from the reintroduction programme, including a variety of pollinating insects taking advantage of the new nectar supply—for example *Ochlodes sylvanus* (large skipper) which uses abundant *M. caerulea* as a larval food plant (Butterfly Conservation accessed 15/1/2023) has become numerous, flying towards the end of the *C. tullia* flight season. Small avian predators *Anthus pratensis* (meadow pipit) (Melling 1987) and *Emberiza schoeniclus* (reed bunting), themselves amber-listed species (Stanbury et al. 2021), are notable within the release area whilst *C. tullia* is flying, with evidence of breeding pairs and fledging young.

Conclusions

This study has enabled us to interpret fine-scale butterfly movements to understand how *C. tullia* uses its habitat and make quantitative estimates of the species' important environmental factors and habitat resources. Taking a quantitative approach to setting goals for habitat restoration prior to future species reintroductions should ensure that a near-optimal abundance of relevant habitat resources is available for the translocated species, increasing the chances of reintroduced populations thriving, and reintroduction programmes achieving long-term success.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10841-024-00589-w.

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Author contributions AO and EC conceived the ideas and designed methodology; AO collected the data; AO analysed the data; AO led the writing of the manuscript. EC, SG and SC contributed critically to the drafts and gave final approval for publication.

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Data availability Data and R scripts are available from Manchester Metropolitan University e-space; http://doi.org/https://doi.org/10.23634/MMU.00633943 (Osborne et al. 2024).

Declarations

Competing interests The authors declare no competing interests.

Ethical approval EthOS Reference Number: 25585. Natural England Consent Reference: 1904211101BL.

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