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RESEARCH ARTICLE

Bringing back the Manchester Argus *Coenonympha tullia* ssp. *davus* (Fabricius, 1777): Quantifying the habitat resource requirements to inform the successful reintroduction of a specialist peatland butterfly

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Abstract

1. The period 2021–2030 has been designated the UN decade of ecosystem restoration. A landscape-scale peatland restoration project is being undertaken on Chat Moss, Greater Manchester, UK, with conservation translocations an important component of this work. The Manchester Argus *Coenonympha tullia* ssp. *davus*, a specialist butterfly of lowland raised bogs in the northwest of England, UK is under threat due to severe habitat loss and degradation. A species reintroduction was planned for spring 2020.
2. This study aimed to quantify the resource thresholds for *C. tullia*, in order to assess potential risks for the project. Thirteen peatland habitat patches with either recent historic or current *C. tullia* populations were surveyed for biotic and abiotic factors based on previous qualitative research on the species' requirements.
3. Percentage cover of two habitat resources was found to be the strongest predictor in models of *C. tullia* presence: cross-leaved heath *Erica tetralix* and hair's-tail cotton-sedge *Eriophorum vaginatum*.
4. Critical inflection points on logistic regression curves were used to make quantitative estimates of the minimum requirement of each resource for population survival and the near-optimum abundance of each resource.
5. The results of this study improve our understanding of *C. tullia*'s ecology and the restoration of peatlands for its reintroduction. Additionally, the method has wider utility for the quantitative assessment of habitat readiness before attempting species reintroductions.

KEYWORDS
Coenonympha tullia, large heath butterfly, lowland raised bog, peatland restoration, resource-based habitat management

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1 | INTRODUCTION

We are currently witnessing what has been described as the Earth's sixth mass extinction event (Butchart et al., 2010; Ceballos et al., 2017). The widespread decline in insect populations has been well documented (Biesmeijer et al., 2006; Hallmann et al., 2017), although the exact scale of the loss is debated (Thomas et al., 2019; van Klink et al., 2020). Loss of pollinating insects (Potts et al., 2010), together with the ecosystem services they provide (Goulson, 2019), has been highlighted as a specific threat to human economies and food production (Losey & Vaughan, 2006; Melathopoulos et al., 2015). There have been significant reductions in numerous Lepidoptera populations worldwide (Thomas, 2016), with around two thirds of species decreasing in abundance across the United Kingdom (Fox et al., 2015; Thomas, 2005). Cited highly among the drivers for these declines are habitat loss and degradation, pollution and climate change (Bubová et al., 2015; Fox et al., 2015).

Peatlands provide important ecosystem services (Bonn et al., 2016), specialist habitat, water storage and filtration and carbon sequestration (Freeman et al., 2012; Hawken, 2018), as well as being an educational resource (Lageard et al., 2017). Carbon sequestration and storage have become a global priority (U.S. Global Change Research Program, 2018), with sub-arctic latitudes containing 90% of total global peatland carbon stores (Yu, 2011).

The large heath butterfly *Coenonympha tullia* has a Holoarctic distribution with 31 described subspecies (Melling, 1987), which are all wetland/peatland specialists. *Coenonympha tullia* is in international decline, primarily due to habitat degradation and destruction (Weking et al., 2013). The butterfly is listed on the IUCN Red List as 'Vulnerable and Declining in Europe' (van Swaay et al., 2010) and as highly threatened, requiring action, under the UK Biodiversity Action Plan (UK BAP) (JNCC, 2010). In Britain, *C. tullia* requires a specialist habitat, found particularly on high-quality lowland bog (Bourn & Warren, 1997). Lowland raised bog is a UK BAP Priority Habitat, of which only 6% remains intact and in England only 500 ha (1.3%) remains in good condition (Maddock, 2008), as a result of drainage, agricultural use and peat extraction.

Coenonympha tullia ssp. *davus* (Fabricius, 1777, p. 259) was first described in Britain on the Manchester mosslands by (Lewin, 1795, p. 50), and became known locally as the Manchester Argus, ranging across the northwest of England between Shropshire and south Cumbria (Melling, 1987) (Figure 1). It is the most threatened of the British subspecies (Bourn & Warren, 1997), with numerous local population losses (Melling, 1987), including extirpation from the Manchester mosslands due to anthropogenic habitat destruction on a landscape scale. Historically, Chat Moss consisted of 35 square miles of impenetrable wilderness (Defoe, 1724–1727); confluent peat domes closely related to other peatlands across the Mersey Valley (Bragg et al., 1984; Hall et al., 1995), now converted to agriculture and urban development.

Due to its prominence, *C. tullia* has been identified as a target species for reintroduction across a suite of peatland nature reserves, with one successful reintroduction onto Heysham Moss, Lancashire in 2013 (BIAZA, 2017). Natural recolonization is unlikely because of *C. tullia*'s poor dispersal ability (Melling, 1984; Wainwright, 2005), and the large distances between suitable habitat remnants (Maddock, 2008): approximately 80 km to the nearest extant population (Figure 1). *Coenonympha tullia* has become a flagship species for the restoration of bog habitats (Lancashire Wildlife Trust, 2019) and therefore has wider relevance for landscape-scale conservation efforts (Bonn et al., 2016; Vasander et al., 2003). U.K. peatlands provide significant natural capital (Ashby et al., 2021; Rouquette et al., 2021) and restoration has been shown to be a cost-effective measure (Moxey & Moran, 2014).

Climate change has, so far, had little impact on *C. tullia* habitat, although this is predicted to become more significant in future decades (Franco et al., 2006). In a recent study using species distribution modelling, Bellis et al. (2021) concluded that predicted climate change scenarios would have only moderate impact on the future viability of *C. tullia* species reintroductions onto the Manchester mosslands.

Species reintroductions have become an established part of conservation practice since the 1970s; however, the chances of success are low without high habitat quality (Griffith et al., 1989). More recent reviews reiterate that species reintroductions are frequently unsuccessful, necesitating more fundamental research (Armstrong & Seddon, 2008; Seddon et al., 2007). A recent meta-analysis of insect translocations found that 52% reported a successful outcome, although only 46% were followed up for 10 years, and underreporting of failed attempts appeared to be likely (Bellis et al., 2019). The IUCN Species Reintroduction Guidelines state the need for a clear understanding of a species' biotic and abiotic habitat requirements, evidence-based decision-making and ongoing monitoring and management adjustment in the light of new evidence (IUCN, 2013). Information from the target species or closely related species can be used to help construct models to inform decision-making and restoration management.

Habitat requirements can be defined using a functional framework taking account of the resources, consumables and utilities needed in different stages of a species' life cycle (Dennis et al., 2003). The habitat resources for the majority of Lepidoptera are nutritional resources for each life cycle stage (O'Brien et al., 2004; Tigreros, 2013); shelter, overwintering sites and suitable substrate for ovipositioning and resting (Dennis et al., 2003). For species with complex life cycles such as Lepidoptera, habitat is therefore defined by the intersection and union of these resources (Dennis et al., 2003). The role of *Sphagnum* hummocks in providing buffering of temperature and humidity for *Boloria aquilonaris* butterfly larvae, especially in the face of climate warming, has also been highlighted (Turlure et al., 2010).

In Britain, the tussock forming hair's-tail cotton-sedge *Eriophorum vaginatum* has been identified as *C. tullia*'s primary larval food plant (Dennis & Eales, 1997, 1999; Melling, 1987). Common cotton-sedge *Eriophorum angustifolium* is noted as a possible alternative food resource; however, few observations have been made of the species using this food plant (Melling, 1984; Wainwright, 2005). Additionally, winter flooding is known to have a marked effect on larval mortality rates (Joy & Pullin, 1997). As such, tussocks provide safe overwintering habitat, permitting larvae to climb up above high water levels (Joy & Pullin, 1999). The density of *E. vaginatum* tussocks has been identified as a limiting factor in the local distribution of adult *C. tullia*



FIGURE 1 Map of habitat 'Patches' on peatland nature reserves in the northwest of England, UK, generated in QGIS. Patches are classified for Presence or Absence of *Coenonympha tullia* ssp. *davus*. Elevation above sea level is also shown. Reserves are low lying and mostly situated near sea level on the coastal plain between Liverpool and Lancaster. The five Absent Patches are on peatland restoration sites, remnants of an extensive area of closely related mires across Chat Moss and the Mersey valley

(Joy, 1991). Ovipositioning has been observed in the dry leaf litter below *E. vaginatum* tussocks (Melling, 1987; Wainwright, 2005). Cross-leaved heath *Erica tetralix* is predictive of *C. tullia* presence (Dennis & Eales, 1997; Dennis & Eales, 1999), and has been observed to be *C. tullia*'s most commonly visited nectar resource (Wainwright, 2005).

Dennis and Eales (1997, 1999) showed that site occupancy is predicted with 91% accuracy by the presence of near confluent cover of *E. vaginatum* tussocks and *E. tetralix*, although site isolation and patch size were shown not to be strongly predictive of site occupancy. These findings are in agreement with Bourn and Warren (1997), who state that patches as small as 1 ha are adequate to sustain a *C. tullia* population. Specific minimum habitat resource requirements have yet to be determined for this species, something which is useful when carrying out restoration projects in preparation for reintroductions.

The aim of this study was to quantify *C. tullia*'s specific habitat resource requirements ('Habitat Resources'), to inform decisions regarding the timing of proposed species reintroductions onto a network of peatland nature reserves, at various stages of restoration.

The objectives were as follows:

1a) Identify the biotic and abiotic environmental characteristics of habitats where *C. tullia* is present or absent.
1b) Determine if the presence or absence of *C. tullia* can be predicted by modelling using these environmental variables.
2) Use breakpoint analysis to identify minimum and 'near-optimal' habitat resource levels and inform ongoing reintroductions.

2 | MATERIALS AND METHODS

We surveyed 12 peatland nature reserves across the northwest of England (map in Figure 1) (QGIS Development Team, 2020), with relevant permissions from site managers. Habitat patches ('Patches') of *Sphagnum* bog, potentially viable *C. tullia* habitat, were identified based on a priori site knowledge. These 'Patches' were usually well-defined, limited in size to a few hectares, with the vegetation type rapidly transitioning from *Sphagnum* bog to a mosaic of other habitats, typically dense purple moor-grass *Molinia caerulea* tussock or scrub.

Patches were classified as 'Present' or 'Absent' based on reserve managers' knowledge of *C. tullia* presence or absence (Wildlife Trusts and Natural England, unpublished data). One nature reserve contained two Patches, both with known butterfly populations, separated by 1 km of inhospitable *Molinia* tussock; these were classified as separate Patches because this is near the likely limit of *C. tullia*'s dispersal ability (Melling, 1984; Wainwright, 2005); hence, these Patches are likely to be functioning as distinct metapopulations.

Thirteen Patches with established *C. tullia* presence ($n = 8$) versus absence ($n = 5$) were included in the analysis. The Absent Patches were situated on a suite of peatland restoration sites to the west of Manchester, with no observation of *C. tullia* presence despite long-term ecological management (unpublished data). As described previously, these nature reserves would originally have formed part of a landscape of closely related peat domes, with historically documented *C. tullia* presence (Lewin, 1795, p. 50). This landscape has been changed beyond

recognition over the centuries of the industrial revolution through into the modern age, resulting in habitat destruction and extirpation of *C. tullia* populations, probably between 100 and 200 years ago (although these losses are undocumented). The peatland restoration sites vary considerably in character (Appendix 1), are currently in poor condition and are at various stages of a decades long process of ecosystem restoration (Osborne et al., 2021).

Data collection took place between July 2018 and July 2019. Measurements of biotic and abiotic environmental factors were recorded. Individual Patches were surveyed on one occasion using a random walk technique, ranging across but remaining within the *Sphagnum* bog habitat Patch. Ten quadrats were surveyed on each Patch (12 on Astley) using a 2 m × 2 m open quadrat.

Biotic data recorded included the percentage area cover of food plants *E. vaginatum* and *E. angustifolium*, and nectar resource *E. tetralix* (Dennis & Eales, 1997, 1999; Melling, 1987), as well as the number of distinct *E. vaginatum* tussocks and the maximum tussock depth. This is recorded as the distance from the top leaf tips of the tussock to the dry plant material below the rosette of leaves, the latter as a measure of larval overwintering habitat resource (Joy & Pullin, 1999) and oviposition site availability (Melling, 1987; Wainwright, 2005). The percentage cover of *E. tetralix* and number of inflorescences were recorded as a measure of adult nectar resource. Percentage cover of other plant species which form a major part of the ground cover was recorded: *M. caerulea*, ling heather *Calluna vulgaris* and mixed moss/liverwort carpet ('Mixed Bryophytes') excluding *Polytrichum* ssp. and *Sphagna* which were recorded separately. *Sphagnum* moss is the keystone species (van Breemen, 1995); therefore, percentage area of *Sphagnum* cover and the greatest hummock depth at the deepest part of *Sphagnum* were recorded. Additionally, presence or absence of common *Sphagnum* species was recorded, using 1 to denote presence and 0 to denote absence. This notation was taken forward into the statistical analysis.

Abiotic data recorded included the percentage area of open water and bare peat. A scoring system was devised to quantify the local topography of each quadrat (Lawrence, 2018). The height of the centre of the quadrat in relation to each of 8 points, 1 m outside of each corner and each side of the quadrat, was scored. The quadrat was given a score of −1 if it lay below the adjacent surface, 0 if it was at the same level and +1 if it was above. Thus, a quadrat could score between −8 for a hollow and +8 for a hummock, for relative height.

Peat chemistry was measured using a single sample from the top layer of peat, in the root zone 10–12 cm below the surface and immediately below the layer of humifying vegetation. Part of the peat sample was mixed with deionized water, and in situ measurements taken as per Hamilton et al. (2004). pH and oxidation–reduction potential (ORP), a marker of waterlogging (Haraguchi, 1991; Rydin & Jeglum, 2013, section 5.7.2), were measured in the field using a Hanna Instruments HI98121 combo-meter. Electrical conductivity (EC), a marker of overall nutrient levels (Rydin & Jeglum, 2013, section 8.5.3.2), was measured on the same peat-deionized water mixture using a Hanna Instruments low reading conductivity meter HI98311. To estimate percentage water content, peat samples were taken in a 30-ml universal container, weighed and oven dried at 105 ± 5°C (O'Kelly & Sivakumar, 2014) and re-weighted until no further weight loss occurred.

Data were collected over a 12-month period because of logistical constraints and permit requirements (mainly to avoid the breeding bird season). *Eriophorum* spp. are evergreen, perennial sedges; hence, percentage cover and tussock size do not vary seasonally. Similarly, *E. tetralix* is an evergreen dwarf shrub, with a long flowering season and which keeps its dry inflorescences overwinter until the next flowering season. All inflorescences were counted; hence, the number was not expected to vary seasonally. ORP and peat water content would be expected to vary seasonally with changing water table. Any variation due to season of sampling ('Season') was accounted for in the statistical analyses as follows: wet months October–March, dry months April–September.

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).

2.1 | Identify the biotic and abiotic environmental characteristics of habitats where *C. tullia* is present or absent

Mean habitat variables calculated for each individual Patch were combined to give overall means and standard deviations for Present and Absent groups. Plant community composition was visualized using a non-metric multidimensional scaling (NMDS) ordination based on a Bray–Curtis dissimilarity distance matrix (Oksanen, 2009, 2015). Present and Absent groups were visualized with ordiellipse, radius set to 1 standard deviation. Environmental variables were fitted using a $p < 0.05$ level of statistical significance. Analysis of similarity (ANOSIM) and Similar percentage analysis (SIMPER) were performed to assess the cumulative contribution of each species (%) to the dissimilarity between Present and Absent groups.

Permutational analysis of variance (PERMANOVA) (Anderson, 2014) was performed to investigate the variation in plant community composition between Patches, using the adonis function in the vegan package with a Bray–Curtis dissimilarity distance matrix (Oksanen et al., 2013). Models were run to estimate the proportion of variation attributable to Present/Absent while accounting for the variation associated with Season, heterogeneity between individual Patches and the interactions between Present/Absent, Season and Patch. In models involving multiple factors, individual Patches were nested within Season, nested within Present/Absent, with the strata set to Present/Absent.

2.2 | Determine if the presence or absence of *C. tullia* can be predicted by modelling using these environmental variables

In order to investigate Habitat Resources which predict *C. tullia* presence, generalized linear mixed-effects models (GLMM)

(Bolker et al., 2009; Harrison et al., 2018) were constructed using the glmer function in the lme4 package (Bates et al., 2011). Models were designed to test the hypothesis that currently recognized Habitat Resources predict *C. tullia* presence. Data were scaled. Individual Patches nested within Season were used as the random effects terms, in order to control for data collection being over multiple Patches and in wet or dry seasons of the year. The choice of predictor variables was guided by a priori knowledge of the species requirements (see Section 1) in addition to variables identified as being important in the NMDS. Highly correlated predictor variables (Appendix 2) were excluded from individual models to avoid issues with multicollinearity (Daoud, 2017). This resulted in the comparison of 26 convergent GLMMs. Finally, a multi-model inference approach (Burnham & Anderson, 2002) was employed, with models selected based on their Akaike information criterion corrected for small samples (AICc) score using the model.sel and importance functions in the MuMin package (Barton & Barton, 2015). Global models were initially run, with the number of predictors then reduced based on variable importance. Variable importance was determined using the sum of the 'Akaike weights' of each candidate model ($\sum \omega i$) for which the variable was present as a predictor (Burnham & Anderson, 2002).

Finally, the most significant Habitat Resources were determined by correlating the most important statistical predictors of *C. tullia* presence with prior knowledge (as discussed previously) of the species' biology.

2.3 | Use breakpoint analysis to identify minimum and 'near-optimal' Habitat Resource levels and inform ongoing reintroductions

Logistic regression models were constructed for individual predictor variables which had been identified as significant Habitat Resources. The logistic models were analysed further using breakpoint analysis to define significant points on the logistic curves. The mid-inflection point ('Midpoint') (Goshu & Koya, 2013) represents the 'mathematical' transition between the binary states for absence and presence. Segmented regression (Muggeo, 2003) was used to define a statistically and biologically meaningful (Passos et al., 2012) upper inflection point, the break of slope of the logistic curve ('Breakpoint').

Logistic curves are asymptotic, only reaching 100% when the predictor variable is at infinity; hence, it is necessary to define an effective upper limit to the dose–response relationship of the curve. Segmented regression defines this point with respect to the characteristics of each individual curve, in preference to setting an arbitrary limit such as 90% (Haanstra et al., 1985; Sharpe et al., 2016). The Breakpoint represents the level of 'near-optimal' (Gass & Harris, 2001) abundance of a habitat resource, where additional supply yields progressively less gain in the probability of maintaining the presence of a *C. tullia* population.

Values for Habitat Resources at the mid inflection point (Midpoint) when the probability of Presence = 50% were calculated using the dose.p function from the MASS package (Ripley et al., 2013) and Habitat Resources at the break of slope (Breakpoint) were calculated using the segmented function from the segmented package (Muggeo & Muggeo, 2017). The odds ratio (OR) and 95% confidence interval (CI) at the Breakpoint were calculated using the oddsratio package (Schratz, 2020). Finally, a multiple logistic model of all four Habitat Resources was constructed.

3 | RESULTS

3.1 | Identify the biotic and abiotic environmental characteristics of habitats where *C. tullia* is present or absent

Mean biotic and abiotic properties of the *C. tullia* Present and Absent Patches are outlined in Table 1.

On the NMDS ordination plot (Figure 2), Present and Absent groups resolved into significantly distinct ellipses—analysis of similarities (ANOSIM) R statistic = 0.573, p = 0.001. Moderate degree of stress = 0.171. From the similar percentages (SIMPER) analysis (Table 2), *E. vaginatum*, *C. vulgaris*, *M. caerulea*, *E. tetralix* and Mixed Bryophytes were the most influential significant contributors to the dissimilarity, these five species contributing 83.3% to the cumulative dissimilarity. *Sphagnum* species *S. papillosum*, *S. capillifolium* and *S. fimbriatum* were weak significant contributors to the dissimilarity.

Of the environmental factors, *E. vaginatum* tussock count, tussock depth, *E. tetralix* inflorescence count and peat water content were significant predictors of *C. tullia* presence. EC and ORP were significant negative predictors of *C. tullia* presence.

The PERMANOVA analysis demonstrated significant difference in plant community composition when aggregated according to Present/Absent ($p = 0.001$), Season ($p = 0.001$) and Patches ($p = 0.001$) (Table 3). Present/Absent explains the greatest proportion of the variation ($R^2 = 0.232$), with the R^2 values for Season, Patch and their interactions ranging from 0.026 to 0.126 (Table 3).

3.2 | Determine if the presence or absence of *C. tullia* can be predicted by modelling using these environmental variables

The top four models reported had the lowest AICc (Harrison et al., 2018), all containing statistically significant predictor variables (Table 4). Overall, the multi-model inference approach identified the most important predictor variables associated with *C. tullia* presence; *E. tetralix* ($\sum \omega i = 0.88$), *C. vulgaris* ($\sum \omega i = 0.86$), *E. vaginatum* ($\sum \omega i = 0.63$), Sphagnum cover ($\sum \omega i = 0.52$) and Mixed Bryophytes ($\sum \omega i = 0.42$) all showed p-values of <0.001 in the best models. The interaction of *E. tetralix* × *E. vaginatum* ($\sum \omega i = 0.23$) had a best p-value of 0.003 (Table 5). Other biotic predictors *E. vaginatum* tussock count ($\sum \omega i = 0.20$) and *E. vaginatum* tussock depth ($\sum \omega i = 0.16$) were identified as moderately

TABLE 1 Mean ± *SD* of biotic and abiotic properties of the *Coenonympha tullia* Present ($n = 8$) and Absent ($n = 5$) Patches

Environmental factor	Present ± *SD*	Absent ± *SD*
Sphagnum cuspidatum (+/−)	0.18 ± 0.13	0.07 ± 0.11
Sphagnum capillifolium (+/−)	0.45 ± 0.40	0.06 ± 0.13
Sphagnum denticulatum (+/−)	0.00 ± 0.00	0.00 ± 0.00
Sphagnum fallax (+/−)	0.39 ± 0.32	0.16 ± 0.36
Sphagnum fimbriatum (+/−)	0.19 ± 0.32	0.57 ± 0.33
Sphagnum magellanicum (+/−)	0.00 ± 0.00	0.00 ± 0.00
Sphagnum palustre (+/−)	0.26 ± 0.26	0.10 ± 0.10
Sphagnum papillosum (+/−)	0.52 ± 0.42	0.12 ± 0.27
Sphagnum squarrosum (+/−)	0.01 ± 0.04	0.00 ± 0.00
Sphagnum subnitens (+/−)	0.10 ± 0.14	0.16 ± 0.25
Sphagnum cover (%)	48.55 ± 31.91	35.61 ± 31.65
Sphagnum hummock height (cm)	13.34 ± 5.66	8.06 ± 6.35
Polytrichum spp. (%)	2.36 ± 5.54	2.67 ± 4.30
Mixed Bryophytes (%)	26.39 ± 27.62	1.09 ± 1.67
Juncus effusus (%)	0.00 ± 0.00	0.86 ± 1.07
Molinia caerulea (%)	5.21 ± 5.29	31.33 ± 27.94
Calluna vulgaris (%)	31.83 ± 19.15	2.18 ± 2.19
Tree species (%)	2.54 ± 3.07	1.56 ± 2.05
Erica tetralix (%)	25.62 ± 11.28	0.70 ± 0.85
Eriophorum vaginatum (%)	41.68 ± 29.63	20.69 ± 10.40
Eriophorum angustifolium (%)	7.85 ± 6.53	15.07 ± 12.91
Inflorescence count	262.00 ± 376.58	26.56 ± 48.35
E.v tussock count	8.94 ± 4.83	4.46 ± 2.39
E.v tussock depth (cm)	7.19 ± 3.28	4.81 ± 3.01
Exposed peat (%)	4.06 ± 4.81	20.27 ± 30.74
Relative hummock height	0.34 ± 0.30	0.25 ± 0.35
Open water (%)	2.33 ± 3.86	3.52 ± 7.87
pH	3.58 ± 0.12	3.55 ± 0.30
EC (μS/cm)	130.20 ± 38.41	185.55 ± 26.30
ORP (mV)	279.06 ± 40.21	326.82 ± 106.34
Peat water content (%)	89.14 ± 3.30	86.27 ± 3.05

Note: (+/−) indicates that presence (1) or absence (0) of Sphagnum species was recorded. (%) indicates that the percentage area cover was recorded.

important. Of the abiotic predictors, peat water content ($\sum \omega i = 0.34$) was moderately important and EC ($\sum \omega i = 0.08$) had a weak predictive value (Table 5).

The results from the NMDS and SIMPER followed a similar overall pattern to the GLMM results. In the GLMM, *C. vulgaris*, *Sphagnum* % cover, Mixed Bryophyte carpet and peat water content were found to be important environmental indicators—however, they did not have a direct role in the biology of various stages of *C. tullia*'s life cycle. The four strongest predictors with direct roles in *C. tullia* biology—*E. tetralix* % cover, *E. vaginatum* % cover, *E. vaginatum* tussock depth and *E. vaginatum* tussock count—were therefore accepted as Habitat Resources and taken forward into the breakpoint analysis.

3.3 | Use breakpoint analysis to identify minimum and 'near-optimal' Habitat Resource levels and inform ongoing reintroductions

Logistic regression models were constructed for the four most important Habitat Resources; *E. tetralix* percentage cover significantly predicted *C. tullia* presence (AIC: 65.35, residual deviance [RD]: 61.35 on 130 degrees of freedom [DF], OR = 76.59, CI: 16.31–658.17, $p < 0.001$), *E. vaginatum* percentage cover significantly predicted *C. tullia* presence (AIC: 167.39, RD: 163.39 on 130 DF, OR = 3.51, CI: 1.76–7.63, $p < 0.001$), *E. vaginatum* tussock count significantly predicted *C. tullia* presence (AIC: 166.39, RD: 162.39 on 130 DF, OR = 5.89,

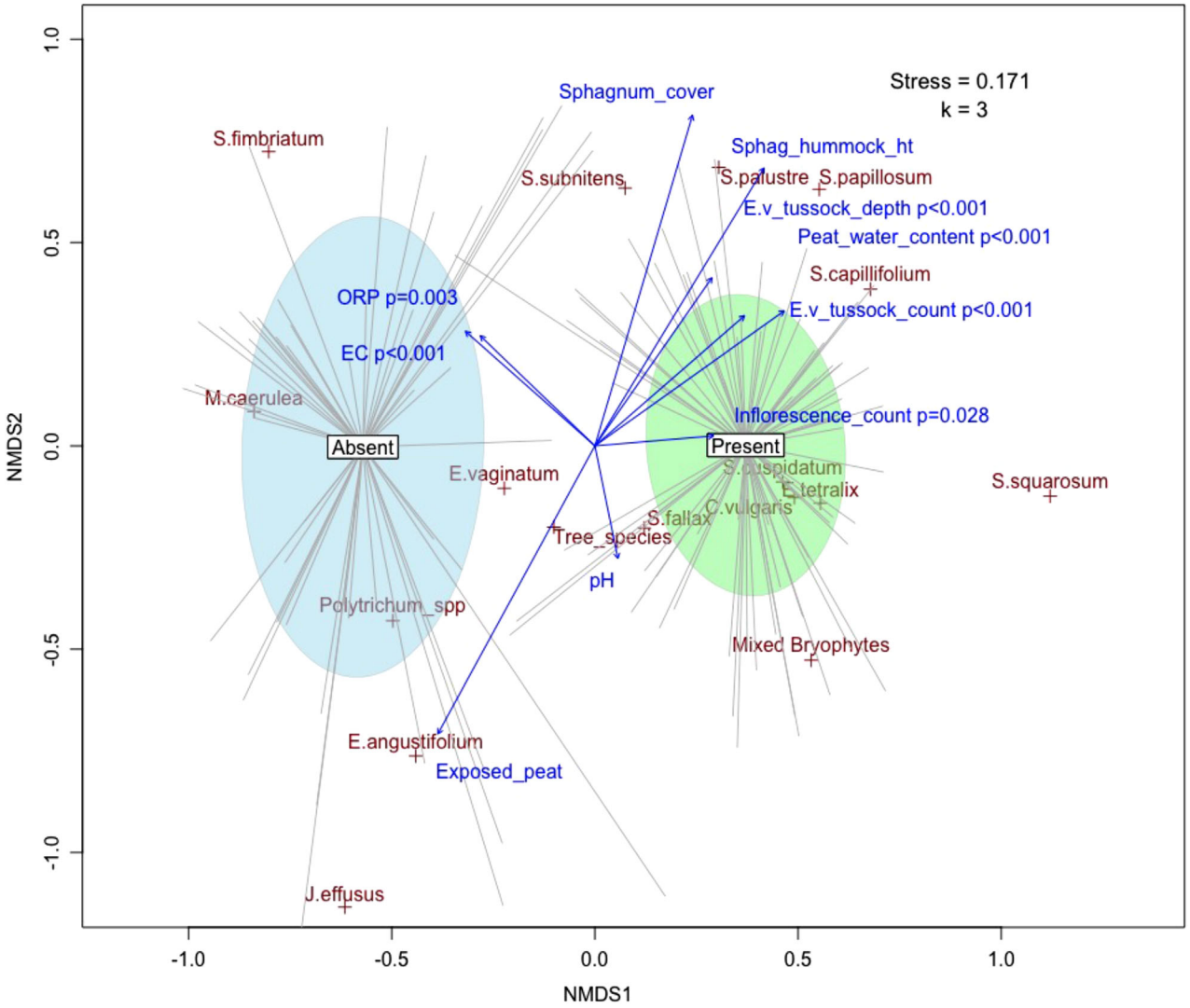


FIGURE 2 NMDS ordination comparing plant communities across the *Coenonympha tullia* Present (green) against Absent (light blue) groups of Patches, ordiellipse radius = 1 *SD*. Present and Absent groups are significantly different with ellipses not overlapping and >2 *SD* distance between group centroids. Plant species (dark red) represent the characteristic species of the Present and Absent Patches. Vector arrows (dark blue) represent the strength of significant ($p < 0.05$) biotic and abiotic factors; *p*-values are given for the drivers of the plant communities. The ordispider diagram (grey lines) shows the dispersion of individual quadrats, linked to the group centroids.

CI: 2.26–17.74, $p < 0.001$) and *E. vaginatum* tussock depth significantly predicted *C. tullia* presence (AIC: 173.48, RD: 169.48 on 130 DF, OR = 4.07, CI: 1.48–12.21, $p = 0.009$). The ORs at the Breakpoint of 76.6 for *E. tetralix* percentage cover and 3.5 for *E. vaginatum* percentage cover underline the distinction between Present and Absent groups of Patches.

The results of the breakpoint analysis (Table 6) gave quantitative estimates for the resource abundance at the Midpoint and Breakpoint of the logistic curves: 5.0% and 11.2% cover of *E. tetralix*; 10.9% and 56.6% cover of *E. vaginatum*; *E. vaginatum* tussock count of 3 and 15 tussocks per 2 m × 2 m quadrat; and 1.8 and 13.5 cm *E. vaginatum* tussock depth. Logistic curves and fitted segmented regression lines are shown in Figure 3. Segmented regression identifies statistically and biologically significant inflection points in the dose–response relationship between habitat resource and the probability of *C. tullia* population presence.

Taken together in a multiple logistic regression model, three of the four predictors remained significant, despite strong autocorrelation between predictors (Appendix 2) (AIC: 58.70, RD: 48.70 on 127 DF, *E. tetralix* percentage cover $p < 0.001$, *E. vaginatum* percentage cover $p = 0.004$, *E. vaginatum* tussock count $p = 0.017$, *E. vaginatum* tussock depth $p = 0.245$).

4 | DISCUSSION

Our analysis revealed significant differences in the environmental conditions across habitat Patches where *C. tullia* was Present and Absent

TABLE 2 Similar percentage (SIMPER) analysis showing the cumulative contribution of each species (%) to the dissimilarity between Present and Absent groups, ordered by decreasing contribution

Species	Average contribution to overall dissimilarity ± SD	Average to SD ratio	Average of Present	Average of Absent	Ordered cumulative contribution	*P*-value
E. vaginatum	0.170 ± 0.14	1.21	41.68	20.96	21.3%	<0.001
C. vulgaris	0.135 ± 0.12	1.17	31.83	2.29	38.1%	<0.001
M. caerulea	0.131 ± 0.13	1.02	5.21	31.31	54.5%	<0.001
E. tetralix	0.118 ± 0.09	1.38	25.83	0.71	69.2%	<0.001
Mixed Bryophytes	0.113 ± 0.13	0.84	26.39	1.06	83.3%	<0.001
E. angustifolium	0.082 ± 0.1	0.80	7.85	15.71	93.5%	0.088
Polytrichum spp.	0.020 ± 0.05	0.40	2.36	2.63	96.0%	0.379
Tree species	0.015 ± 0.026	0.60	2.54	1.50	97.9%	0.473
J. effusus	0.004 ± 0.016	0.26	0.00	0.83	98.4%	0.248
S. fimbriatum	0.003 ± 0.002	1.04	0.19	0.58	98.7%	<0.001
S. papillosum	0.003 ± 0.003	0.96	0.53	0.12	99.0%	<0.001
S. capillifolium	0.002 ± 0.002	0.86	0.45	0.06	99.3%	<0.001
S. fallax	0.002 ± 0.003	0.80	0.39	0.15	99.5%	0.016
S. palustre	0.002 ± 0.002	0.63	0.26	0.10	99.7%	0.125
S. cuspidatum	0.001 ± 0.002	0.51	0.18	0.08	99.9%	0.209
S. subnitens	0.001 ± 0.002	0.51	0.10	0.15	100.0%	0.274
S. squarrosum	0.000 ± 0.000	0.11	0.01	0.00	100.0%	0.410
S. denticulatum	0.000 ± 0.00	NA	0.00	0.00	100.0%	1.000
S. magellanicum	0.000 ± 0.00	NA	0.00	0.00	100.0%	1.000

Note: Mixed Bryophytes consists of a mixed carpet of mosses and liverworts, excluding *Sphagna* and *Polytrichum* ssp. which are recorded separately. Tree species were most commonly *Betula* sp., although *Pinus sylvestris* was prominent in some Patches. In descending order *E. vaginatum*, *C. vulgaris*, *M. caerulea*, *E. tetralix* and Mixed Bryophyte carpet are the most influential significant contributors to the dissimilarity.

TABLE 3 PERMANOVA outputs comparing plant community composition between Present/Absent, Season, Patch and their interactions

Model	*df*	Sums of squares	Mean squares	Model *F*. statistic	R^2	*P*-value
Present/Absent	1	7.93	7.93	39.18	0.232	0.001
Season	1	2.56	2.56	10.52	0.075	0.001
Patch	1	4.32	4.32	18.80	0.126	0.001
Present/Absent × Season	1	0.88	0.88	4.49	0.026	0.002
Present/Absent × Patch	2	3.44	1.72	9.63	0.100	0.001
Present/Absent × Season × Patch	2	3.33	1.66	9.56	0.097	0.001

Note: The proportion of the variation explained is represented by the R^2 values. Present/Absent accounts for the largest proportion of the variation. Season accounts for the smallest proportion of the variation, less than one third of Present/Absent.

(Table 5). Key predictors of the butterfly's presence included the cover of *E. tetralix* and *E. vaginatum*, but certain abiotic conditions and the presence of other lowland raised bog plant species also contributed to the overall models. By applying statistical techniques not traditionally used in ecological studies (Figure 3; Table 6), we are able to make suggestions as to 'near-optimal' habitat conditions for *C. tullia*, and therefore increase the chances of successful reintroductions going forward.

Community analysis showed significant differences in the vegetative communities when habitat Patches were grouped according to Present/Absent, and to a lesser extent, individual Patches and Season. Differences between Present/Absent were explained by five main variables—*E. vaginatum*, *C. vulgaris*, *M. caerulea*, *E. tetralix* and Mixed Bryophyte carpet (Table 2). Abiotic conditions were also shown to be distinctly different across Present and Absent habitat Patches, with high peat water content, anoxia and low nutrient levels predicting

TABLE 4 Top four models (lowest AICc scores) predicting *Coenonympha tullia* presence from the multi-model inference approach including model terms, AICc score and model weight

Model	*df*	Log likelihood	AICc	Delta	Weight
Mod.z	9	−1.96	23.40	0.00	0.22
C.t_presence ~ C.vulgaris + Mixed_Bryophytes + E.tetralix × E.vaginatum + (Season | Patch_no)					
Mod.e	9	−2.28	24.00	0.65	0.16
C.t_presence ~ C.vulgaris + E.tetralix + E.vaginatum + Mixed_Bryophytes + Sphagnum_cover + (Season | Patch_no)					
Mod.p	9	−2.14	24.1	0.66	0.16
C.t_presence ~ C.vulgaris + E.tetralix + E.vaginatum + Sphagnum_cover + Peat_water_content + (Season | Patch_no)					
Mod.c	9	−2.31	24.40	1.00	0.14
C.t_presence ~ C.vulgaris + Sphagnum_cover + Peat_water_content + E.tetralix + E.v_tussock_depth + (Season | Patch_no)					

TABLE 5 Variable importance, number of models, average and most significant *p*-values for *Coenonympha tullia* presence predictor variables—derived from the GLMMs as part of the multi-model inference approach

Fixed effect	Sum of weights ($\sum \omega i$)	Number of models	Average *P*-value	Most Significant *P*-value
E. tetralix	0.88	13	0.098	<0.001
C. vulgaris	0.86	9	0.132	<0.001
E. vaginatum	0.63	8	0.542	<0.001
Sphagnum cover	0.52	9	0.560	<0.001
Mixed Bryophytes	0.42	8	0.415	<0.001
Peat water content	0.34	6	0.547	<0.001
E. tetralix × *E. vaginatum*	0.23	2	0.482	0.003
E.v tussock count	0.20	8	0.671	<0.001
E.v tussock depth	0.16	6	0.603	0.080
EC	0.08	5	0.752	0.665

Note: Importance refers to the sum of 'Akaike weights' for all candidate models in which a specific term was a predictor. The 10 most important predictors are listed, ordered by descending sum of weights ($\sum \omega i$). *E. tetralix*, *C. vulgaris*, *E. vaginatum*, *Sphagnum* cover and Mixed Bryophytes are the most influential significant predictors.

TABLE 6 Calculated values for the Midpoint and Breakpoint for the four Habitat Resources which are strongest predictors of *C. tullia* presence

Habitat resource	Midpoint ± *SE*	Breakpoint ± *SE*
E. tetralix (% cover)	4.96 ± 0.99	11.15 ± 0.04
E. vaginatum (% cover)	10.91 ± 9.63	56.57 ± 0.19
E.v tussock count (per 2 m quadrat)	2.76 ± 1.82	15.18 ± 0.07
E.v tussock depth (cm)	1.78 ± 2.29	13.50 ± 0.34

Note: Midpoint represents the 'mathematical' mid-inflection point of the logistic curve, where the probability of *C. tullia* presence is 50%—below this level, a population is vulnerable to extirpation. Breakpoint is a statistically and biologically significant estimate of the upper inflection point of the logistic curve, the 'near-optimal' abundance of each habitat resource.

C. tullia presence, along with the number and depth of *E. vaginatum* tussocks and number of *E. tetralix* inflorescences (Figure 2). These findings are supportive of previous work which has identified the importance of *E. vaginatum* tussocks for ovipositioning, overwintering and as the species' main larval food plant, as well as the nectar resources of *E. tetralix* (Dennis & Eales, 1997, 1999; Joy & Pullin, 1997, 1999; Melling, 1987; Wainwright, 2005). *Calluna vulgaris* flowers too late to be considered an important nectar resource (Miller, 1979), but is associated with damp, acidic, low-nutrient substrates found in good-quality peatlands (BSBI, n.d.) and therefore could be considered an indicator of overall site condition.

These results were further supported by the results of GLMMs (Table 5), which identified the top significant predictors of *C. tullia* presence, their relative strength quantified using the sum of the

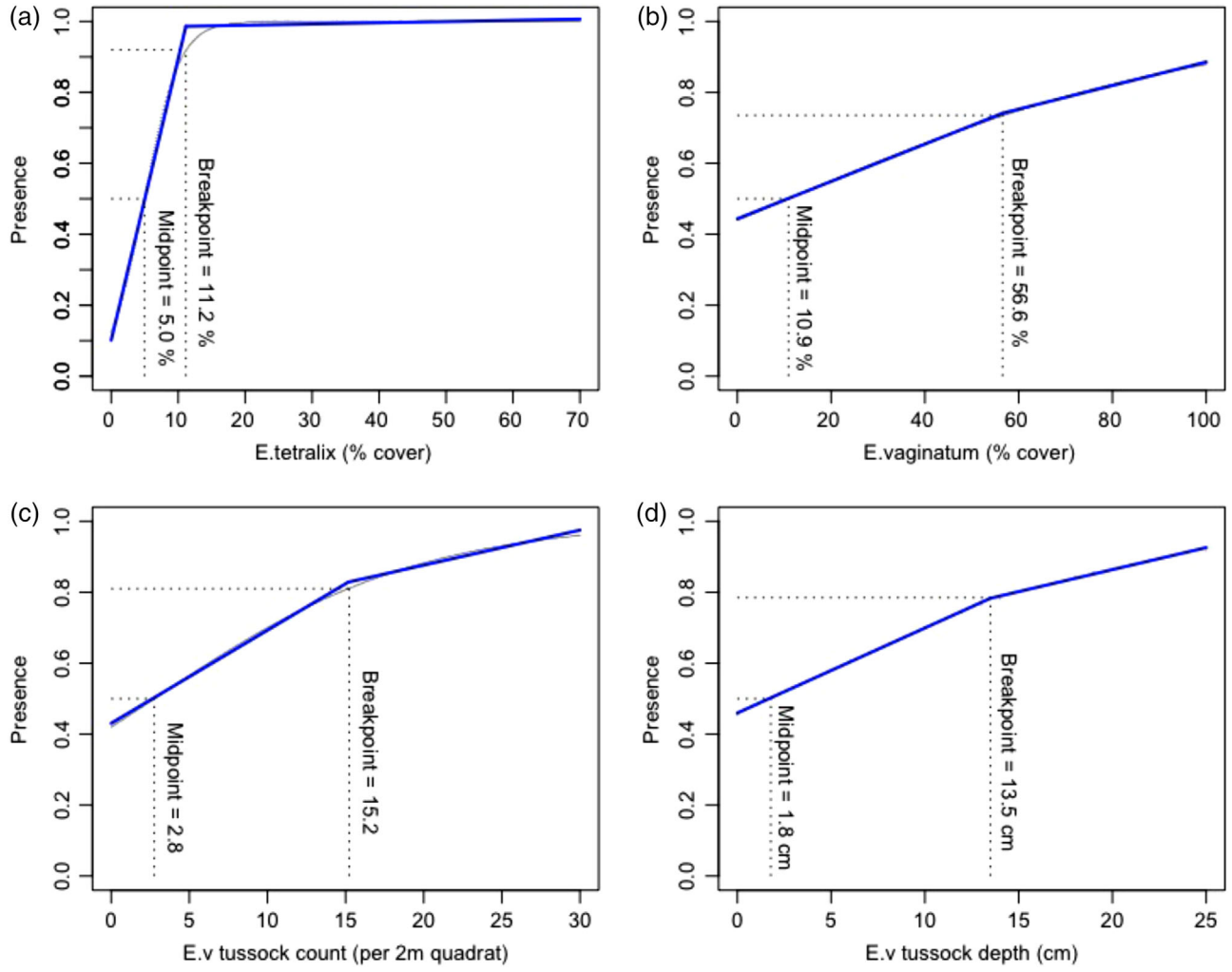


FIGURE 3 Segmented regression lines (blue) for the four Habitat Resources which are important predictors of the presence of *Coenonympha tullia*, overlying their logistic curves (grey). Dotted lines show the calculated values for Midpoint and Breakpoint (Table 6). (a) *Erica tetralix* percentage cover; (b) *Eriophorum vaginatum* percentage cover; (c) *E. vaginatum* tussock count and (d) *E. vaginatum* tussock depth. The Midpoint is the mid-inflection point on the logistic curve when the possibility of a Habitat Resource supporting a *C. tullia* population is 50%. The Breakpoint is the statistically and biologically significant upper inflection point on the logistic curve when the abundance of Habitat Resource is 'near-optimal'.

'Akaike weights' ($\sum \omega i$). Of the plant species with known direct relevance to *C. tullia* life cycle biology, *E. tetralix* ($\sum \omega i = 0.88$) and *E. vaginatum* ($\sum \omega i = 0.63$) were strong predictors, and *E. vaginatum* tussock count ($\sum \omega i = 0.20$) and *E. vaginatum* tussock depth ($\sum \omega i = 0.16$) were weaker predictors. The strongest plant indicator species were *C. vulgaris* ($\sum \omega i = 0.86$), Sphagnum cover ($\sum \omega i = 0.52$) and Mixed Bryophyte carpet ($\sum \omega i = 0.42$). The abiotic environmental factors peat water content ($\sum \omega i = 0.34$) and EC ($\sum \omega i = 0.08$) were weaker predictors of *C. tullia* presence.

Our findings support those of Dennis and Eales (1997, 1999) and Melling (1987), which suggest that *C. tullia* is a specialist of good-quality lowland raised bogs. As such, healthy populations of *C. tullia* can be used as a bioindicator of peatland sites in optimal condition (Bourn & Warren, 1997) and any work to restore sites for this species should have positive implications for a whole raft of other associated species, as well as the overall health of the ecosystem (Bonn et al., 2016; Burkmar, 2018; Maddock, 2008) and peatland carbon balance (Freeman et al., 2012; Hawken, 2018; U.S. Global Change Research Program, 2018; Yu, 2011).

Logistic or 'dose–response' curves are widely used in trails of therapeutic (Dershwitz et al., 1998) or toxic effects (Haanstra et al., 1985; Lappi & Luoranen, 2018; Sharpe et al., 2016), whereby they can be implemented to identify 'breakpoints' in the effectiveness (Goshu & Koya, 2013; Muggeo, 2003). Here, we use this method to predict minimum and 'near-optimal' thresholds for the presence of *C. tullia*, using the identified Habitat Resources *E. tetralix* and *E. vaginatum*. These analyses revealed that the 'near-optimal' percentage cover (at the Breakpoint/point of diminishing returns on the logistic curve) of just over 11% of *E. tetralix* was associated with approximately 90% chance of *C. tullia* presence, and that around 57% cover of *E. vaginatum* resulted

in approximately 75% chance of *C. tullia* presence (Table 6; Figure 3). Further work to quantify the interaction between individual Habitat Resources would be useful but would require additional data relating to the species' habitat use, beyond the scope of this study.

This information is important, given that vast amounts of money are spent on species reintroductions, often with mixed success (Bellis et al., 2019; IUCN, 2013). This novel application of a well-established statistical method could be used to build on qualitative habitat descriptions to establish the quantitative 'breakpoints' for essential habitat resources. This is important during the initial habitat assessment stages of any potential species reintroduction to significantly improve the chances of success, particularly when the species has specific habitat resource requirements (Dennis et al., 2003; O'Brien et al., 2004; Tigreros, 2013).

The results of this study have been used to inform site selection for the reintroduction of *C. tullia* onto Chat Moss in 2020 (Weston, 2020), and will be used to inform future restoration works and ongoing site monitoring, with the hope of ensuring the success of the species colonization across the Manchester mosslands.

Other abiotic factors not measured in this study are also likely to have an impact on the overall habitat quality and suitability at the sites, with factors such as climate, agricultural use, peat quality and site management all playing a role (Bonn et al., 2016; Rydin & Jeglum, 2013). Additionally, the success of terrestrial invertebrate reintroductions is influenced by the numbers of individuals released and the genetic diversity of the populations, as well as factors such as dispersal ability and seasonal conditions (Bellis et al., 2019; Bellis et al., 2021; IUCN, 2013).

5 | CONCLUSIONS

Our results demonstrate a practical method for defining and quantifying the Habitat Resources required for supporting a specialist invertebrate species, in order to facilitate species reintroductions and target ongoing works. The use of logistic regression and breakpoint analysis particularly can be applied to help reduce costs in targeted site restorations and help ensure positive outcomes of associated reintroductions, where specific resources are crucial to a species success. The 'near-optimal' abundance of each habitat resource represents an aspirational target for the ecosystem restoration, prior to species reintroduction.

On-going monitoring of habitat Patches will ensure necessary Habitat Resources are available to support *C. tullia*, and will improve the success of any further translocations. Adding extra data to our models, as current Absent sites mature and prove themselves sufficient to maintain a *C. tullia* reintroduction population, will improve overall model robustness. Planned work using spatial statistical techniques to relate detailed environmental surveys with *C. tullia*'s habitat use will help to clarify how the various Habitat Resources co-relate. Further work on the species' dispersal abilities and genetic diversity will also be crucial to the long-term success of this project.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Andrew Osborne (AO), Mike Longden (ML), Dave Bourke (DB) and Emma Coulthard (EC) conceived the ideas and designed methodology; AO, ML and EC collected the data; AO, DB and EC analysed the data; AO led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.d7wm37q3j (Osborne et al., 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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