

Research article

Landscape-scale dynamics of a threatened species respond to local-scale conservation management

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Landscape-scale approaches are increasingly advocated for species conservation but ensuring landscape level persistence by enlarging the size of patches or increasing their physical connectivity is often impractical. Here, we test how such barriers can be overcome by management of habitat at the local (site-based) level, using a rare butterfly as an exemplar. We used four surveys of the entire UK distribution of the Lulworth skipper *Thymelicus acteon* over 40 years to test how local habitat influences population density and colonization/extinction dynamics, and parameterized, validated and applied a metapopulation model to simulate effects of varying local habitat quality on regional persistence. We found the total number of populations in four distribution snapshots between 1978 and 2017 varied between 59 and 84, and from 1997 to 2017 34% of local populations showed turnover (colonization or extinction). Population density was closely linked to vegetation characteristics indicative of management, namely height and food plant frequency, both of which changed through time. Simulating effects of habitat quality on metapopulation dynamics 40 years into the future suggests coordinated changes to two key components of quality (vegetation height and food plant frequency) would increase patch occupancy above the range observed in the past 40 years (50–80%). In contrast, deterioration of either component below threshold levels leads to metapopulation retraction to core sub-networks of patches, or eventual extirpation. Our results indicate that changes to habitat quality can overcome constraints imposed by habitat patch area and spatial location on relative rates of colonization and local extinction, demonstrating the sensitivity of regional dynamics to targeted in situ management. Local habitat management therefore plays a key role in landscape-scale conservation. Monitoring of population density, and the monitoring and management of local (site-level) habitat quality, therefore represent effective and important components of conservation strategies in fragmented landscapes.

Keywords: connectivity, habitat fragmentation, habitat quality, in-situ conservation, landscape-scale, Lepidoptera, metapopulation dynamics, *Thymelicus acteon*



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Introduction

Land abandonment, urbanization and the conversion of land to agriculture (for example, through fertilization, reseeding or ploughing), have caused widespread habitat loss and fragmentation, increasing the vulnerability of species to environmental change (Hanski 1998, 2011, Warren et al. 2001). Smaller habitat patches support smaller and more extinction-prone populations, and increasing isolation reduces the likelihood of colonization following local extinction or in conservation recovery programs (Dolman et al. 2007, Lawson et al. 2012, Oliver et al. 2013). Therefore, creating and maintaining well-connected landscapes that facilitate persistence and expansion is key to species conservation; and policy objectives such as Favorable Conservation Status (FCS) for the EU Habitats Directive (92/43/EEC) recognize key goals of long-term viable dynamics, a stable or increasing natural range, and a sufficient area of habitat to maintain populations across the range (Mehtälä and Vuorisalo 2007, Epstein 2016). Landscape scale approaches to species conservation are promoted for maintaining viable and connected populations across fragmented landscapes (Lawton et al. 2010) and are increasingly advocated in nature recovery strategies, but implementation can involve significant challenges (Donaldson et al. 2017). Local habitat management is an important tool within such approaches, improving conditions for species in situ (Greenwood et al. 2016) with implications for population survival and metapopulation viability (Johansson et al. 2019).

Long-term species viability in fragmented habitats can often be understood in terms of metapopulation dynamics, where patch size and connectivity influence local extinction and colonization across networks of sub-populations (Hanski 1998). In metapopulation dynamics, patch size is indicative of population size, thus larger patches are assumed to have a lower extinction rate than small patches and well-connected patches a higher likelihood of colonization than isolated patches (Hanski 1998). Landscape-scale management based on these metapopulation principles with a focus on increasing the size, quality and connectivity of sites (bigger, better, more joined up) is widely advocated (Lawton et al. 2010, Isaac et al. 2018) and has been applied in conservation projects (Ellis et al. 2011). However, the practical implementation of landscape-scale conservation remains a focus of discussion (Hodgson et al. 2011a, Donaldson et al. 2017), as creating new patches, or increasing connectivity by forming physical linkages between them, can be difficult to achieve following extensive habitat loss, or where land is limited and subject to competing demands (Balmford et al. 2012). Particularly in the US and Europe where a significant amount of land is privately owned, enhancing physical connectivity involves working across landholdings and boundaries (Merckx et al. 2009), requiring co-ordination across landowners and stakeholders with different priorities. Creation or restoration of the semi-natural habitats required by many specialist species in highly modified landscapes can therefore be complex due to restricted access and ownership (Wimberly et al. 2018)

as well as time consuming and costly, particularly where land is degraded (Walker et al. 2004, Woodcock et al. 2011, Chimner et al. 2017).

In the landscape-scale paradigm, there is often greater emphasis on connectivity and spatial configuration of habitat (Heller and Zavaleta 2009, Wimberly et al. 2018) and a pre-disposition towards conserving larger and more connected patches (Wintle et al. 2019). However, prior to the widespread adoption of landscape-scale conservation, local-level in situ approaches aiming to improve quality within individual habitat patches were the main focus for habitat specialist species, though primarily with the intention of increasing site-abundance as opposed to metapopulation viability. The habitat quality of a patch can be altered by active management practices (e.g. opening woodland, adding shelter or grazing) (Dolman et al. 2007, Ellis et al. 2011, Bruton et al. 2016, Greenwood et al. 2016, Johansson et al. 2019), that lead to changes in the characteristics of the microhabitat (Grundel and Pavlovic 2007, Poniatowski et al. 2018, Dallas et al. 2020). The resulting variation in habitat quality is known to influence metapopulation dynamics through its effects on population density (Thomas et al. 2001, Heisswolf et al. 2009, Bruton et al. 2016) and therefore local carrying capacity (Heinrichs et al. 2016, Poniatowski et al. 2018). Because increasing local population size can increase dispersal beyond that achieved by manipulating patch configuration or physical connectivity alone, such management may also improve functional connectivity (Hodgson et al. 2009). Coordinated manipulation of habitat quality at a local level thus increases metapopulation viability (Heinrichs et al. 2015) and may offer solutions where true (physical) landscape-scale interventions are problematic. For example, in situ approaches to management could be adopted for species where low habitat quality impedes range expansion through fragmented landscapes (Wilson et al. 2009) or where changes in management intensity improve metapopulation functioning (Johansson et al. 2019) without the need to create new habitat patches or implement direct connectivity measures. Nevertheless, though there is evidence of the role changing habitat quality has on landscape-scale dynamics (Ozgul et al. 2006, Lawson et al. 2012, Heinrichs et al. 2015, Bruton et al. 2016, Johansson et al. 2020), how habitat requirements translate to population density and regional persistence, and the practical implications for management, is a topic of active debate (Dallas et al. 2020, Mestre et al. 2020, Schulz et al. 2020).

Here, using as an exemplar a rare butterfly, the Lulworth skipper *Thymelicus acteon*, we examine how landscape-scale distribution and dynamics are affected by habitat quality at the local patch level, indicative of impacts of habitat management on factors known to influence occupancy (vegetation height and larval food plant abundance) (Thomas 1983a, Thomas et al. 2001). The entire UK distribution of habitat and populations has been mapped at a fine-scale four times over 40 years. This patch-level information on population turnover and the relationship between habitat quality and local abundance allows us to parameterize a metapopulation

model, and to investigate the effects of local habitat management interventions on the dynamics and distribution of the species for an equivalent time period into the future. We show how understanding these effects can help to anticipate the results of changed management for regional persistence, to identify core populations or population networks that are most likely to withstand suboptimal conditions, and to quantify management requirements for long-term viability in a fragmented landscape. In this way we demonstrate the role of local, patch-level management in overcoming the barriers associated with species conservation in fragmented landscapes.

Methods

Study system

The butterfly *Thymelicus acteon* is classified as Near Threatened in Europe (Van Swaay et al. 2010), and reaches its northern range edge in the UK, where it is restricted to a 40 km stretch of coastline in the county of Dorset. Here, populations inhabit extensively managed south-facing calcareous grasslands which have not experienced intensive agricultural practices such as fertilizer application or ploughing. Eggs are laid on tall (> 10 cm) plants of the larval host Tor-grass *Brachypodium rupestre*, and larval density is more than ten times greater in turf over 25 cm tall, compared with 5 cm or shorter (Thomas 1983a, Thomas et al. 2001). Previous research has shown that the highest population densities of *T. acteon* occur where the vegetation is 30–50 cm in height (Thomas 1983a, Thomas et al. 2001) achieved where livestock grazing is either absent or at a low density. The abundance of *T. acteon* over time has also been shown to respond to the effects of changed management on vegetation height and structure (Thomas 1983a, Thomas et al. 2001). *Thymelicus acteon* has a single annual life cycle, flying from May to August, when females lay batches of up to 15 eggs. The species overwinters as first instar larvae, which begin feeding in spring in the UK. *Thymelicus acteon* persists in closed localized populations observed as concentrations of individuals or in discrete patches of suitable habitats with limited dispersal between these concentrations or habitat patches (Thomas 1983a, b), and the probability of colonization decreasing with distance (Thomas et al. 1992, Thomas et al. 2001): thus, it exhibits characteristics typical of a species demonstrating metapopulation dynamics (Hanski and Thomas 1994). Prior surveys of its full British distribution were conducted in 1978 (Thomas 1983a), 1997 (Thomas et al. 2001) and 2010 (Jones et al. 2013). We combined these data with information from a new comprehensive survey to test for evidence of colonization and local extinction, and how these are influenced by changes in habitat quality and availability.

Population and habitat surveys

A comprehensive distribution survey for *T. acteon* and its habitat was carried out in 2017 based on the full geographic extent of its UK range from prior surveys (though two very

small patches visited in previous surveys were not visited in 2017 due to a coastal landslip). Potential habitat up to 5 km away from the observed distribution of populations was surveyed in 2018 to gather information on possible longer distance colonizations and wider habitat availability. This 2018 survey involved visiting mostly new habitat patches not previously surveyed. If *T. acteon* was detected in a new patch the search radius was extended outwards (a further 5 km). Habitat was defined as areas of suitable grassland (*B. rupestre* > 10 cm), separated from the next nearest patch by 100 m of unsuitable habitat (Thomas et al. 2001). Patches with vegetation shorter than 10 cm but *B. rupestre* present were surveyed to enable modelling the effects of changed management, but were not classified as habitat. As it is not possible to count all butterflies within a patch, we calculated an index of 'relative density' (number per hectare) for each patch (hereafter referred to as 'population density'). Population density was generated by counting *T. acteon* on a 4 m wide transect, as detection of this species is high within 4 m (Thomas 1983b), and the length of the transect was proportional to the area of the patch. We conducted these transect surveys across the full range of patches during the peak annual flight period from late June to August, as determined by weekly counts from six populations included in the UK Butterfly Monitoring Scheme (UKBMS), a systematic national program that quantifies butterfly population density and phenology (UKBMS 2020). If *T. acteon* were not detected in a patch after two transects and up to two further searches throughout the habitat patch then it was assumed to be unoccupied. The likelihood of false absences based on our sampling approach is small because: 1) distance-sampling for congeneric species with similar size, color, behavior and habitat shows high detectability and no drop-off in detectability across 5 m transects (Isaac et al. 2011); 2) transect counts of *T. acteon* repeated on the same day give consistent numbers (Thomas 1983b); 3) transect counts of this species are closely correlated with abundance estimated from mark–release–recapture and 4) over 75% of the peak size of a population is estimated to be flying for the peak month (Thomas 1983b).

In 1997, 2010 and 2017 vegetation height and food plant frequency were recorded using the same methodologies (Thomas et al. 2001, Jones et al. 2013), allowing us to determine habitat changes between surveys. The methods used to measure habitat attributes in 1978 were not directly comparable to 1997, 2010 and 2017 surveys, therefore the 1978 data are not used in the statistical analysis of habitat changes or habitat quality, but we use 1978 occupancy data in metapopulation parameterizations. Vegetation height was measured systematically along the butterfly transect using a 30 cm drop disk (Stewart et al. 2002), noting if *B. rupestre* was present within 50 cm of each drop disk measurement, to calculate the proportion of measurements where the food plant was present on each habitat patch (hereafter 'food plant frequency'). Measurements were taken systematically along the butterfly transect, with the number of measurements collected (once every 5 m on transects < 300 m in length, once every 10 m on transects between 300 and 600 m in length,

or once every 20 m on transects > 600 m long) proportional to transect length and hence patch area. In 2017, habitat patches were broadly classified as grazed, partly grazed or ungrazed based on field observations, differences in average vegetation height and food plant frequency were compared using Kruskal–Wallis tests. Habitat patches and transects were mapped in the field, using a GPS and satellite imagery in QGIS ver. 3.4.14 Madeira (QGIS Development Team 2019). For occupied *T. acteon* patches surveyed in 1997, 2010 and 2017 (not including 2018), we tested whether the average *T. acteon* population density, vegetation height and food plant frequency for a patch had changed between survey years using paired Wilcoxon signed ranks tests.

Colonizations and extinctions

Presence or absence of *T. acteon* was recorded in each habitat patch in 1978, 1997, 2010 and 2017/2018 and habitat parameters in 1997, 2010, 2017/2018. Due to the limited dispersal capacity of this butterfly (Thomas 1983a, b) if one or more *T. acteon* adult was detected in a habitat patch the butterfly was considered present. Habitat data recorded in 1997 ($n=84$), 2010 ($n=83$) and 2017 ($n=86$), were used to understand effects of habitat (vegetation height, quadratic term for vegetation height and food plant frequency), habitat patch size and connectivity on occupancy (1 or 0). Connectivity was represented by S_i , a measure of connectivity based on distance from, occupancy and size of surrounding patches (see calculation described for the parameterization of the metapopulation model) (for the full set of models see the Supporting information). Data were analyzed using a binomial generalized linear mixed model (GLMM) and the lme4 package (Bates et al. 2015) in RStudio Ver. 1.2.1335 (www.r-project.org), comparing models by AICc. We controlled for the year of observation and multiple years' data for the same patches as patch and year were incorporated as random effects (intercept only).

Turnover between successive survey years (e.g. 1997–2010, 2010–2017) was determined as follows: patches that were occupied by the species in a snapshot then unoccupied in the next were 'local extinctions', in contrast with patches which remained occupied or 'survived'. Patches that were unoccupied in the earlier snapshot then occupied in the next were 'colonizations', in contrast with those remaining unoccupied. As each patch could only appear once in each model (i.e. as an observation of colonized (1) versus absent (0); or extinct (0) versus survived (1)), Binomial generalized linear models (GLMs) were used to analyze the effects of habitat (vegetation height and food plant frequency), habitat patch size and connectivity (represented by S_i) on colonization, survival or local extinction. Binomial GLMs were used also to analyze the effects of habitat change (proportional change in vegetation height and food plant frequency between two survey years), connectivity (represented by S_i) and habitat patch size on turnover (for the full set of models see the Supporting information). Habitat patch size and connectivity values were based on patches in the later of the compared survey periods

(e.g. when analyzing turnover between 1997 and 2010, patch area and connectivity in 2010 were used). Data were analyzed using binomial GLMs for each turnover period where there was sufficient data for analysis (survival versus extinction; 1997–2010 ($n=72$) and colonization versus absent 2010–2017 ($n=32$)), comparing models within 2 Δ AICc from the top model. To assess if climate could be driving observed turnover patterns, 1km gridded data on average annual mean temperatures (1978–2017) was sourced from the Met Office (Hollis et al. 2019). Kruskal–Wallis tests were used to test for differences in climate between sites by turnover (colonization, survival or extinction) and whether temperatures were on average warmer or cooler on sites where the butterfly had persisted from those in which colonizations or extinctions had occurred in each turnover period (Supporting information).

Population density and habitat quality

To derive our model for habitat quality, we modelled relationships between population density and food plant frequency, vegetation height and the quadratic term of vegetation height to account for a potential deterioration of quality as vegetation becomes too tall (Thomas 1983a). We analyzed the habitat and population data from occupied patches in 1997, 2010 and 2017 visited within the four-week period from late-June to late-July when at least 70% of peak numbers are observed, determined from the UK Butterfly Monitoring Scheme data. Occupied patches were used in this analysis as we only wanted to model the effects of habitat on butterfly density, and inclusion of patches absent due to recent local extinction (e.g. habitat loss caused by development or agricultural intensification) or a failure to colonize (e.g. due to isolation) would not be informative for the model. We used a generalized linear mixed model (GLMM) with a negative binomial error structure and *log link* function, using the lme4 package (Bates et al. 2015) in RStudio ver. 1.2.1335. The dependent variable was maximum count in each year, with transect length included as an offset term to account for difference in sampling effort at each patch (Zuur et al. 2009). The independent variables included as fixed effects, food plant frequency and average sward height, were scaled by predictor standardizing to improve model stability and convergence (Harrison et al. 2018). To control for the year of observation and multiple years' data for the same patches, patch and year were incorporated as random effects (intercept only). Using the model with the lowest AICc, the count (relative to transect length) was estimated and then converted into patch population density for different combinations of sward height and host plant frequency as well as the habitat quality at which population density was maximized.

Metapopulation parameterization and simulations

SPOMSIM (stochastic patch occupancy modelling simulator) software (Moilanen 2004), an implementation of the incidence function model (IFM) (Hanski 1994), was used for metapopulation parameter estimation and simulations.

Stochastic patch occupancy models (SPOMs) have been shown to provide reliable estimates of metapopulation dynamics (Mestre et al. 2020). SPOMs can be widely applied to systems for which occupancy (presence or absence) data are available, because within-patch dynamics are omitted and only patch colonizations and extinctions are modelled (Moilanen 2004). Habitat quality can be incorporated by weighting patch area (Hanski 1994), meaning a low quality patch has a smaller 'effective area' than a high quality patch of the same size (Johansson et al. 2019, 2020). Patches with a higher quality are assumed to support larger populations and to increase functional connectivity more. For parameterization and simulations, we used our habitat quality GLMM to derive population density estimates for each patch to weight the observed patch area, generating an 'effective area' (A) as:

$$A = a \frac{D}{D_{\max}}$$

where a is patch area (ha), D patch density and D_{\max} is the maximum modelled population density based on the habitat quality model, to enable effective area to be scaled to a realistic area equivalent to but not exceeding observed area.

The IFM is based on the assumption that the colonization probability C_i between surveys of each patch i is given by:

$$C_i(t) = \frac{S_i(t)^2}{S_i(t)^2 + y^2}$$

where y scales the relationship between connectivity and colonization probability, and S_i is the connectivity of patch i based on the distribution of populations in surrounding patches, given by:

$$S_i(t) = \sum p_j \exp(-\alpha d_{ij}) A_j^b$$

where p_j is the occupancy (1 = occupied, 0 = unoccupied) of each patch j . The parameter d_{ij} is the distance between patches i and j (here the Euclidean edge to edge distance) and α is the slope of a negative exponential dispersal kernel (the rate at which dispersal decreases with distance). Emigration rate from patch j is scaled by b which is set at 0.5 to account for higher per capita emigration from smaller patches. The extinction probability (E_i) of each occupied patch is given by:

$$E_i(t) = \left(\frac{\mu}{A_i^x} \right) (1 - C_i(t))$$

where, μ defines the probability of local extinction in a patch of unit area in one time-step (one year) and x scales the relationship between area and extinction probability. Here, extinction probability is adjusted for by the rescue effect

($1 - C_i(t)$) to account for a reduced extinction risk in well-connected patches owing to dispersal from nearby patches (Moilanen 2004).

IFM parameters μ , x and y were estimated in SPOMSIM from starting values of $x=1$, $\mu=0.01$ and $y=5$. Following tests of a range of values (Supporting information) taken from other butterfly species breeding in fragmented landscapes in the UK, α was fixed at 1.5 to improve model convergence in the derivation of other parameters and b was fixed at 0.5 (Thomas et al. 2002, Gutiérrez 2005, Bulman et al. 2007). Parameters were estimated using a Monte Carlo Markov chain approach (with a high effort of 19 200 iterations) from occupancy snapshots and turnover between 1978, 1997 and 2010 using 81 patches from the main distribution (Fig. 1). Patch area used in parameterization was the effective area based on 1997 habitat conditions (vegetation height and food plant frequency) as 1997 represented the mid-point of the three parameterization snapshots (1978, 1997 and 2010). We estimated two sets of parameters, based on the alternative assumptions that colonization and local extinction were or were not at a steady state (equilibrium versus non-equilibrium assumptions). Whether snapshots of occupancy represent an equilibrium between colonization and extinction can influence parameter estimation and thus model predictions (Moilanen and Hanski 1998) as non-equilibrium assumptions assume occupancy fluctuations represent a trend rather than natural fluctuations in dynamics (Moilanen 2004), therefore modelling with both equilibrium and

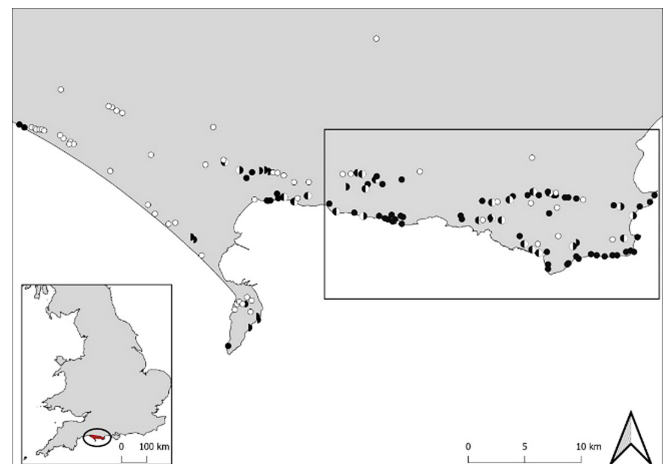


Figure 1. Distribution and turnover of *Thymelicus acteon* populations in southern England between 1997 and 2017. Filled symbols show habitat patches where populations were present in both 1997 and 2017. Left-filled symbols show local extinctions (occupied 1997, absent 2017); right-filled symbols show colonizations (absent 1997, occupied 2017). Filled semi-circles show populations found in 2017 (or the wider survey in 2018) in habitat patches that had not previously been searched. Open symbols show patches where habitat was present but the species was not found. The rectangle contains habitat patches ($n=81$) used in metapopulation parameterization (surveyed 1978, 1997 and 2010). Inset map shows, highlighted in red and contained in the circle, the distribution of *T. acteon* in southern England.

non-equilibrium parameters gives an indication of the range of potential metapopulation responses over time. Parameters were tested by running 1000 simulations from the starting distribution of *T. acteon* in 1978, allowing both a comparison of modelled versus observed occupancy for patches visited after 19, 32 and 39 years (which corresponds to the timings of surveys in 1997, 2010 and 2017), and an independent test of occupancy (i.e. using the 2017 occupancy data not used to estimate the parameters, and the newly surveyed sites visited from 2018). The equilibrium and non-equilibrium parameter sets with the lowest AICc values for parameters which accurately reflected observed occupancy were selected for use in metapopulation simulations (Supporting information).

To simulate how local management could influence metapopulation dynamics, we used the habitat quality model to estimate population density and thus effective area for each patch based on a set of scenarios. We varied vegetation height and food plant frequency incrementally to represent 'low' to 'high' quality (Supporting information). For each scenario, as a simplification, we simulated uniform vegetation height or food plant frequency across time over all patches ($n = 148$; Table 1). We varied vegetation height in increments of 5 cm for the range of vegetation heights at which *T. acteon* populations are known to occur (10–45 cm), and in increments of 1 cm in 'marginal' habitat quality scenarios outside this range (≤ 10 and ≥ 45 cm) to identify threshold conditions for metapopulation persistence. In the vegetation height simulations, food plant frequency values were kept at observed values for each patch in 2017, thus retaining some variation in quality across patches. Simulations were also run to investigate the effects of food plant frequency, with proportions increased in 0.05 increments from low (0.05)

to high frequency (1) retaining observed vegetation heights from 2017. We used simulations to identify core patches, as those which showed occupancy in $> 50\%$ of simulations at scenarios of low habitat quality (e.g. 5 cm vegetation height). Lastly, we modelled the effect of changing all patches to 'optimum' quality (based on the habitat quality model), in order to investigate the importance of managing both key components of habitat quality (vegetation height and food plant frequency) instead of either in isolation. Regional stochasticity, an important consideration in metapopulation dynamics, reflects the extent to which dynamics are synchronized across patches under environmental stochasticity (e.g. during climate extremes or other environmental perturbations). Effects of regional stochasticity on model projections were tested by setting regional stochasticity at 0.3, a relatively high value used in previous studies (Moilanen 2004, Gutiérrez 2005, Bulman et al. 2007) and observing effects on model projections (Supporting information). Simulations were run for 500 replicates over 40 years maintaining the simulated habitat conditions as constant over time, using equilibrium and non-equilibrium parameter sets starting with the observed distribution of *T. acteon* in 2017.

Results

Effects of habitat variables on occupancy and abundance

Descriptive statistics

We visited 150 patches in total, of which 42 were patches visited for the first time outside the known *Thymelicus acteon* distribution in 2018. The remaining 108 patches

Table 1. Colonization–extinction dynamics of *Thymelicus acteon* populations from four distribution surveys. For consecutive surveys, the number of survived (occupied in both years), colonizations (unoccupied to occupied), discoveries (not surveyed in the previous year), unoccupied (unoccupied in both years) and local extinctions (occupied to unoccupied). Habitat area shows the suitable area in each survey year, defined by the physical area of patches of *Brachypodium rupestre* > 10 cm. The final column shows total colonies, habitat and percentage when including the new patches surveyed in the extended area in 2018.

Survey year	1978	1997	2010	2017	Total 2017 and newly surveyed sites (2018)
<i>T. acteon</i> status					
Total sites occupied	84	79	59	72	77
Total sites surveyed	93	96	101	106	148
Percentage occupancy	90%	82%	57%	68%	52%
<i>T. acteon</i> turnover between surveys					
Survived		66	53	54	52
Colonizations		3	1	14	14
Discoveries	84	10	5	4	9
Unoccupied	9		17	29	66
Local extinctions		17	25	5	5
<i>T. acteon</i> habitat and occupied area					
Total habitat area (ha)	588	504	640	584	647
Area occupied (ha)	554	461	544	513	514
Percentage area occupied	94%	91%	85%	88%	79%
Median occupied patch size (ha)	2.5	3	5	3.3	3
Interquartile range (0.25–0.75)	1.2–6.4	1.5–6	2.7–10	1.5–8.6	1.1–7.6
Median extinct patch size (ha)		0.01	2.8	2	2
Interquartile range (0.25–0.75)		0.001–1.7	1.2–4.2	1.4–2.6	1.4–2.6

were targeted for surveys in 1997, 2010 and 2017 (Table 1). Though the number of populations of *T. acteon* in 1997 and 2017/18 were similar (79 versus 77), 37 local populations (34%) showed turnover over the twenty years (Fig. 1) as there was a period from 1997 to 2010 in which local extinctions outnumbered colonizations, followed by a period between 2010 and 2017 in which colonizations outnumbered local extinctions.

Results from occupancy model

Occupancy was influenced by vegetation height, vegetation height squared, food plant frequency, patch size and connectivity (all years). When controlling for site and year, high food plant cover, patch size and connectivity had a positive effect on occupancy, whilst vegetation had a quadratic effect (Supporting information). Patch area, food plant frequency and vegetation height had a positive effect on colonization, and connectivity had a positive effect on survival whilst vegetation had a quadratic effect (Supporting information). Increasing food plant cover between 1997 and 2010 had a negative effect on survival but increases in vegetation height and connectivity had a positive effect, whilst patch area and

increases in vegetation height had a positive effect on colonization between 2010 and 2017 (Supporting information).

Results from abundance model

From 1997 to 2017, *T. acteon* population density (number per hectare on occupied patches visited in the peak flight period, $n = 70$) declined (Median₁₉₉₇ = 66, Median₂₀₁₇ = 33, $V = 1153$, $p = 0.004$, $n = 31$ pairs), food plant frequency on these patches also declined (Median₁₉₉₇ = 1.0, Median₂₀₁₇ = 0.89, $V = 1097$, $p < 0.001$), but vegetation height increased (median₁₉₉₇ = 19.7 cm, median₂₀₁₇ = 21.6 cm, $V = 391$, $p < 0.001$) (Fig. 2, Supporting information). Vegetation height was lower on patches which were grazed (median = 15.9 cm) compared to ungrazed (median = 23.5 cm) or partly grazed (median = 21.7 cm) patches ($H(2) = 16.3$, $p < 0.001$).

The most parsimonious model relating population density to habitat included effects of food plant frequency, vegetation height and vegetation height squared (Fig. 3, Table 2), and no other model had $\Delta AICc < 2$. After controlling for time (year) and location (patches), patches with taller vegetation and greater food plant frequency had higher population densities.

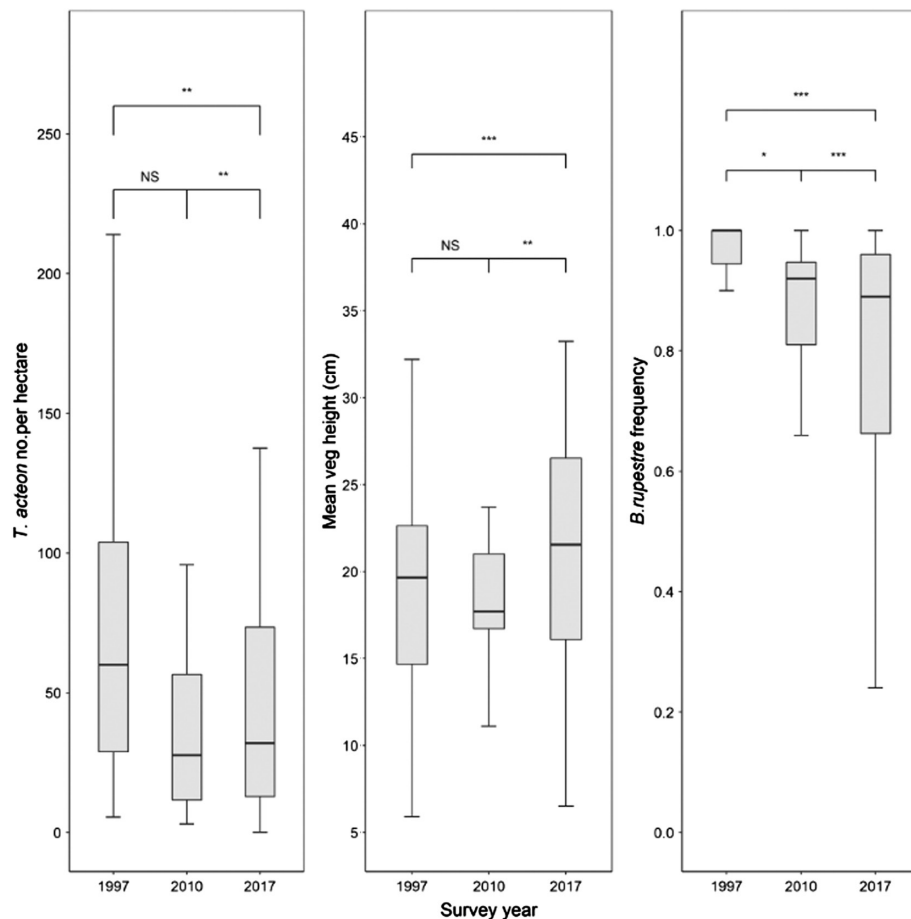


Figure 2. Differences between survey years in *Thymelicus acteon* population density (left), vegetation height (middle) and food plant frequency (right) for occupied sites visited in the peak flight period (comparisons between 1997 and 2017: $n = 70$; comparison with 2010, $n = 24$).

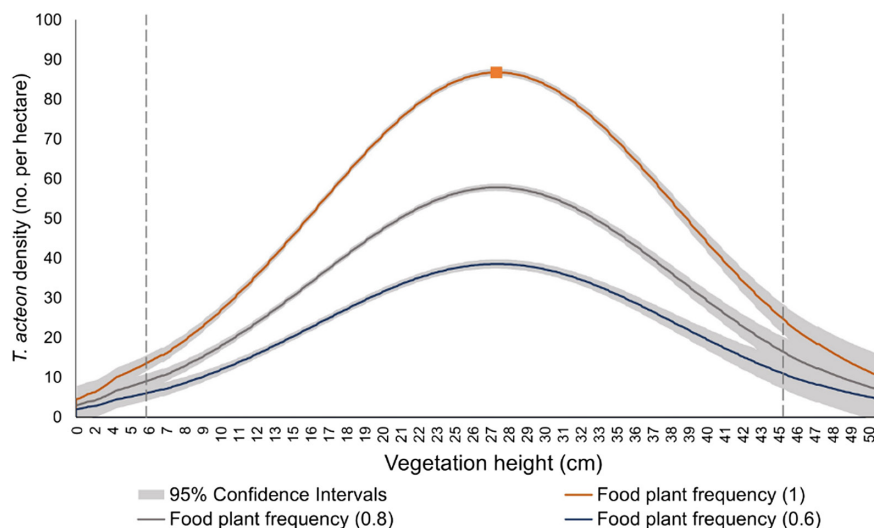


Figure 3. Modelled relationship between *Thymelicus acteon* population density and vegetation height for three food plant frequencies (0.6, 0.8, 1), shading represents 95% confidence intervals, the orange square represents maximum density at optimum vegetation height (27.2 cm) and food plant frequency (1), the grey dashed lines represent the maximum (45.3 cm) and minimum (5.9 cm) vegetation heights observed.

Modelled population density was greatest for a vegetation height of 27.2 cm and food plant frequency of 1 (100%).

Metapopulation modelling

We obtained Spomsim parameter estimates of $x=0.315$, $\mu=0.129$ and $y=8.258$, assuming that occupancy in 1978, 1997 and 2010 represented a metapopulation at equilibrium with habitat availability. In model validation, empirically observed patch occupancy in 2017 (68%) was close to median patch occupancy after 39 years in simulations run from 1978 (Supporting information). Minimum and maximum patch occupancy for these simulations ranged between 60 and 80% over 39 years. Parameters estimated without assuming equilibrium dynamics ($x=0.292$, $\mu=0.156$, $y=9.270$) led to

slightly lower predictions of patch occupancy from 1978 to 2017 (Supporting information).

Simulated changes in the effective area (patch size weighted by expected population density based on different modelled habitat quality) influenced the extent of *T. acteon*'s regional distribution after 40 years from the 2017 distribution (Fig. 4). Results from scenarios run with the equilibrium parameter estimates suggested no metapopulations would go extinct in 40 years when vegetation height ranged from 8 to 46 cm and food plant frequency was > 0.3 , compared with slightly more restrictive conditions of 15–40 cm and > 0.5 food plant frequency in the scenarios run with the non-equilibrium parameter estimates. In equilibrium simulations with vegetation heights of 15–40 cm, or food plant frequencies exceeding 0.5, patch occupancies remained above minima

Table 2. Multi-model inference of relationships between population density and habitat attributes (*Brachypodium rupestre* frequency, vegetation height and vegetation height squared). AICc is the Akaike information criterion (corrected for small sample size), Δ AICc the difference in AICc from the best model and Wi is the Akaike weight. The direction of the effect is indicated by model coefficients, with standard errors shown in brackets. Models were fitted using data from occupied patches visited during peak flight period, using a generalized linear mixed model with a negative binomial error structure, transect length as an offset term, and patch and year (1997 (n=70), 2010 (n=22), 2017 (n=70)) as random intercepts.

Model	AICc	Δ AICc	Wi	Intercept	Food plant frequency	Vegetation height	Vegetation height ²	Food plant frequency \times vegetation height	Food plant frequency \times (vegetation height) ²
Model 1	1257.8	0	0.84	-3.818 (0.15)	0.367 (0.08)	0.374 (0.08)	-0.168 (0.05)		
Model 2	1261.9	4.2	0.11	-3.819 (0.15)	0.352 (0.10)	0.384 (0.09)	-0.160 (0.06)	-0.056 (0.11)	-0.006 (0.09)
Model 3	1264.2	6.5	0.03	-3.970 (0.15)	0.3769 (0.09)	0.2962 (0.09)			
Model 4	1265.2	7.4	0.02	-3.968 (0.15)	0.3354 (0.09)	0.3185 (0.08)		-0.1189 (0.1)	
Model 5	1271.5	13.7	0.00	-3.852 (0.21)		0.480 (0.08)	-0.171 (0.05)		
Model 6	1273.1	15.3	0.00	-3.863 (0.08)	0.486 (0.08)				
Model 7	1277.7	19.9	0.00	-4.01 (0.33)		0.398 (0.08)			
Intercept only	1295.3	37.5	0.00	-4.02 (0.20)					

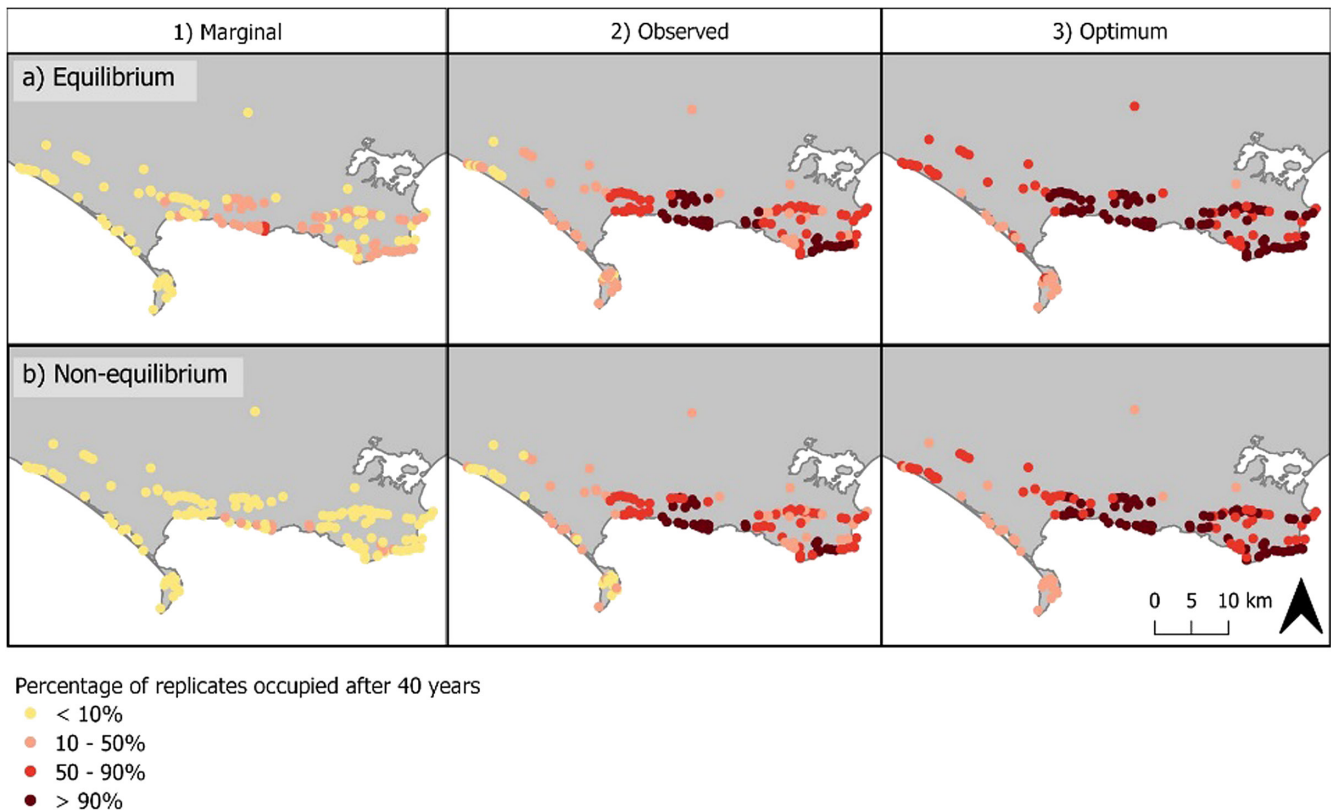


Figure 4. Percentage of simulations in which patches were occupied by *Thymelicus acteon* after 40 years in southern England, using (a) equilibrium and (b) non-equilibrium assumptions in three different scenarios 1) marginal (5 cm vegetation height; food plant frequency as observed in 2017/2018) 2) observed (habitat quality as observed in 2017/2018); 3) optimum (27.2 cm vegetation height; food plant frequency 1).

observed in the past 40 years (Fig. 5). At vegetation heights between 20 and 35 cm or food plant frequency above 0.9, more than 90% of the available area was occupied; under non-equilibrium parameters this reduced to 86–90% (Fig. 5). Approximately 25% of patches remained unoccupied in equilibrium scenarios (35% in non-equilibrium), unless both vegetation height and food plant frequency were simulated as optimal, when estimated patch and area occupancy increased to 85% and 96% respectively after 40 years in equilibrium scenarios (79% and 92% non-equilibrium). Incorporating regional stochasticity into scenario projections had a minimal effect on occupancy projections (Supporting information).

At marginal quality (i.e. ≤ 8 cm or ≥ 46 cm vegetation height or $\leq 30\%$ food plant cover), the species retracted to a group of core patches in the centre of the landscape as exemplified in the marginal quality scenario set at 5 cm vegetation height (Fig. 4, panel 1), where the average metapopulation lifetime was 31 years (23 years for non-equilibrium). In marginal quality non-equilibrium scenarios, the proportion of the 500 replicates an individual patch was occupied at 40 years was < 50% of replicates in all patches (Fig. 4, panel 1). The observed effective area in 2017 maintained metapopulation persistence for both equilibrium and non-equilibrium parameters, but no patches beyond the current distribution were occupied after 40 years in more

than 30% of replicates (Fig. 4, panel 2). Maximum effective area, under optimum vegetation height and food plant frequency, was the only scenario in which persistence after 40 years outside the current distribution was consistently observed for either equilibrium or non-equilibrium parameter sets (Fig. 4, panel 3).

Discussion

We show how local habitat quality can influence the landscape-scale dynamics and conservation of species breeding in fragmented habitats through its effects on local population density. The colonization–extinction dynamics of a rare butterfly over the past four decades responded to changes in local habitat quality, and metapopulation simulations for the next 40 years suggested that extending its current distribution would require improved habitat quality or availability. The results increase understanding of the role of local-level management in landscape-scale conservation; show the role of metapopulation modelling approaches for evaluating potential management approaches and have implications for other species in fragmented landscapes that would benefit from coordinated management to overcome constraints imposed by the spatial location of habitat.

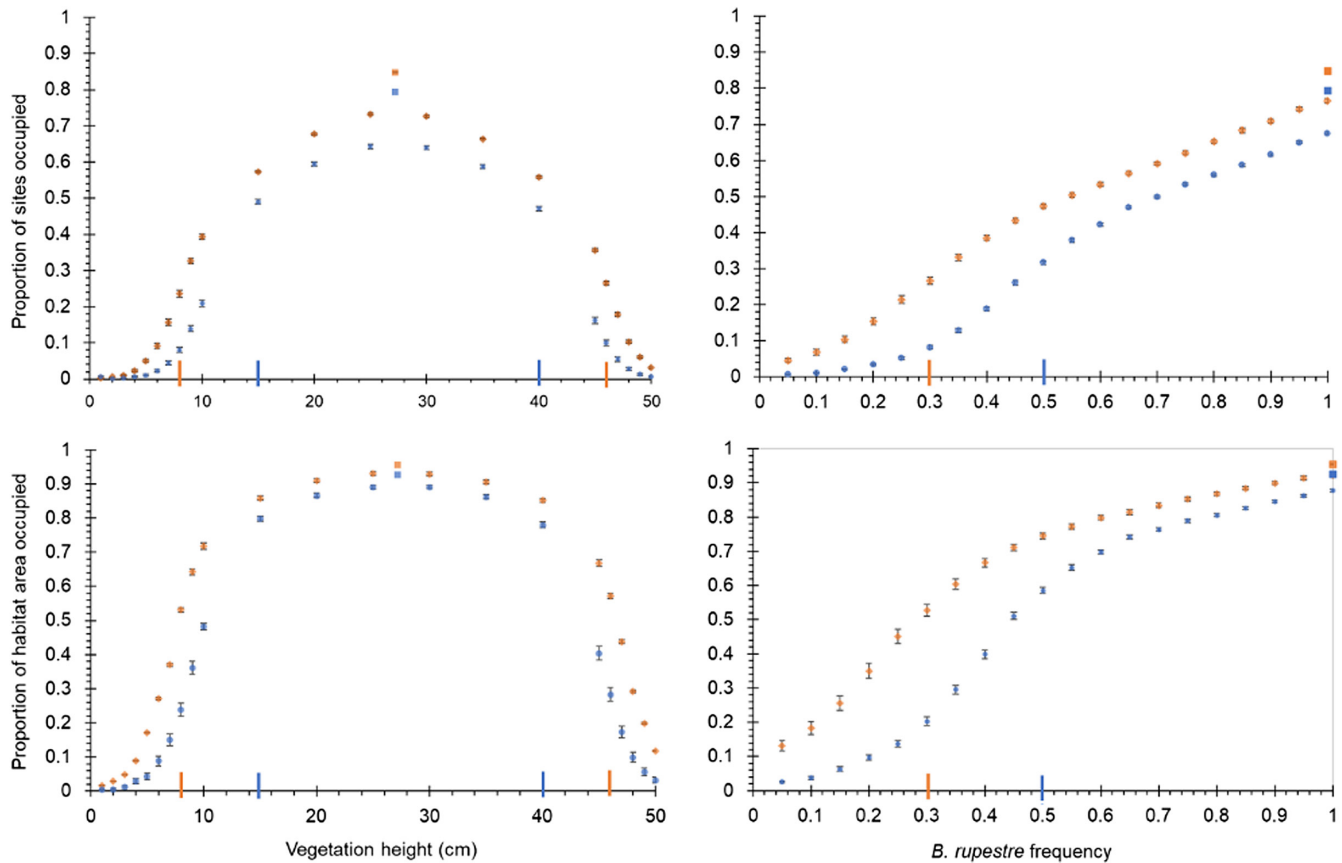


Figure 5. *Thymelicus acteon* occupancy from metapopulation simulations run through the distribution in southern England, showing median proportions (\pm 99% confidence intervals) of habitat patches occupied (top) and habitat area occupied (bottom) after 40 years from 500 metapopulation simulations starting with 2017 occupancy from equilibrium (orange diamonds) and non-equilibrium (blue circles) simulations. Left hand panels show vegetation height simulations, keeping food plant frequency at 2017 values; right hand panels show food plant simulations, at 2017 vegetation heights. Solid vertical lines across the x-axis show thresholds for indefinite metapopulation survival for equilibrium (orange) and non-equilibrium (blue) scenarios. The proportion of habitat patches and proportion of habitat area occupied at optimum habitat quality (vegetation height of 27.2 cm and food plant frequency of 1) is shown by an orange square (equilibrium) and blue square (non-equilibrium).

Changes to habitat, population density and distribution over 39 years

The local population density of *Thymelicus acteon* decreased between 1997 and 2010, then increased from 2010 to 2017. These changes accompanied a decrease then overall increase in vegetation height, but ongoing declines in food plant availability. Habitat models, when controlling for time, showed that increased food plant cover promoted higher population densities, and that *T. acteon* was positively associated with intermediate vegetation heights (shown by the quadratic effect of vegetation height on *T. acteon* densities), with lower densities occurring at short (< 15 cm) or tall (> 40 cm) vegetation. *T. acteon* is thus limited by food availability, but also by vegetation height, which may influence microclimatic conditions affecting insect development (Turlure et al. 2009, Thomas et al. 2011, Curtis and Isaac 2015).

The declining, then increasing abundance of *T. acteon* was mirrored by its colonization and local extinction dynamics, which have been driven by changes in habitat quality over

time associated with changing management intensity (Thomas 1983a, Thomas et al. 2001). Yet no major changes to the extent of habitat or the species distribution were observed since 1978. When local population densities increased as a result of improved habitat quality, driven by taller vegetation, likely linked to reductions in grazing intensity after 2010, metapopulation dynamics shifted from net local extinction to net colonization, because larger populations were less extinction prone and resulted in greater functional connectivity via increased dispersal (Hodgson et al. 2009). Simulated effects of local habitat on population density and metapopulation dynamics resulted in realistic simulations of observed patch occupancy in 2017, whether or not we assumed that rates of colonization and local extinction were in equilibrium between 1978 and 2010, giving confidence in our parameter values.

Application to conservation practice

In our focal system, in situ management including approaches to increase food plant cover or manipulate vegetation height

towards an optimum is required to maintain or expand the distribution of *T. acteon*. Results from the non-equilibrium assumption gave narrower bounds of habitat quality for *T. acteon* to maintain its current distribution (15–40 cm vegetation height and > 50% food plant frequency), suggesting minimum requirements for the species. The modelling suggests that outside such threshold limits of quality, patches may be unlikely to become and stay occupied, leading to metapopulation contraction and extirpation, as may be observed following correlated declines in environmental favorability in metapopulations (Schulz et al. 2020).

The *T. acteon* is sensitive to management, particularly throughout the egg and larval stages (Thomas 1983a) when eggs and larvae can be removed by cutting or grazing, but our results show management interventions are required to avoid vegetation exceeding maximum height thresholds and succession to scrub and secondary woodland. Management approaches to increase food plant cover or manipulate vegetation height towards an optimum for *T. acteon* could include relaxing or increasing management intensity. Extensive cattle grazing can create a mix of long and tall vegetation to help maintain suitable habitat conditions. The temporary removal of livestock or a reduction in grazing intensity may be required if vegetation is too short, whereas grazing or cutting can be reinstated where vegetation is becoming too tall for *T. acteon*. The challenge of managing habitat for mid-successional species in fragmented landscapes (Dolman et al. 2007, Ellis et al. 2019, Johansson et al. 2020, Mestre et al. 2020) could therefore be met using intermediate management intensity or frequency, for example by coordinated rotational management among networks of habitat patches.

Our simulations show how changes in local habitat quality, for example through targeted management interventions influences the overall quality of a landscape with implications for the carrying capacity of a focal species (Heinrichs et al. 2015), and thus the physical area of habitat required to meet or exceed such minimal thresholds. Increasing local population sizes by improving habitat quality could therefore diminish the importance of the spatial location of patches for metapopulation persistence (Heinrichs et al. 2016). In our simulations, the estimated proportion of patches occupied after 40 years increased as habitat quality improved from marginal to optimal, showing that when average quality improves, small or isolated patches may be occupied more often, enabling them to act as stepping stones in range recovery (Hodgson et al. 2011b, Kuussaari et al. 2015, Poniowski et al. 2018) or to enhance regional persistence (Ozgul et al. 2006). In the long term, therefore, maintaining habitat quality even in unoccupied or small patches can contribute to functional connectivity and persistence (Ellis et al. 2011, Wintle et al. 2019).

There is conservation value in restoring the size and connectivity of fragmented habitat patches (Johansson et al. 2022), however physical space for increasing habitat can be limited in fragmented landscapes, making the in situ management of small habitat fragments an important tool for conservation (Wintle et al. 2019). In our case study region, 70%

of calcareous grassland was lost between 1930 and 2015, primarily to agricultural conversion (Ridding et al. 2020), thus patch or corridor creation would generally require habitat restoration on heavily enriched farmland. Restoring habitat on agricultural or degraded land can be a complex and long-term process of which restoration success is dependent on a number of factors (Walker et al. 2004, Fagan et al. 2008, Woodcock et al. 2011, Chimner et al. 2017) and often with additional complexities of management of appropriate thermal environments of food plants (e.g. restrictions to certain aspects or elevations) (Grundel and Pavlovic 2007). We show how increasing carrying capacity and functional connectivity through management in situ can help to overcome some of these challenges.

Funding mechanisms, such as agri-environment schemes are an important tool to support the delivery of targeted in situ management. Though in situ management can be less complex and costly than habitat creation, there is still a cost to interventions such as the clearance of vegetation (e.g. scrub or secondary woodland) to restore habitats, management of low productivity land (e.g. reinstating grazing on semi-natural habitat) or reductions in grazing intensity resulting in temporary loss of grazing pasture (e.g. through grazing exclusions). Policy instruments, agri-environment schemes or grants can help provide financial support and guidance to facilitate appropriate management and encourage coordinated approaches between networks of habitat (Ellis et al. 2011). Furthermore, our approach to identifying suitable habitat thresholds for species can help provide clear habitat prescriptions with metapopulation model outputs facilitating the spatial targeting of interventions.

The demographic or physical factors that drive local population dynamics and extinction risk mean that some species, such as amphibians at risk from chytrid fungus (Heard et al. 2018), species with very low dispersal ability (for example, saproxylic beetles, small mammals) (Bełcik et al. 2019, Smith 2020) or terrestrial mammals at high risk from human–wildlife conflicts and requiring expansive migratory routes (Harris et al. 2009, Peters et al. 2015), may benefit more from habitat creation, assisted colonization or increasing physical connectivity than managing existing patches. However, in cases where the structure or composition of vegetation appears to determine population density, in situ management can help overcome constraints associated with the area and spatial configuration of patches that might otherwise require more complex habitat creation or schemes working across different landholdings to create physical linkages.

Metapopulation modelling presents a useful tool for projecting extinction–colonization dynamics in response to changes in habitat area or quality (Bennie et al. 2013, Johansson et al. 2019), however the projections themselves should be interpreted with some caution because they are based on outputs from models which incorporate some simplifications. Firstly, habitat quality did not vary across time within our 40-year simulations, but quality will vary temporally in response to biotic and abiotic factors. Secondly, and related to the first point, effects of climate change were not

incorporated in these models, and climate can affect habitat quality and population dynamics for grassland invertebrates, altering equilibrium regional distribution sizes (Davies et al. 2006). Nevertheless, the conclusions about medium term metapopulation dynamics are supported by the congruence between the results of simulations based on assumptions of recent equilibrium versus non-equilibrium dynamics: in the latter case, a progressive increase or reduction in occupancy would be expected (based on improving or deteriorating environmental conditions, respectively). Under a deteriorating climate we might also expect evidence of regionally synchronized dynamics as populations within a landscape are synchronously exposed to sub-optimum climatic conditions, however sensitivity testing of the effects of regional stochasticity on simulation outputs showed little apparent effect of regional stochasticity on model projections of occupancy. There was also a close match between observed and projected changes in patch occupancy and metapopulation dynamics over 39 years, giving confidence that we are able to project conditions for species persistence an equivalent period into the future.

Metapopulation modelling for landscape management under environmental change

Landscape-scale conservation is recognized as an appropriate approach to achieve stable or increasing ranges under environmental change (e.g. habitat loss, climatic change), particularly for policy objectives such as EU Favorable Conservation Status (FCS) or Nature Recovery Networks (Isaac et al. 2018) and can play a role in the Recovery plans for species listed under the U.S. Endangered Species Act (Dunk et al. 2019).

Our results show how metapopulation modelling approaches present a useful tool to assess effectiveness of such landscape-scale strategies prior to implementation, identifying where in situ management in remnant natural or semi-natural habitats could improve our ability to manage for species in landscapes with limited scope for restoration and where there might be multiple management conflicts. The loss of semi-natural habitats can limit resources for a range of species with different habitat requirements, potentially resulting in management conflicts and trade-offs (Botham et al. 2015). Metapopulation models incorporating habitat quality can help identify minimum thresholds of habitat for viability and the core patches within a landscape (Bulman et al. 2007, Johansson et al. 2019, 2020). Understanding these lower thresholds of habitat and the contribution of patches can help identify the core patches important for the targeting of resources and restoration (Schultz and Crone 2005, Scroggie et al. 2019).

Metapopulation model projections demonstrate that for species in highly modified and fragmented landscapes where there is often limited scope for habitat creation, optimal habitat management of existing patches has an important role for facilitating range expansion thus helping to achieve FCS policy goals for maintaining a stable and increasing range. In our study system as quality and effective area increased in high-quality simulations, the excess of colonizations over

extinctions led eventually to expansion beyond the current distribution (Fig. 4). However, even under scenarios of high habitat quality, long-term persistence probability for small and isolated patches remained low. These outputs have relevance for the role of local habitat quality in facilitating species range shifts in response to climate change (Årevall et al. 2018), although in some circumstances habitat may be too fragmented for natural expansion and targeted introductions may be required (Widhalm et al. 2020).

Simulations of marginal habitat conditions highlight the locations of core populations that may be vital to withstand suboptimal conditions under periods of population contraction and that would benefit from targeted management or protection. For *T. acteon* in low habitat-quality simulations, the proportion of occupied habitat decreased as the number of local extinctions outweighed colonizations, reducing the long-term viability of the metapopulation and resulting in contraction to a cluster of large well-connected patches (Fig. 4). Core populations might be more resilient to extreme events provoking regionally synchronous crashes (Johansson et al. 2020, 2022, van Bergen et al. 2020) or are larger and more central patches (Schultz and Crone 2005, Dolman et al. 2007). Alternatively, core patches might help buffer a metapopulation from other external drivers e.g. human-wildlife conflict or coastal exposure (Eaton et al. 2014, Peters et al. 2015), acting as source patches to rescue populations following such stochastic events. Therefore, applying simulations ranging from marginal to optimal conditions helps identify patches where local management may be important for buffering populations or facilitating expansion in conservation strategies under scenarios of changed policy or climate.

Conclusion

Conservation interventions to overcome fragmentation by making patches bigger and more connected (Lawton et al. 2010) present practical challenges. Applying snapshots of species distribution and habitat quality to metapopulation models, we linked local habitat conditions to regional dynamics, demonstrating the key role of patch-level habitat quality in landscape-scale conservation. Metapopulation model projections show how improving habitat quality within patches affects overall dynamics, through enhancing patch carrying capacity and increasing colonizations, thus helping to promote metapopulation viability. Local-level management is useful partly because it can facilitate expansion by overcoming barriers imposed by fragmented habitat. For the rare butterfly *T. acteon* and other habitat specialists, applying the understanding gained through targeted in situ management of protected areas or via approaches such as agri-environment schemes, could thus help to meet goals of stable or increasing ranges.

Speculations

In recent decades enhancing connectivity has emerged as one of the most commonly suggested approaches for enhancing species persistence in fragmented landscapes, particularly in

light of the requirement for range shifts in response to climate change. Connectivity is therefore frequently advocated in landscape-scale conservation initiatives and associated policy instruments (such as those seeking to establish protected area or nature recovery networks). However, the evidence for this is at best equivocal, and it is often contended that site-based measures such as increasing the size or quality of habitat patches are at least as effective for supporting larger and more stable populations with greater capacity to (re)colonize surrounding habitat patches. Our results lend support to this premise, indicating that long-term metapopulation viability can indeed be secured through site management. In fragmented landscapes such as those in the United Kingdom, in which the sizes of intact areas of habitat are frequently small and partially degraded, we speculate that the importance of connectivity has been over-emphasized. Rather we contend that improving the quality and size of existing habitat patches is of greater priority.

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Author contributions

Rachel Jones: Conceptualization (equal); Formal analysis (lead); Investigation (lead); Methodology (equal); Visualization (lead); Writing – original draft (equal); Writing – review and editing (equal). **Nigel A. D. Bourn:** Conceptualization (equal); Funding acquisition (equal); Methodology (equal); Supervision (equal); Writing – review and editing (equal). **Ilya M. D. Maclean:** Conceptualization (equal); Funding acquisition (equal); Supervision (equal); Writing – review and editing (equal). **Robert J. Wilson:** Conceptualization (equal); Funding acquisition (equal); Methodology (equal); Supervision (equal); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.dncjsxkzp> (Jones et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

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