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Mapping the habitat quality of patch networks for the marsh fritillary *Euphydryas aurinia* (Rottemburg, 1775) (Lepidoptera, Nymphalidae) in Wales

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Abstract

The marsh fritillary is widely distributed in Wales, with over 200 populations identified in the past 15 years. However, agricultural improvement, habitat fragmentation and changes in agricultural practices continue to impact on status and a decline in range of 23.5% was recorded over a 10-year period. Solutions must be applied at the landscape scale to improve metapopulation viability and, since 2000, surveys of habitat extent and quality have been carried out on 116,373 ha of grassland surrounding 111 populations. Analysis of the results for standard 'core landscapes' (based on circles of 1 km radius around known populations) shows that overall cover of suitable breeding habitat is 3.44%. However, only 11.85% of the grassland that was suitable for marsh fritillaries was classified as being in Good Condition. The remainder was regarded as having sub-optimal vegetation structure and/or the foodplant was at low density; 33% of the habitat resource that was not in Good Condition was regarded as inappropriately or excessively managed and 67% was suffering from neglect. An Index of Landscape Quality is used to rank landscapes for evaluation. Thirty-five 'core landscapes' (incorporating 98 marsh fritillary populations) were assessed and just four exceeded a threshold value deemed to represent viable landscape configurations. The results have demonstrated that most marsh fritillary populations in Wales exist within depauperate patch networks that lack sufficient breeding habitat of the right quality for long-term persistence. Without targeted conservation action the marsh fritillary will continue to decline in Wales. This paper reports on efforts to collect information on the quality of breeding habitat for marsh fritillaries across Wales in order to identify priorities for conservation action.

Introduction

The marsh fritillary *Euphydryas aurinia* has experienced substantial declines across much of its European range in recent decades (van Swaay and Warren 1999), leading to its inclusion on Annex II of the EEC/EU Habitat and Species Directive, requiring Member States to designate Special Areas of Conservation (SACs) for its protection. In Britain the marsh fritillary was once widespread but decades of decline have seen its range significantly reduced to the point where it is now extinct from the eastern half of the country. Strongholds for the species now only remain in areas supporting an extensive land cover of unimproved semi-natural grassland in central-southern and south-western England, Wales, and western Scotland, but even here populations continue to be lost at an alarming

rate and there is a steady contraction to a handful of core areas (Asher et al. 2001).

Systematic surveys of marsh fritillary populations in Wales began in the 1980s and since 1990 the Countryside Council for Wales (CCW) has commissioned surveys of all known and historic sites throughout the Principality (Thomas 1992; Hurford 1993; Lewis 1994; Hack 1995; Poole 1996; Howe 1997; Woolley 1997; Lloyd 1998; Clarke 1999; Woodman 1999; Smith 2000; Wheeler et al. 2000). Additional information has been provided by volunteer effort, largely through the work of members of Butterfly Conservation and the Wildlife Trusts (CCW, unpublished data). Overall, the species has been lost from 51.5% of the 10 km squares it has been recorded from and, despite recent conservation efforts, losses are continuing. For example, 23.5% of tetrads (4×4 km^2) occupied during the 1980s were found to be unoccupied during comprehensive surveys undertaken during the 1990s. During the recent survey period 213 marsh fritillary populations (defined as distinct aggregations of butterflies separated by more than 500 m of unsuitable habitat from other aggregations) have been recorded in Wales, but 12 of these are known to have become extinct since the initial survey and, of a further 90 populations that have been surveyed on more than one occasion, no evidence of marsh fritillaries was found at 35 of them during the repeat visits.

Difficulties in confirming presence during low population levels (the 'observation threshold' whereby individual webs may be overlooked because they are scarce) may account for some of this apparent loss, but nonetheless it is evident that current conservation measures are failing this characteristic species of Welsh lowland grassland. Conventional site-based approaches to conservation have been unable to halt the decline. Whilst 70 marsh fritillary populations still occur on Sites of Special Scientific Interest (SSSIs) in Wales it has also become extinct on 27 SSSIs since 1980. Currently 51.7% of all post-1990 populations are covered by positive conservation management initiatives, such as management agreements or as nature reserves, but despite these efforts 79.6% of the existing populations support less than 25 larval webs and can be considered extremely vulnerable to local extinction. In the vast majority of cases this is due to inappropriate grazing management. CCW surveys across Wales identified threats to populations at 89 sites and at 77 of these it was considered that agricultural neglect or unsuitable stocking levels (either under- or over-grazing) were factors limiting population size.

With a high proportion of Welsh marsh fritillary populations being small and threatened by unsympathetic management further extinctions are inevitable. However, as the marsh fritillary exhibits metapopulation dynamics (Warren 1994), whereby local extinction and re-colonisation is a natural process, these factors by themselves should not necessarily lead to overall decline. Unfortunately these problems are exacerbated by habitat fragmentation such that re-colonisation becomes less likely as habitat patches become more and more isolated (Bulman 2001). Recent research indicates that a minimum of 100 ha of suitable habitat is required within a landscape for marsh fritillary metapopulations to persist in the long-term and models developed from this research predict that the marsh fritillary will become extinct over most of its UK range by 2020 if conditions remain the same (Bulman 2001).

Increasingly, butterfly conservationists recognise the importance of the extent and distribution of habitat patches at a landscape scale, in addition to the traditional emphasis placed on habitat quality (Moilanen and Hanski 1998; Thomas et al. 2001). The survival of butterfly metapopulations (for species such as the marsh fritillary) is dependent upon due regard being placed upon both issues, as neglect of either will result in the extinction of the metapopulation sooner or later. Our traditional focus on the maintenance of habitat quality on individual occupied sites needs to be strengthened by a much wider recognition of the role that currently unoccupied habitat patches play in metapopulation persistence. To maximise opportunities for survival the entire patch network needs to be safeguarded and as many patches as possible brought into Good Condition through sympathetic management. As Anthes et al. (2003) observed, "management exclusively focusing on optimising within patch habitat quality might increase local environmental capacity and thus decrease the local extinction probability, but it will not alter the principle [*sic*] dynamics of the entire metapopulation".

Knowledge of the distribution of the marsh fritillary in Wales, as a result of more than a decade of concerted survey effort, is very good and hence there is sufficient information with which to address habitat quality issues for occupied sites. However, across Wales there is much less of an understanding of the extent and quality of the entire patch network within metapopulation landscapes. Fortunately, CCWs comprehensive Phase One Survey of lowland habitats (Howe et al. 2005) provides an ideal platform on which to base any landscape scale assessments and GIS software now supplies an excellent tool to harness this invaluable data source. Given knowledge of the occurrence of marsh fritillaries in a particular area, the situation now exists whereby pragmatic limits for survey can be established and within this boundary land can be surveyed to determine any potential contribution to the marsh fritillary breeding resource. Habitat patches across Wales can, therefore, be mapped such that the resultant data are compatible and can contribute to Wales-wide analysis of the extent and quality of the habitat resource for the marsh fritillary.

Habitat degradation and loss has led to a sustained decline in the fortunes of the marsh fritillary in Wales and considerable effort will be necessary to secure the future of this flagship species. Targeting resources where they may have the most effective medium-long term impact and benefit is an irrefutable strategy but to do so we need some mechanism by which landscapes can be compared. The developing science of landscape ecology has generated a considerable array of indices to describe landscape heterogeneity, spatial distribution of habitat patches and connectivity. For overviews, see Haines-Young and Chopping (1996) and Gustafson (1998). Existing indices are inadequate for comparisons relevant to the quality of landscapes for the marsh fritillary. Cale and Hobbs (1994) pointed out that individual species utilise landscapes in various ways and the use of generic landscape indices can be misleading unless the index is tailored to their specific requirements. Whilst indices undoubtedly over-simplify real situations, as long as efforts are made to account for the most significant factors in a landscape as they relate to the target organism then landscape indices are likely to prove to be a beneficial tool.

Methods

Habitat mapping

The change of emphasis from surveying for the presence of adult butterflies or larval webs to landscape scale mapping of habitat quality required the development of standard categories for the condition of habitat patches (Table 1). The surveys described here focussed on patches of breeding habitat supporting the larval foodplant, devil's-bit scabious *Succisa pratensis* Moench. Given that the marsh fritillary in Wales occurs over an area extending for 220×150 km^2, it is inevitable that habitat quality surveys will involve numerous different observers and take place over several years. To reduce error from these sources as far as possible, a guidance document (Fowles 2003) was produced and a training workshop for interested parties was held. Initially habitat quality was only recorded as either 'Good' or 'Suitable' (Table 1), but experience gained during the mapping surveys helped to refine the categories used to classify habitat quality. The Suitable category was split into three on the basis of foodplant density and vegetation structure. Different approaches have also been taken with regard to the dominant sward species. Most breeding areas occur in lowland purple-moor grass *Molinia caerulea* (L.) pasture (generally referred to as 'rhos' in Wales) and, with the exception of populations based on dune slacks, this is where marsh fritillaries seem to prosper best. However, other grassland types are occasionally utilised and some surveys mapped these separately as 'Overspill Grassland (OG)' in recognition of the fact that they are often only occupied where they abut *Molinia* pasture. This distinction has now been removed and patch quality is now mapped regardless of dominant sward species (Fowles 2005).

A fundamental problem to overcome was the question of what constitutes the boundaries of the survey area. Marsh fritillaries have been reported colonising habitat patches up to 15 km from existing populations (Warren 1994) and it could be argued that the landscape should be defined by plotting circles of that radius from known populations. Although such events are significant for metapopulation dynamics, they are undoubtedly rare and a more pragmatic boundary is needed in recognition of the fact that surveys covering such

Table 1. Condition categories for mapping habitat quality for the marsh fritillary.

Good Condition (GC):	Grassland where, for at least 80% of sampling points, the vegetation height is within the range of 12–25 cm and *Succisa pratensis* is present within a 1 m radius. Scrub (>0.5 m tall) covers no more than 5% of area. (cf. Figure 3).
Suitable (Under-grazed) (SU):	Grassland where *Succisa pratensis* is occasional/frequent/abundant and vegetation height is above 25 cm, or in which sward height is between 12–25 cm but scrub (>0.5 m tall) covers more than 5% of area.
Suitable (Over-grazed) (SO):	Grassland with frequent/abundant *Succisa* but which is currently over-grazed such that the sward is below 12 cm on average. Mown swards may also come under this category.
Suitable (Sparse) (SS):	Grassland with sparse (rare-occasional) *Succisa* and vegetation height less than 25 cm on average.
Potential (Rank) (PR):	Grassland with rare *Succisa* which is currently under-grazed or neglected such that the sward is above 25 cm on average and *Succisa* occurs as scattered plants, usually in a rank, tussocky sward.
Unsuitable Habitat (NS):	All other habitat types are mapped under this category. This will include patch types that potentially could be restored to support marsh fritillaries but this is likely to involve a considerable resource input to correct former agricultural practices or to alter soil hydrology.

extensive areas are prohibitively expensive. Dispersal studies (e.g. Wahlberg et al. 2002; Konvicka et al. 2003) have shown that the marsh fritillary is generally sedentary, with maximum distances for female dispersal recorded as 510 m in Finland and 2.3 km in the Czech Republic. Habitat patches close to occupied sites will be more likely to be colonised periodically than those further away and hence efforts to improve habitat quality are likely to be more cost-effective near to existing populations than if effort is diluted across a wider landscape. In the Finnish study, males were recorded dispersing up to a maximum of 1.3 km from their origin (Wahlberg et al. 2002). We, therefore, regarded the landscape defined by circles of 2-km radius from known populations as containing the 'functional landscape', within which most colonisations will occur and where regular exchange of genetic material through male dispersal, potentially of benefit to long-term fitness of the metapopulation, takes place.

To construct the boundaries, post-1990 marsh fritillary records were plotted on a map and then circles of a 2-km radius were drawn from each record. The resultant overlapping circle areas were then combined to produce the final landscape boundary (Figure 1).

Phase One land cover maps of lowland Wales were then investigated by over-laying the functional landscapes, using MapInfo GIS software, to identify parcels of land for field survey. Marsh fritillaries will breed in a range of biotopes if their foodplant is present in the right conditions and hence a range of unimproved and semi-improved grassland, heathland and mire biotope types was included: Unimproved and Semi-improved Acid Grassland (B.1.1 & B.1.2), Unimproved and Semi-improved Neutral Grassland (B.2.1 & B.2.2), Marshy Grassland (B.5), Wet Heath (D.2), Wet Heath/Acid Grassland mosaic (D.6), Lowland Blanket Mire (E.1.6.1), Wet and Dry modified Bogs (E.1.7 & E.1.8), Valley Mire (E.3.1), Basin Mire (E.3.2), Floodplain Mire (E.3.3), Dune slack (H.6.4), Coastal Heathland (H.8.5) (Nature Conservancy Council 1990). Survey teams then visited each identified parcel and mapped patches of habitat as belonging to one of the Condition categories (Table 1; Appendix 1).

Each enclosure was walked over and the location of patches corresponding to the categories of GC, SU, SO, SS and PR mapped individually onto recent 1:10,000 scale Ordnance Survey maps or aerial photographs and subsequently transferred to a GIS database (Figure 2). Once the surveyor was confident of the nature of each patch type most surveying could be done without the need to collect detailed sample data. For instance, visual assessments of sward height were made rather than laboriously recording samples across a patch. Similarly, estimates of scrub cover could usually be judged by eye. Occasionally, in borderline cases, it was necessary to establish the frequency of *Succisa* in the sward and this could be done relatively quickly by noting presence or absence in a 1-m radius every three or five paces (depending on the area to be assessed) during a W-walk across the patch. Patches amounting to less than 25 m^2 in extent were amalgamated with the surrounding patch type.

Further guidance (Fowles 2003) was provided on the interpretation of the category definitions:

Frequency of Succisa: 'Frequent' represented *S. pratensis* distributed throughout the patch, with plants occurring within a one metre radius of at least 80% of sample points. 'Occasional' referred

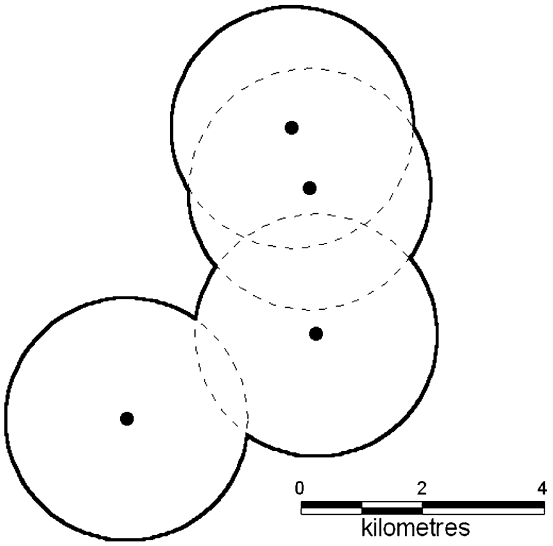

Figure 1. Construction of survey boundary based on circles of 2 km radius around known marsh fritillary populations.

to *S. pratensis* occurring within a 1 m radius of at least 50% of sample points. Cover values corresponding to these frequency estimates were in the order of 10% for 'Frequent' and 2% for 'Occasional', although for the latter category it would be inappropriate to measure cover values over the areas involved.

Scrub: The extensive grazing regimes necessary to maintain marsh fritillary habitat frequently result in a degree of scrub encroachment. On damper soils this is usually in the form of willow, birch or occasionally alder, whilst on drier soils gorse, bramble, blackthorn, etc. may become established. Some scrub may be beneficial in providing shelter for the adult butterflies during windy conditions, but if scrub development continues then shading will reduce the amount of breeding habitat (Konvicka et al. 2003). The 5% cover value utilised here is taken as representing situations where scrub is sparsely established within the patch and at present does not pose a threat of encroachment. Marsh fritillaries may

Figure 3. Good Condition habitat on Rhos Llawr-cwrt NNR, Ceredigion, Wales.

Figure 2. Part of Gower Commons candidate Special Area of Conservation showing the distribution of habitat patches.

actually tolerate a higher percentage cover by scrub but in such cases it is likely that grazing levels are too low and detrimental encroachment will follow in the near future requiring costly management intervention.

Vegetation height: Several studies of marsh fritillaries across their British range have identified optimal sward heights for marsh fritillaries. Hobson et al. (2002) reported optimal swards as 12–25 cm for southern English populations on purple-moor grass *Molinia caerulea* grasslands, whilst BUTT (1986) considered 4–12 cm as ideal on chalk grasslands. In Scotland lower swards of 5–10 cm are regarded as optimal in the cooler, wetter climate of north-western Britain (Ravenscroft and Gaywood 1996). The threshold here for Welsh populations of 12–25 cm is taken from Hobson et al. (2002), but is considered appropriate for all Welsh rhos pasture populations and is confirmed by extensive studies carried out over 10 years by Woolley (2001) at Rhos Llawr-cwrt National Nature Reserve in Ceredigion (where the optimal height was 10–20 cm). It should be remembered that sward height measurements vary with the method used (Stewart et al. 2001), as the Boorman drop disk (used by BUTT 1986; Ravenscroft and Gaywood 1996; Woolley 2001) compresses the vegetation and hence results in lower values than sward stick or direct measurement. The thresholds given here for optimal sward height are by direct measurement.

Landscape index

A simple index for evaluating the quality of the patch network, termed the Index of Landscape Quality (ILQ), has been developed for marsh fritillary metapopulations in Wales (Fowles 2005). This incorporates aspects of habitat quality, spatial distribution, and land cover and is calculated as:

$$\mathrm{ILQ} = (10\mathrm{Ao} + \mathrm{Ah})(\mathrm{Aa}/\mathrm{L}) \times 100$$

where Ao = the total area of optimal habitat; Ah = the total area of sub-optimal habitat; Aa = the total area of available habitat; and L = the landscape area (as defined above).

Optimal Habitat is defined as distinct patches of habitat in Good Condition (GC) exceeding 2 ha, or Good Condition patches which are greater than 1 ha and less than 500 m from other Good Condition patches greater than 1 ha.

Sub-optimal Habitat is Good Condition habitat that is less than 1 ha, or between 1 and 2 ha in area and isolated from other Optimal patches.

Available Habitat is the sum of all Good Condition and Suitable Habitat in the Landscape (Aa = GC + SU + SO + SS).

ILQ is a measure of the importance of connected patches of habitat in Good Condition ($10 \times$Ao), taking into account the contribution of isolated patches of Good Condition habitat (Ah), moderated by the relative proportion of Available habitat within the landscape (Aa/L). The multiplier of 10 for Ao is an arbitrary figure and it could be argued that a higher value should be assigned to these large or connected patches of Good Condition habitat. In practice, however, multiplying Ao by 100 rather than 10, for instance, makes little difference to the rankings of the landscapes, largely because of the modifying influence of Aa/L. In other words, the major influence on ILQ is the relative amount of overall Good and Suitable Habitat within a landscape, reflecting the significance for metapopulation viability of reduced fragmentation. This emphasis is appropriate as, in neutral landscape models, With et al. (1997) found that "one factor variable described almost all the variation in distributional patterns … the relative abundance of habitat exerted a large effect on population dispersion, reflecting the threshold phenomenon of percolating networks". For the purposes of ILQ the 'core landscape' (constructed from 1 km radii from known populations) is utilised. This focuses on patches that are most likely to be colonised in the short-term and are therefore the most cost-effective for habitat restoration.

For the marsh fritillary, autecological studies have demonstrated (e.g. Bulman 2001) that the most important elements of a landscape are the quantity of habitat patches, their quality, and their proximity to other suitable patches. Landscape quality will also be affected by the influence of barriers to dispersal (overgrown hedgerows, blocks of woodland, major roads, broad expanses of unsuitable land, etc.) (Mader et al. 1990). However, not enough is known about the relative importance of these features to be able to quantify their effects. Indeed, Gustafson and Gardner (1996) point out that "the landscape matrix between habitat islands is not homogenous, and the dynamics of organism movement between habitat islands in such a

matrix has not been widely studied and is poorly understood''. Factoring in the complex mathematics associated with barriers would make the index unduly complicated without any guarantee that it truly reflected the quality of a landscape as experienced by marsh fritillaries. Hence consideration of barrier effects (frequently referred to in the literature as landscape permeability or viscosity) is omitted from the index described here.

Results

Habitat condition

Between 2000 and 2004 fourteen separate habitat condition surveys have taken place in Wales (Figure 4), over an area covering 116,373 ha (Smith 2000, 2004, 2005a, b; Wheeler et al. 2000; Woodman and Fowles 2002; Smith et al. 2002, 2003; Boardman 2003, 2004; Powys Local Biodiversity Action Plan Partnership 2003; Graham 2005; Smith and Gander 2005; unpublished data). In total, 12,405 ha of grassland have been surveyed, but there is a degree of overlap between surveys and the actual amount of land reported on equals 11,470 ha. The area of grassland actually surveyed ranged in size from 45 ha based around a candidate Special Area of Conservation (cSAC) to 3266 ha encompassing all potential grassland within the administrative district of Rhondda Cynon Taff. Within the survey areas lie 111 marsh fritillary populations, 55.2% of the known post-1990 Welsh resource. Of the grassland that was surveyed, 1822 ha (15.9%) were mapped as being capable of supporting marsh fritillary populations on the basis of the presence of the foodplant (Figure 5a–c).

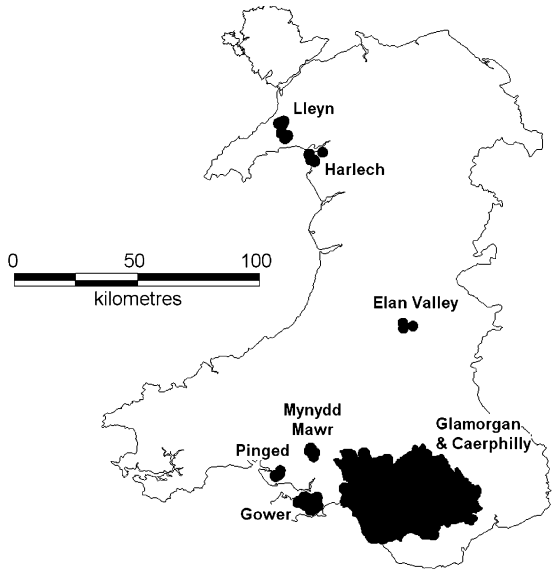

Figure 4. Areas of Wales surveyed for marsh fritillary habitat quality.

Only 216 ha of the grassland that was potentially suitable for marsh fritillaries (11.85%) was classified as being in Good Condition (Table 2). The remaining 1606 ha were recorded as being capable of supporting populations but were regarded as having either an unsuitable vegetation structure and/or the foodplant was at low density. Of the 452 ha of Suitable habitat that was assigned to a sub-category, 55 ha were classed as Over-grazed, 94 ha were classed as Sparse (which is often the result of sheep grazing), 214 ha were classed as Under-grazed and 89 ha were classified as Rank. Thus, 33% of the potential habitat area can be regarded as inappropriately or excessively managed and 67% was suffering from neglect.

Patch size

Patch size, along with habitat quality, is considered to be an important factor in the successful persistence of butterfly species that exist in metapopulations (Schoener and Spiller 1987; Thomas 1992). The largest continuous patch of Good Condition (GC) habitat found in these surveys was 18.68 ha, forming the stronghold of the candidate SAC of Corsydd Eifionydd in North Wales. However, most patches of GC were small (Figure 6), with patches less than 0.5 ha accounting for 85.3% of the 573 GC patches recorded, and the average GC patch size was 0.37 ha. For the other categories of suitable habitat (excluding GC), the average patch size was 1.1 ha (n = 1462), with 58.6% of patches less than 0.5 ha.

The marsh fritillary will breed, albeit at lower density, in patches that are not in Good Condition and hence the overall size of patches of breeding habitat, regardless of their current condition, will have a major bearing on population persistence. Many grasslands consist of mosaics of habitat in different categories of condition as a result of soil

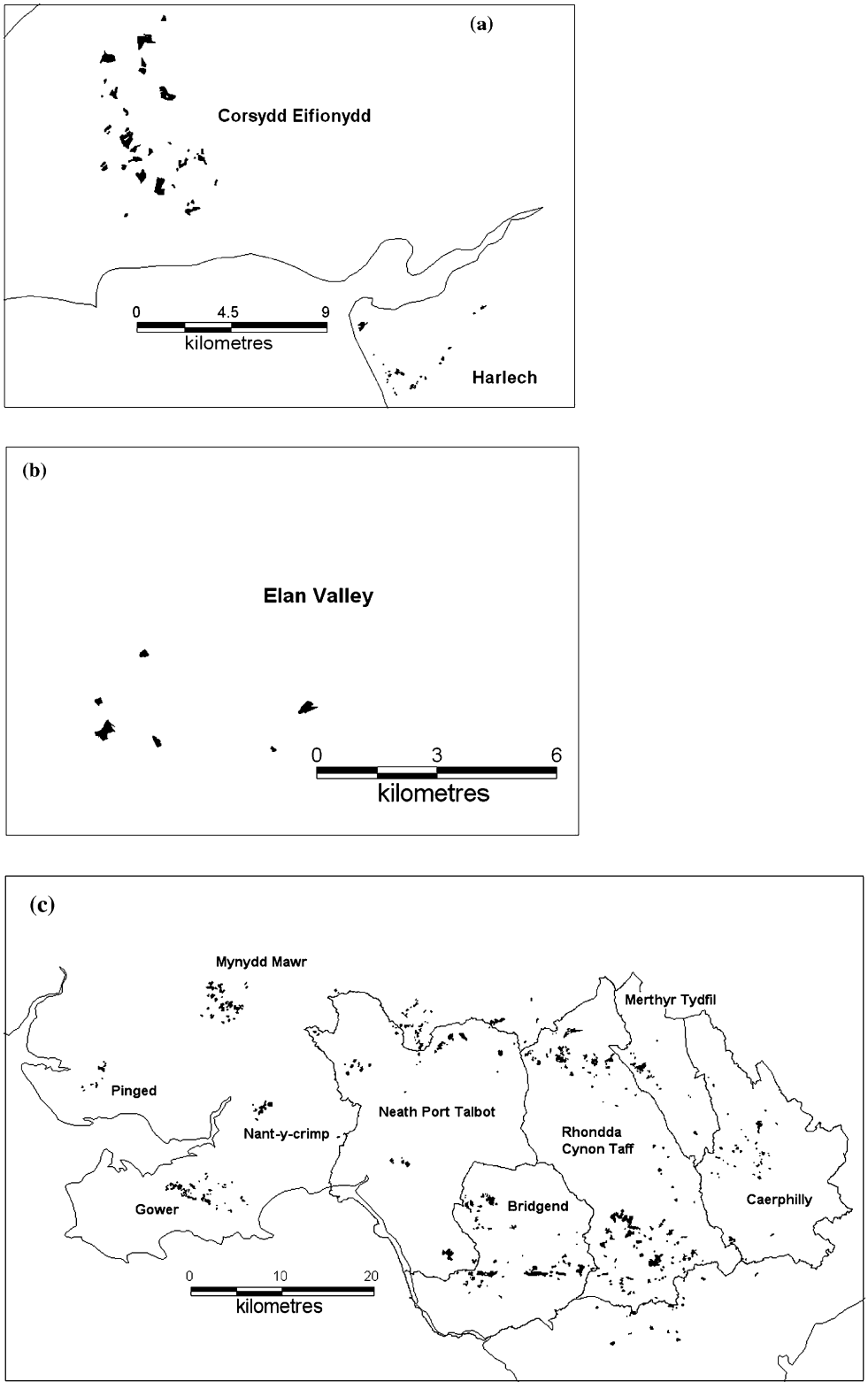

Figure 5. Distribution of available breeding habitat in the areas surveyed: (a) North Wales; (b) Mid Wales; (c) South Wales.

Table 2. Area of grassland in different habitat condition categories.

Survey district	Area surveyed (ha)	Condition category (ha)							Total available habitat (ha)
		GC	SO	SS	SU	OG	S	PR	
South Wales 2000	553.60	50.27	n	n	n	n	158.05	n	208.32
Mynydd Mawr	780.88	10.72	n	n	n	14.88	105.56	n	131.16
Corsydd Eifionydd	1141.00	38.88	11.36	28.39	109.68	21.75	n	9.90	219.96
Bridgend CBC	723.90	21.58	n	n	n	45.46	189.68	n	256.72
Nant-y-crimp SSSI	84.70	4.50	n	n	n	4.85	32.82	n	42.17
Aberbargoed cSAC	45.00	2.37	0	0	7.52	2.37	n	0.22	12.48
Neath Port Talbot CBC	1499.00	14.63	17.53	23.8	74.70	16.38	n	57.00	204.04
Rhondda Cynon Taff	3265.90	49.40	n	n	n	n	585.11	n	634.51
Merthyr Tydfil CBC	306.50	1.12	0	0.08	0	0.57	n	0	1.77
Elan Valley	170.66	0.21	0	17.95	0.03	0	n	6.91	25.10
Gower Commons	1108.37	7.70	19.40	13.36	9.68	0	n	2.23	52.37
Morfa Harlech	1740.00	7.00	6.06	0.80	1.50	0	n	1.53	16.89
Ystradgynlais	418.60	5.40	6.03	5.78	10.69	4.39	n	8.52	40.81
Caerphilly	566.80	4.40	0.67	2.99	1.26	8.21	n	1.40	18.93
Total	12404.91	218.18	61.05	93.15	215.06	118.86	1071.20	87.71	1865.23
% of area surveyed		1.76	0.49	0.75	1.73	0.96	8.64	0.71	15.04
Combined survey data	11470.67	215.96	55.09	94.14	213.74	129.78	1024.40	89.38	1822.46
Available habitat (%)		11.85	3.02	5.17	11.73	7.12	56.21	4.90	
% of area surveyed		1.88	0.48	0.82	1.86	1.13	8.93	0.78	15.89

Values for the combined survey data differ from the total of individual surveys because of boundary overlaps. (For Condition Categories, see Table 1; n = category not included in survey).

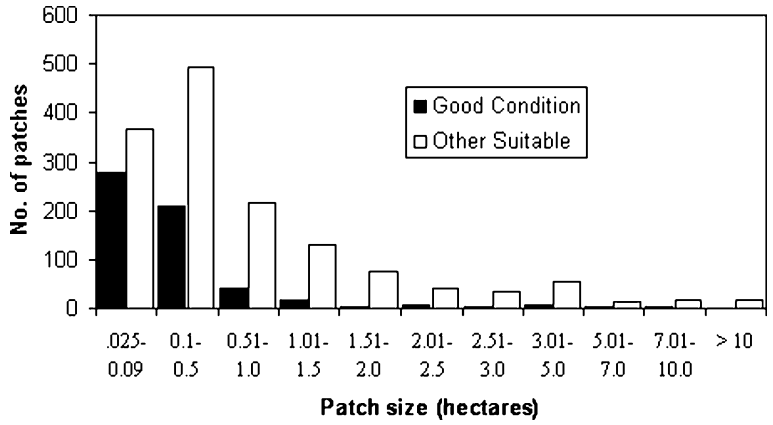

Figure 6. Patch size of Good Condition and other suitable habitat.

moisture, vegetational growth in response to climate, and grazing intensity. These variables effectively combine to produce the patch dynamics so characteristic of these landscapes (Blackstock et al. 1998). When contiguous patches of suitable habitat are amalgamated the average patch size increases to 1.62 ha (n = 1111) but 56.5% of these merged patches are still less than 0.5 ha (Figure 7). Bulman (2001) found that breeding did not occur in suitable patches less than 0.1 ha in size. In the present study there were 293 patches (26.4%) below this threshold, but together they account for only 15.39 ha, less than 0.01% of the total resource. In area terms these small patches may be insignificant but they indicate grasslands that have the potential to support more suitable habitat if appropriate management is instigated.

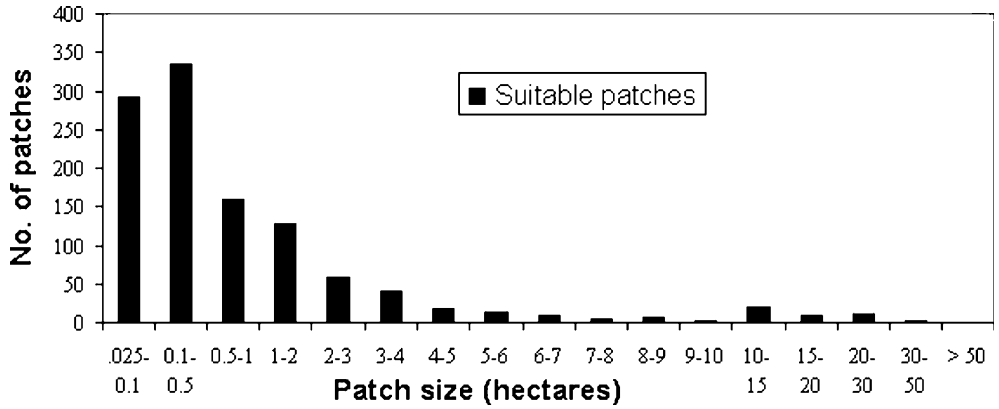

Figure 7. Size of amalgamated patches of suitable breeding habitat.

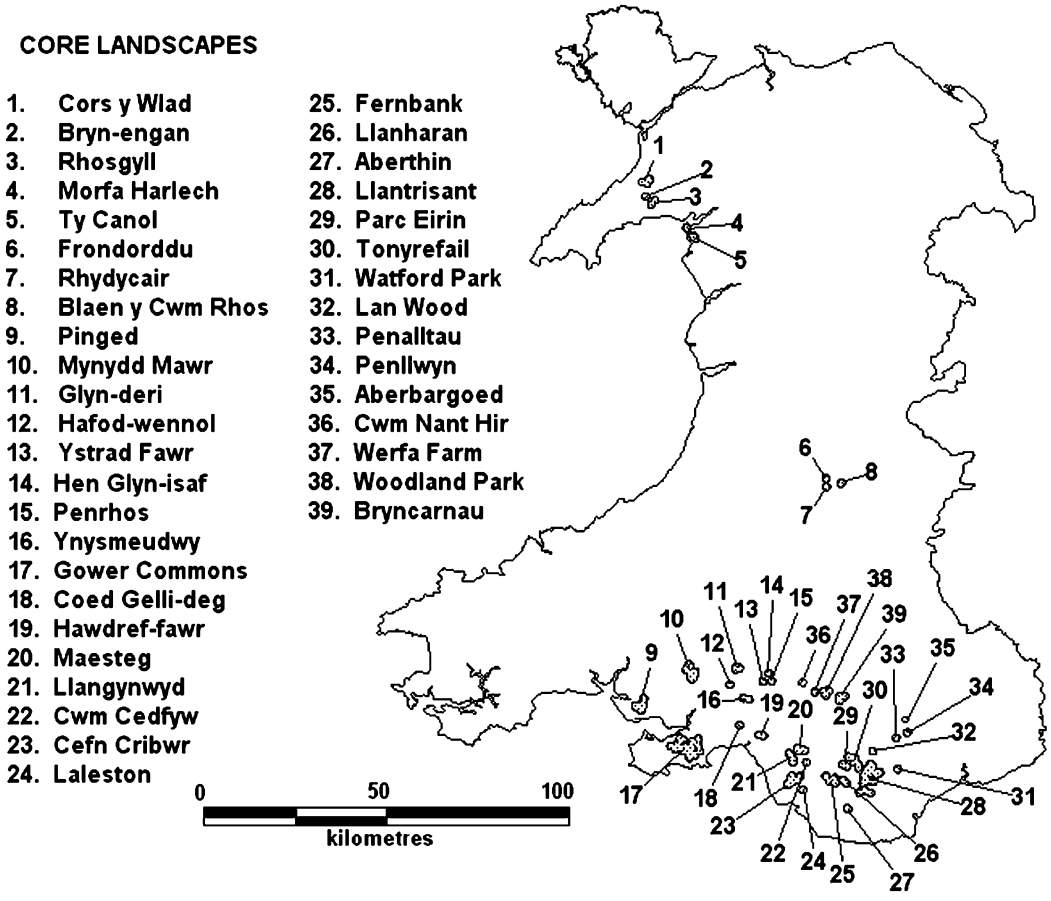

Figure 8. Location of 'core' marsh fritillary landscapes.

Land cover

We calculated percentage cover of suitable habitat for 39 'core landscapes' based on interlocking circles of 1 km radii from known marsh fritillary populations (Figure 8; Table 3). This accounted for 107 of the 111 populations included within surveys to date; the other four had incomplete

Table 3. Area (ha) and percentage land cover of available habitat within 'core' marsh fritillary landscapes.

Core landscape	No. of populations	Landscape area	Available habitat	% Available
30. Tonyrefail	3	1300.28	145.81	11.21
38. Woodland Park cSAC	4	783.84	69.07	8.81
2. Bryn Engan	2	313.79	23.98	7.64
3. Rhosgyll	1	580.64	41.69	7.18
10. Mynydd Mawr cSAC	5	1670.28	119.89	7.18
36. Cwm Nant Hir	1	313.79	20.70	6.60
1. Cors y Wlad cSAC	3	836.08	54.64	6.54
39. Bryncarnau	3	790.39	44.36	5.61
23. Cefn Cribwr	7	1498.42	77.69	5.18
16. Ynysmeudwy	2	600.77	28.93	4.82
37. Werfa	1	313.79	14.78	4.71
21. Llangynwyd	4	830.74	38.07	4.58
13. Ystrad Fawr	1	313.79	14.23	4.53
20. Maesteg	5	844.23	37.35	4.42
25. Fernbank	4	1162.38	44.99	3.87
19. Hawdref-fawr	2	562.22	20.13	3.58
35. Aberbargoed cSAC	1	313.79	10.84	3.45
28. Llantrisant	15	3797.98	110.84	2.92
31. Watford Park	1	313.79	7.87	2.51
29. Parc Eirin	2	560.18	12.57	2.24
15. Penrhos	1	313.79	5.43	1.73
12. Hafod-wennol	1	313.79	5.38	1.71
7. Rhos Rhydycair	1	358.39	6.06	1.69
27. Aberthin	1	353.75	5.91	1.67
26. Llanharan	2	558.98	8.68	1.55
22. Cwm Cyfedw	1	313.79	4.79	1.53
14. Rhos Hen Glyn-isaf	1	313.79	4.72	1.50
17. Gower Commons cSAC	13	4357.90	62.10	1.42
5. Ty Canol	3	645.51	8.62	1.34
9. Pinged	5	1200.26	16.10	1.34
18. Coed Gelli-deg	1	313.79	3.90	1.24
4. Morfa Harlech	1	366.10	4.29	1.17
8. Blaen Cwm Rhos	1	313.79	2.86	0.91
32. Lan Wood	1	313.79	2.63	0.84
6. Rhos Frondorddu	1	313.79	2.58	0.82
34. Penllwyn Grasslands	1	313.79	2.37	0.76
24. Laleston	1	313.79	2.19	0.70
11. Glyn-deri	3	592.64	3.41	0.58
33. Penalltau	1	313.79	0.72	0.23
Total	107	29586.40	1091.17	3.69

survey data for the full core landscape. Recent modelling (Bulman et al. unpublished data) based on data taken from 12 networks across England and Wales has shown that, within 4×4 km^2 sample plots, marsh fritillary metapopulations were estimated to require a minimum of 100 ha of suitable habitat for a 95% probability of long-term persistence. This equates to 6.25% of the land surface. Further simulations of larger landscapes (up to 16,000 ha) gave a Minimum Viable Metapopulation (MVM) size of about 4% of the land surface area. Only three of the core landscapes exceeded the 1600 ha used in the initial models and only one of these, the candidate SAC of Mynydd Mawr in Carmarthenshire, had habitat cover above 6.25%. In total, just seven of the core landscapes exceeded this threshold and hence it can be assumed that most marsh fritillary populations in Wales currently exist within landscapes with inadequate habitat resource to sustain their metapopulations in the long term.

Table 4. Index of Landscape Quality values for 'core' landscapes.

Core landscape	ILQ
Cors y Wlad cSAC	1287.25
Rhosgyll	594.43
Bryn Engan	580.57
Tonyrefail	427.92
Llantrisant	339.20
Fernbank	338.86
Mynydd Mawr cSAC	205.72
Cefn Cribwr	201.95
Ynysmeudwy	159.15
Werfa Farm	131.41
Gower Commons cSAC	106.18
Morfa Harlech	50.27
Bryncarnau	35.98
Rhos Hen Glyn-isaf	31.39
Woodland Park cSAC	17.89
Maesteg	14.02
Parc Eirin	11.29
Llangynwyd	10.22
Hawdref-fawr	9.06
Aberbargoed cSAC	8.19
Ystrad Fawr	3.99
Ty Canol	2.64
Pinged	2.55
Llanharan	2.05
Penrhos	1.92
Watford Park	1.33
Coed Gelli-deg	0.96
Cwm Cyfedw	0.69
Penllwyn Grasslands	0.65
Aberthin	0.42
Rhos Frondorddu	0.17
Cwm Nant Hir	0.13
Glyn-deri	0.05
Hafod-wennol	0.03
Penalltau	0.03
Laleston	0.00
Lan Wood	0.00
Rhos Rhydycair	0.00
Blaen Cwm Rhos	0.00

Table 5. Index of Landscape Quality for a hypothetical viable landscape (see text).

		Model landscape
Landscape area	L	1600.00
Area of Good Condition habitat (Ao + Ah)	Ag	11.85
Area of optimal habitat	Ao	6.10
Area of sub-optimal habitat (Ag − Ao)	Ah	5.75
Area available habitat	Aa	100.00
Index of Landscape Quality		417.19

Index of Landscape Quality

We calculated ILQ for 39 core marsh fritillary landscapes across Wales (Table 4; Appendix 2), with the intention of identifying those landscapes with the most potential for restoration. What we do not know at present is what value constitutes an acceptable ILQ for long-term viability of marsh fritillary metapopulations. Population data associated with individual patches would be required to validate any threshold and these data are not currently available. However, we can propose a minimum baseline threshold for indicative purposes by analysing a model landscape based on the sample areas of Bulman (2001) and the amount of GC habitat as a proportion of available breeding habitat across Wales. For a landscape of 1600 ha, the MVM models indicated that 100 ha need to be capable of supporting marsh fritillary populations, whilst across Wales 11.85% of available habitat was in Good Condition. There is no evidence on which to estimate what proportion of the GC habitat should be Optimal (i.e. large or connected patches), but if we take as a starting point the value of 50.3% that was observed in these surveys, we would expect 6.1 ha of the model landscape to be classed as Optimal. The resultant ILQ for this 'model' landscape is 417.19 (Table 5) and hence we may consider, at least until further studies are available, that this represents a minimum ILQ for a viable habitat network.

There are just four 'core landscapes' that exceed this threshold. Three of these are on the Lleyn peninsula in North Wales and are part of the functional landscape in which lies the Corsydd Eifionydd cSAC. Some of the habitat patches here were mapped at a coarse resolution and it is likely that the amount of available breeding habitat has been over-estimated (leading to an elevated ILQ), but it is clear that this is an important area for marsh fritillaries in Wales. The other core landscape exceeding the hypothetical threshold surrounds the South Wales town of Tonyrefail in Glamorgan. The strength of the marsh fritillary population here has only recently been recognised and at present the area has no protection. However, the Countryside Council for Wales, in partnership with Rhondda Cynon Taff County

Borough Council and Butterfly Conservation, has just embarked on a targeted project to encourage sympathetic management in this area. It is worrying that none of the other four cSACs for marsh fritillaries in Wales analysed in this study approach the suggested threshold and this suggests that urgent efforts are required to improve habitat quality and extent in order to secure Favourable Conservation Status.

Discussion

There is a growing awareness amongst conservationists that global problems of habitat fragmentation require solutions at a landscape scale (Burke 2000; Melbourne et al. 2004; Opdam and Wascher 2004). Whilst the protection of important localities for wildlife will remain a cornerstone of conservation, without considerable efforts to restore semi-natural habitats to the wider countryside biodiversity will inevitably decline. Given the fact that relatively few insect species have had their population dynamics investigated, it seems inevitable that more species operate at a metapopulation level than we currently know about and unless fragmentation is halted it seems certain that we will witness local extinctions of more and more species. The studies reported here are examples of the way in which we need to shift emphasis. No longer is it sufficient to monitor trends in the abundance of butterflies; we need to address the extent, configuration and quality of their habitat resources in the landscape (Dennis et al. 2003).

Many of the sites with low ILQ values contain single populations, that is, they are isolated by at least 1 km in all directions from other populations. With the exception of Rhosgyll (one of the Lleyn populations discussed above) and Werfa Farm (a landscape with one large patch of GC habitat), all single population core landscapes have very low ILQs, demonstrating that isolated populations usually lie within landscapes containing insufficient or poor quality habitat. If the landscapes contained better patches of habitat it would be expected that they would have been colonised and hence hold more populations. Several multi-population landscapes also have low ILQ values. Three of these (Ty Canol, Pinged and Llanharan) occur in areas that used to hold greater quantities of breeding habitat but agricultural improvement or neglect has led to substantial declines. The marsh fritillary populations surviving in these core landscapes are all relatively small and are probably examples of extinction debt. Nine of the lowest-scoring landscapes have all had a maximum of less than 15 adult butterflies or larval webs recorded at any time since 1990. Indeed, several have not produced records of marsh fritillaries for some years and may already be extinct.

Conclusion

The studies described here represent an attempt to translate metapopulation theory into conservation practice. Detailed modelling has established the necessary principles but conservation organisations rarely have the resources to collect data of the quality necessary to populate the models. Instead pragmatic compromises have to be taken, especially with regard to species that occur over large areas of the countryside, to apply the lessons learnt from academic research.

The habitat quality surveys aim to provide the information on which to tackle the issues of metapopulation dynamics for the marsh fritillary in Wales. With over half of the areas recently supporting marsh fritillaries assessed, we now have a much better understanding of the extent, distribution and quality of the breeding habitat and are able to focus conservation action on priority landscapes and identify those landscapes where habitat restoration would be difficult. There is clearly considerable scope to improve the condition of marsh fritillary breeding habitat in many areas, given that only 11.85% of the suitable habitat was classified as being in Good Condition. Much of the grassland that was economically viable to improve agriculturally has already been destroyed as breeding habitat and neglect is now a much more significant threat, as evidenced by the fact that 67% of suitable grassland was either rank or under-grazed. This is a familiar problem for unimproved grassland in lowland Britain and initiatives such as

agri-environment schemes, to pay landowners for sympathetic management, have been introduced to restore appropriate grazing regimes. Extensive areas are also over-grazed or stocked with sheep, leading to substantial declines in the abundance of the foodplant. Agri-environment schemes can help to reduce stocking density but it is much more difficult to encourage farmers to change their livestock.

The status of the marsh fritillary in England and Wales will continue to deteriorate unless significant resources are devoted to addressing the problems of habitat fragmentation and impoverishment. There are several innovative projects that have recently been established, such as the Mynydd Mawr and Tonyrefail schemes in Wales and the Mid-Cornwall, Salisbury Plains and Culm Grasslands projects in England, to focus on landscape-scale conservation for the marsh fritillary. If we are to secure a future for this species then urgent action must take place to address the dominant issues that threaten its populations. In particular, efforts must be taken at landscape scale to address the deterioration in habitat quality as a result of changes in farming practices and to prevent further isolation of habitat patches due to succession or habitat loss.

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Appendix 1. Criteria table for marsh fritillary patch types.

		Succisa			Vegetation height			Scrub <5% cover
		Frequent – Abundant	Occasional	Rare	< 12 cm	12–25 cm	> 25 cm	
Good condition	GC	✓				✓		✓
Suitable (under-grazed)	SU	✓	✓				✓	
Suitable (over-grazed)	SO	✓			✓			✓
Suitable (sparse)	SS		✓	✓	✓	✓		✓
Potential (rank)	PR			✓			✓	
Unsuitable	NS							

Appendix 2. Index of Landscape Quality (ILQ) and amount of habitat (ha.) assigned to each condition category for 'core' landscapes (see Table 1 and Figure 8)

Core Landscape	O.S. 10 km square	Survey Area	Condition Category (ha)								Available habitat	ILQ
			GC Optimal	GC sub-Optimal	SO	SS	SU	OG	S	PR		
Cors y Wlad cSAC	SH44	836.08	19.49	2.07		5.41	5.92	21.75			54.64	1287.25
Rhosgyll	SH44	580.64	8.25	0.29	4.71		28.10			0.34	41.69	594.43
Bryn Engan	SH44	313.79	7.56	0.37	4.97		9.05			2.03	23.98	580.57
Tonyrefail	ST38	1300.28	2.81	10.06					132.90		145.81	427.92

Appendix 2. (Continued).

Core Landscape	O.S. 10 km square	Survey Area	Condition Category (ha)								Available habitat	ILQ
			GC Optimal	GC sub-Optimal	SO	SS	SU	OG	S	PR		
Llantrisant	ST08	3797.98	10.99	6.33					93.52		110.84	339.20
Fernbank	SS98	1162.38	8.53	2.25					34.21		44.99	338.86
Mynydd Mawr cSAC	SN51	1670.28	2.30	5.66				13.82	98.11		119.89	205.72
Cefn Cribwr	SS88	1498.42	2.77	11.25				27.66	35.35	0.66	77.69	201.95
Ynysmeudwy	SN70	600.77	3.07	2.35	1.90	3.28	5.08	10.65		2.60	28.93	159.15
Werfa Farm	SN90	313.79	2.67	1.20					10.91		14.78	131.41
Gower Commons cSAC	SS59	4357.90	6.70	7.51	19.50	14.30	9.49	0.77		3.91	62.10	106.18
Morfa Harlech	SH53	366.10	4.29								4.29	50.27
Bryncarnau	SN90	790.39		6.41					37.95		44.36	35.98
Hen Glyn-isaf	SN71	313.79	2.07	0.17	0.20	1.53	0.61			0.14	4.72	31.39
Woodland Park cSAC	SN90	783.84		2.93					67.04		69.97	17.89
Maesteg	SS89	844.23		3.17				2.27	31.91		37.35	14.02
Parc Eirin	SS98	560.18		5.03					7.54		12.57	11.29
Llangynwyd	SS88	830.74		2.23				5.43	30.41		38.07	10.22
Hawdref-fawr	SS79	562.22		2.53		8.24	8.26	0.45		0.65	20.13	9.06
Aberbargoed cSAC	ST19	313.79		2.37			7.42	0.83		0.22	10.84	8.19
Ystrad Fawr	SN71	313.79		0.88	3.30	6.69	0.67			2.69	14.23	3.99
Ty Canol	SH53	645.51		1.98	6.06		0.27			0.31	8.62	2.64
Pinged	SN40	1200.26		1.90					14.20		16.10	2.55
Llanharan	SS98	558.98		1.32					7.36		8.68	2.05
Penrhos	SN71	313.79		1.11		0.04	3.15	0.31		0.82	5.43	1.92
Watford Park	ST18	313.79		0.53				0.20	7.14		7.87	1.33
Coed Gelli-deg	SS79	313.79		0.77		2.17			0.55	0.41	3.90	0.96
Cwm Cyfedw	SS88	313.79		0.45				0.24	4.10		4.79	0.69
Penllwyn	ST19	313.79		0.86		0.02	0.04	0.26		1.19	2.37	0.65
Aberthin	ST07	353.75		0.25					5.66		5.91	0.42
Frondorddu	SN96	313.79		0.21		2.37					2.58	0.17
Cwm Nant Hir	SN80	313.79		0.02					20.68		20.70	0.13
Glyn-deri	SN71	592.64		0.09	1.35	1.16	0.56	0.25			3.41	0.05
Hafod-wennol	SN60	313.79		0.02			0.79	3.84		0.73	5.38	0.03
Penalltau	ST19	313.79		0.11		0.13		0.14	0.28	0.06	0.72	0.03
Laleston	SS88	313.79						2.19			2.19	0.00
Lan Wood	ST09	313.79							2.63		2.63	0.00
Rhydycair	SN96	358.39								6.06	6.06	0.00
Blaen Cwm Rhos	SN96	313.79				2.86					2.86	0.00
		TOTAL:	84.91	83.78	42.00	48.20	79.40	91.06	642.49	22.82	1091.17	

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