



Conservation implications of long-term changes detected in a lowland heath plant metacommunity



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ABSTRACT

Conservation management that is focused on the scale of individual habitat patches rarely considers the implications for conservation of metacommunities at the regional scale. Here we examine the conservation implications of long-term changes identified in a vascular plant metacommunity associated with lowland heathland in Dorset, UK. This was achieved by re-surveying 150 patches that were first surveyed in the 1930s and assessing changes in species distributions, diversity, community composition and metacommunity structure. Results were compared for two sets: (i) all remaining heathland patches and (ii) intact heaths, excluding partly degraded sites. Overall, patterns of change were similar for the two sets. Values of γ - and α -diversity both decreased over time as individual patches shifted towards either woodland or improved grassland communities. However, only the intact heaths set exhibited a significant decrease in β -diversity. Both sets lost metacommunity structure over time, suggesting a change in underlying processes. These changes were attributable both to management regimes adopted at local sites, relating to their differing ownership, and to wider processes of environmental change. These results highlight the need to place site-based conservation actions in the context of regional-scale processes, to ensure the long-term conservation of metacommunity structure and function.

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1. Introduction

Conservation management has experienced a paradigm shift in recent years, from strategies focused solely on individual sites towards the development of conservation approaches at larger spatial scales (Gimona et al., 2012; Lawton et al., 2010). This reflects growing recognition that different ecological processes operate across different spatial and temporal scales (Cousins and Vanhoenacker, 2011; McGill, 2010), and are capable of significant interaction (Noss, 2001; Skórka et al., 2010). Consequently, it has become increasingly evident that ecological processes should be considered at multiple scales to enable conservation actions to be designed and implemented effectively (de Bello et al., 2010; Jones, 2011). The concept of metacommunities, namely sets of local communities that are linked by dispersal, has particular value in this context (Leibold et al., 2004). Analysis of metacommunity

dynamics can provide insights into the viability of multi-species communities and their responses to environmental change, which can inform the development of appropriate conservation responses at both site and regional scales (Devictor and Robert, 2008; Siqueira et al., 2012).

Here we examine the application of metacommunity theory to conservation management by measuring the long-term change in species diversity and composition within a heathland plant metacommunity. Lowland heathland is a European priority habitat for nature conservation found predominantly on acidic soils on the Atlantic seaboard of Europe (Gimingham, 1994; Loidi et al., 2010). It is largely an anthropogenic plagioclimax habitat, arising from humans preventing succession to woodland by using the vegetation for grazing livestock and as a supply of fuel, building and bedding materials (Bokdam and Gleichman, 2000; García et al., 2013; Gimingham, 1994). Economic and cultural changes over the last century have led to a decline in traditional uses of heathland, so its continued existence depends increasingly on conservation management interventions (Hardtle et al., 2007; Webb, 1998). In addition to local-scale processes such as succession, heathlands across Europe are impacted by larger-scale disturbances. For example, atmospheric environmental change such as decreased rainfall (Paxman, 1992), increased temperature (Peñuelas and Boada, 2003) and atmospheric deposition of

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anthropogenic nitrogen (Britton and Fisher, 2007; Hansen and Nielsen, 1998; Marrs, 1993), could potentially affect the distribution of species, community composition, and metacommunity structure. Such factors have been found to influence long-term dynamics of other metacommunities (Ernest et al., 2008; Keith et al., 2009, 2011; Newton et al., 2012). However, currently heathland management decisions are primarily made at the local patch scale, with little reference to the dynamics or processes occurring at the metacommunity scale.

Our aim here is to evaluate the conservation implications of long-term change in heathland communities at patch and metacommunity scales. We assess the effects of both local management and wider environmental change and examine whether a failure to consider functioning of the entire metacommunity may be limiting the effectiveness of management interventions. Specifically, we test the hypotheses that:

- (1) Patterns in species distributions, diversity, community composition and metacommunity structure have undergone similar changes over a 70 year interval in both all remaining heathland patches (AP) and in relatively intact patches (IP).
- (2) Metacommunity dynamics have been influenced by: (a) local differences in management strategies of different owners of individual patches, and (b) large-scale environmental change (e.g. nutrient availability, temperature, precipitation).

2. Materials and methods

2.1. The study system

The Dorset Heaths (UK) consist of heathland patches that vary in quality, from intact to very degraded. Patches are managed for a range of outcomes which results in them differing in the extent of intactness as heathland. This includes: biodiversity conservation; recreation; military training; forestry and pasture. Fragmentation and loss of the Dorset Heaths has been well documented (Rose et al., 2000). From the 1930s to the 1980s, heathland underwent major declines in extent (Horsfall, 1989), largely attributed to a decrease in traditional heathland management and conversion to alternative land uses (Hooftman and Bullock, 2012). Our study compared the current vegetation assemblages associated with patches of Dorset Heath with those recorded in the 1930s.

2.1.1. The “1930s” survey

Data on vascular plant species distribution were collected by Professor Ronald Good from 1931 to 1939 in 505 heathland patches selected using what Good referred to as the “stand” method (Fig. A1). Stands were “...reasonably distinct topographical and ecological entit[ies]...” and were required to be “...as evenly scattered as possible” across Dorset (Good, 1937). All vascular plant species encountered during a survey of approximately one hour were recorded within each stand, generating a species list, and stand locations were recorded on six inch Ordnance Survey (OS) maps, which were subsequently digitised by the Dorset Environmental Records Centre (DERC).

2.1.2. 2010 Resurvey of heathland patches

For clarity, henceforth we refer to Good’s stands as ‘patches’ and the species list for a patch as a ‘community’. Good surveyed a total of 505 patches of heathland vegetation. We re-visited a random selection of the 227 patches still recorded as surviving “relatively unchanged” in the 1980s by Horsfall (1989). A total of 160 patches were visited between mid-June and mid-August 2010. Ten of these patches were found to have been completely destroyed since 1989, i.e. they had no plant species in 2010 that were recorded in the

original 1930s survey. These had been lost to quarrying (four patches), housing (two patches) or arable crops (four patches) and so were not resurveyed. The 150 remaining patches varied in size from 0.12 to 21.00 ha, with a mean size of 4.60 ha (SD = 4.34). They varied in their extent of intactness but all had a perennial vegetation cover including at least one species recorded from the 1930s survey. All 150 were resurveyed to form the All Patches “AP” set. A subset of 65 of these patches had a vegetation cover sufficiently intact to classify as “heathland” (of any type) according to a Phase 1 Survey, the standard UK method of assigning habitat types (JNCC, 2010). These were considered as the Intact Patches “IP” subset.

Patches were relocated in the field using a hand held Global Positioning System (GPSmap 60CSx, Garmin Ltd., Southampton, UK) supported by digital maps of the Good patches supplied by DERC and 1:25,000 scale raster OS tiles. Each patch was surveyed for approximately one hour to match as closely as possible the survey intensity applied by Good. Detailed maps are available of the Good patches and care was taken to re-survey the exact and total patch area surveyed by Good. All vascular plant species were recorded as presence only data (i.e. without recording a measure of abundance) to follow Good’s method as precisely as possible. In a few cases, Good identified species of *Agrostis* and *Pinus* only to genus. We applied the conservative assumption that these were the same species as encountered in 2010.

2.2. Data analysis

Analyses were conducted in R ver. 2.9.2 (R Development Core Team, 2008) using package *vegan* ver. 1.17-6 (Oksanen et al., 2011) and *Primer* ver. 6 (Clarke and Gorley, 2006).

2.2.1. Patterns of change in species distribution, diversity, community composition and metacommunity structure

Significance of change in patch occupation by individual species was tested with McNemar’s test for paired dichotomous values, determined using Eq. (1) with a Yates’ correction:

$$\chi^2 = \frac{((b - c) - 0.5)^2}{b + c} \quad (1)$$

where b represents the number of patches at which the species became locally extinct, and c represents the number of patches that the species has colonised. We also calculated extinction rate and colonisation rate for each species as a proportional rate of extinction/colonisation per patch. Extinction rate was the number of patches from which a species became extinct (n_{ext}) divided by the number of patches in which that species was present in the 1930s survey. Colonisation rate was the number of patches that were colonised by each species (n_{col}) divided by the number of patches in which each species was present in 2010.

We assessed the significance of change in γ -(regional) diversity between the two survey times with a bootstrap method (Jost, 2006; Supplementary methods A1.1). Change in β -diversity between the two surveys was assessed for APs and IPs using Sorensen’s similarity indices (S) (Eq. (2)) to assess the homogenisation of community composition which is a measure of β diversity change (Koleff et al., 2003).

$$S = \frac{2a}{2a + b + c} \quad (2)$$

where a is the number of species present in both surveys, b is number of species present only in the Good 1930s survey, and c is the number of species present only in the 2010 survey. The significance of differences in β -diversity between surveys was tested for APs and IPs using a Wilcoxon paired ranks test (Wilcoxon, 1945). To

determine whether there had been a significant change in α -diversity (species richness within patches) or species patch occupation between the two surveys, we used paired Wilcoxon tests. We calculated the mean change in range extent across species for each community between the 1930s and 2010 surveys and assessed significance of this change using a Wilcoxon paired test. The individual range extent for each species was based on the number of 10 km grid squares occupied in Great Britain (Hill et al., 2004).

Change in community composition between the 1930s and 2010 surveys and between owner groups (described below) was assessed by a one-way Analysis of Similarity (ANOSIM) (Clarke and Gorley, 2006) with 999 permutations, based on a Bray–Curtis similarity matrix for presence-absence data. ANOSIM generates a global R statistic that represents similarity and generally ranges from 0 (total similarity) to 1 (total dissimilarity). We used SIMPER (Clarke and Gorley, 2006) to identify which species most characterise each group and to identify which species most contribute to differences between groups. We ran SIMPER using a 50% contribution cut-off point. Broad habitat types associated with each of these species were obtained from the PLANTATT database (Hill et al., 2004).

To determine the structure that best described the metacommunity in the 1930s and 2010 surveys for AP and IP, we used elements of metacommunity structure (EMS) analysis (Leibold and Mikkelsen, 2002; Presley et al., 2009; Supplementary methods A1.2). To prevent bias when calculating the number of gaps within species ranges (coherence), we removed species that occurred in one site only (Presley et al., 2009) – it is not possible for such species to have gaps in their ranges, thus these species would inflate the overall coherence of species distributions within the metacommunity. Changes over time in individual elements of coherence, species turnover through space, and coincidence of species range boundaries were assessed with z scores ($z = (X - \mu) / \sigma$; where X = observed value, μ = mean, σ = standard deviation), following Keith et al. (2011). A z score difference between the two surveys of more than twice the standard deviation was interpreted as statistically significant.

2.3. Effects of local management and large-scale environmental change

Each patch surveyed in 2010 was assigned into one of the ownership type groups with different primary management objectives: (i) Forestry Commission (“FC”), the UK’s national forest service; (ii) individual private owners (“Private”); (iii) non-governmental organisations or Ministry of Defence (“NGO/MoD”). FC patches were managed primarily for plantation forestry but sustained an understorey of heathland species. Privately owned patches were managed as grazing land for domestic herbivores by individual farmers. NGO patches were managed primarily for nature conservation. The MoD owned patches were grouped with the NGO owned patches for this analysis as although the patches are used as military training grounds, they are otherwise managed primarily for nature conservation. We explored differences in community composition between APs and IPs under different ownership types for both years using non-metric multi-dimensional scaling (NMDS) plots and a one-way ANOSIM with 999 permutations between ownership types at each survey time. NMDS was performed using a Bray–Curtis Similarity Index. We performed SIMPER analysis to determine which species were characteristic of each ownership type. Potential environmental drivers were assessed using species’ Ellenberg values from the PLANTATT database (Hill et al., 2004) as indicators of environmental conditions. To determine whether the change in plant community was related to environmental conditions, we tested for significant Spearman’s correlations between NMDS species axis scores and Ellenberg plant characteristic scores

(as a proxy for environmental variables, which were unobtainable for the historical survey).

3. Results

3.1. Patterns of change in species distribution, diversity, community composition and metacommunity structure

A total of 452 vascular plant species were identified over the two combined surveys of 150 patches. Of these, 189 species were only found in the 1930s survey, 72 were only found in 2010 and 191 were found during both surveys (Table A1a). There was a significant change between the two surveys in how species were distributed across patches for both APs (McNemar test, $W = 65917$, $p < 0.001$) and IPs (McNemar test, $W = 37218$, $p < 0.001$). In both cases, changes were caused by a combination of significant decreases in the number of patches occupied by some species and increases in patch occupancy by other species. Similar heathland species were lost from APs and IPs and species loss occurred to a similar extent (47 species decreased significantly across the 150 APs while 26 species decreased significantly across the 60 IPs; Table A1b). High proportional patch extinction rates between 0.9 and 1.0 were commonly observed in both APs and IPs (Fig. A2). Overall, the species that decreased significantly in occupancy most were the ericoids (*Calluna vulgaris*, *Erica tetralix*, *Erica cinerea*) and species of wet heathland such as *Drosera intermedia*, *D. rotundifolia*, *Eleocharis multicaulis*, *Hydrocotyle vulgaris*, *Hypericum elodes*, *Juncus acutiflorus*, *J. bulbosus*, *Narthecium ossifragum*, *Rhynchospora alba* and *Trichophorum cespitosum* (Table A1b). Although all are currently listed as of Least Concern in the Red List, many are declining nationally (Table A1b). In addition we found significant declines in all species present in the 1930s that are currently Red listed as Endangered (*Lycopodiella inundata*), Vulnerable (*Chamaemelum nobile*, *Cuscuta epithimum*) and Near Threatened (*Anagallis minima*, *Genista anglica*, *Radiola linoides*).

There were also few overall differences between the APs and IPs in the pattern of species gain: mean range extent scores increased significantly for species within APs (McNemar test, $W = 1871$, $p < 0.001$) and IPs (McNemar test, $W = 964.5$, $p < 0.001$). A total of 24 species increased significantly across the 150 APs while 12 species increased significantly across the 60 IPs (Table A1b and Fig. A2). Species tended to have either very low or very high colonisation rates for both APs and IPs (Fig. A2). Species with high colonisation rates whose distribution increased most were either predominantly woodland species (e.g. *Betula pendula*, *Hedera helix*, *Ilex aquifolium*, *Quercus robur*, *Rubus fruticosus* agg.) or mesotrophic grassland species (e.g. *Dactylis glomerata*, *Lolium perenne*, *Plantago lanceolata*, *Ranunculus repens*, *Trifolium repens*, *Urtica dioica*) (Table A1b).

Examination of changes in diversity between the 1930s and 2010 found significant decreases in γ -diversity in both APs and IPs. Species richness in APs decreased from 380 to 263 species ($\text{abs}(z) = 6.723$, $p < 0.001$), whereas and IPs decreased from 291 to 173 species ($\text{abs}(z) = 5.216$, $p < 0.001$). Mean α -diversity decreased significantly in both cases: APs from 17.5 to 16 ($W = 6196$, $p = 0.023$) and IPs from 18 to 11 α -diversity ($W = 1373$, $p = 0.002$). β -diversity of APs did not significantly change between surveys (median values for both surveys = 0.21, $V = 1064942$, $p = 0.432$) but IPs became significantly more homogenised (median for 1930s survey = 0.18, median for 2010 survey = 0.24, $V = 810905$, $p < 0.001$).

In the 1930s survey there was no overall significant difference in community composition between the patches that would, in 2010, be classed as IPs and APs ($R = 0.02$, $p = 0.07$). However, by 2010 these patch sets had diverged significantly ($R = 0.164$,

$p = 0.001$) and had changed significantly in species composition over time (APs: $R = 0.30$, $p < 0.001$; IPs: $R = 0.14$, $p < 0.001$). In both sets, species axis scores for the NMDS plots, and SIMPER analysis of characteristic species, indicated communities had shifted from heath and mire towards either mesotrophic grassland (axis 1) or woodland (axis 2) (Fig. 1 and Table 1). These shifts were most pronounced for APs (axis 1: $U = 5805$, $p < 0.001$; axis 2: $U = 2803.5$, $p = 0.022$), but were also significant for IPs (axis 1: $U = 2872$, $p = 0.002$; axis 2: $U = 1382.5$, $p < 0.001$); overall the APs shifted more towards grassland and the IPs more towards woodland. In both cases acid grassland communities and scrub communities were an intermediate stage in the transition to mesotrophic grassland and woodland, respectively.

EMS analysis indicated a general loss of structure over time; metacommunities became closer to random in structure. On the primary axis, which represents the dominant gradient influencing biological structure, the metacommunity structure of IPs was Clementsian in the 1930s. This indicates that species co-occurred with high fidelity to form multiple distinct communities, and transitions between communities were relatively abrupt. However, transitions between community types were less abrupt, i.e. quasi-Clementsian (Presley et al., 2010), in the resurvey data. The secondary axis, shifted over time from quasi-Clementsian to one that did not differ significantly from randomly assembled null matrices (EMS analysis, $p < 0.001$; Table 2). In contrast, when APs were analysed, the dominant axis maintained a Clementsian structure at both survey times. However, the secondary axis shifted from a nested structure (where species are lost in a predictable sequence from high richness to lower richness communities), to a random structure (EMS analysis, $p < 0.001$; Table 2). No significant change in either contiguity of species ranges ($z = 3.61$) or spatial turnover ($z = 0.02$) over time was indicated by the z score analyses on the primary axis for APs.

3.2. Effects of local management and large-scale environmental change

In the 2010 survey, significant differences were found between all owner groups in the AP set (Fig. 2, ANOSIM: FC vs Private,

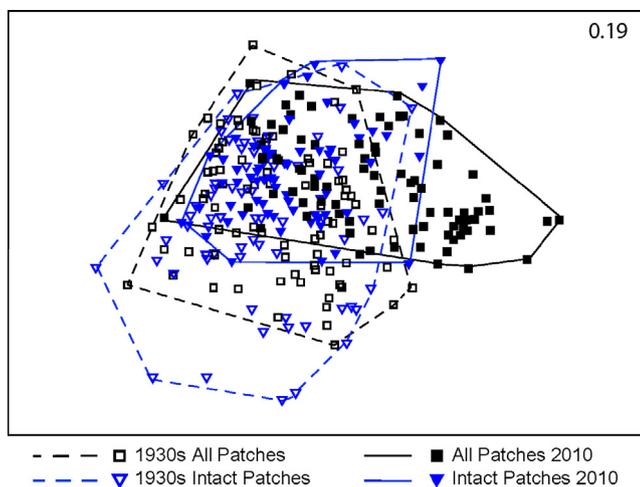


Fig. 1. Differences in plant community composition between patches in the the AP and IP sets in 2010 and the 1930s survey. The plot was generated with non-metric multidimensional scaling using Bray-Curtis similarity. (a) Shifts in overall species composition of patches along axis 1 (horizontal) and axis 2 (vertical). (b) Shifts in frequency of occurrence of 5 characteristic species of heathland (solid line), mesotrophic grassland (dotted line) and woodland (dashed line) along each NMDS axis (excluding the edges of each axis range where group sizes fell below 50 patches).

$R = 0.251$, $p = 0.001$; FC vs NGO/MoD, $R = 0.052$, $p = 0.046$; Private vs NGO/MoD, $R = 0.33$, $p = 0.001$) and between NGO/MoD and privately owned patches in the IP subset (Fig. 2, $R = 0.478$, $p = 0.001$). In particular, the latter patches contained more grassland-associated species such as *Agrostis curtisii* and *A. capillaris*, and scrub- or woodland-associated species such as *Quercus robur*, *Ulex minor* and *Rubus fruticosus* agg. The main difference between APs and IPs in species composition change over time was that *Rhododendron* became more prevalent in the IPs (Table A2). Comparison of changes between surveys in both the AP and IP set showed that private patches contained more grassland and scrub-associated species and contained fewer ericaceous species by 2010 (Table A2). Medians of species richness change between the 1930s and 2010 surveys were similar across APs and IPs, with values of +4/+3.5 (All/Intact) for the NGO/MoD owned patches, +3/+5 for the FC and $-17/-18$ for the privately owned patches.

Analysis of environmental change found that NMDS axis scores for species were significantly correlated ($p < 0.001$, Table A3) on axis 1 for all PLANTATT variables except for January temperature for both AP and IP sets. The directions of the changes in PLANTATT variable compositional changes for both APs and IPs in the 70+ years between the two surveys are: increasing summer temperatures, increasing pH; increasing nitrogen availability; decreasing light availability; decreasing precipitation and decreasing moisture. (Table A3).

4. Discussion

4.1. Patterns of change in species distribution, diversity, community composition and metacommunity structure

The Dorset Heath metacommunity lost significant γ -diversity over the seven decade interval in both APs and IPs, with a total of 189 species lost from the regional species pool since the 1930s. Species with high proportional patch extinction rates were primarily those that were rare in the 1930s, including nationally rare and heathland specialist species, while those with low proportional patch extinction rates were primarily those that were initially common (Table A1). In common with other comparable studies where long-term data sets are assembled by different surveyors, our results may be affected by pseudo-turnover (Nilsson and Nilsson, 1985) as each survey of a patch was conducted only once in the 1930s and again only once, by different surveyors, in 2010. Although our results should consequently clearly be viewed with caution, they provide evidence of a substantial decline in the number of species associated with this metacommunity, particularly of heathland specialist species.

The observed decline in species richness at the regional scale was accompanied by a decline in α -diversity, with a 39% decline in mean α -diversity recorded in IPs, reflecting the local-scale loss of rare species. Changes in α -diversity were accompanied by parallel losses of β -diversity for IPs but not APs. This result may be attributed to differential changes in patch occupancy for rare and common species. Rare species underwent dramatic and widespread loss across both intact and degraded patches, whilst relatively common species tended to increase in occupancy. Homogenisation of IPs but not APs was a result of a combination of (i) IPs losing proportionally more species than APs and these species often being rare, early successional species with scattered distributions across the patches, (ii) IPs gaining fewer generalist common species than APs so experiencing less mitigation of the homogenisation caused by the loss of rare species.

To some extent our results for heathlands contrast with those from those found in two parallel investigations of changes over almost identical time intervals in neighbouring woodlands

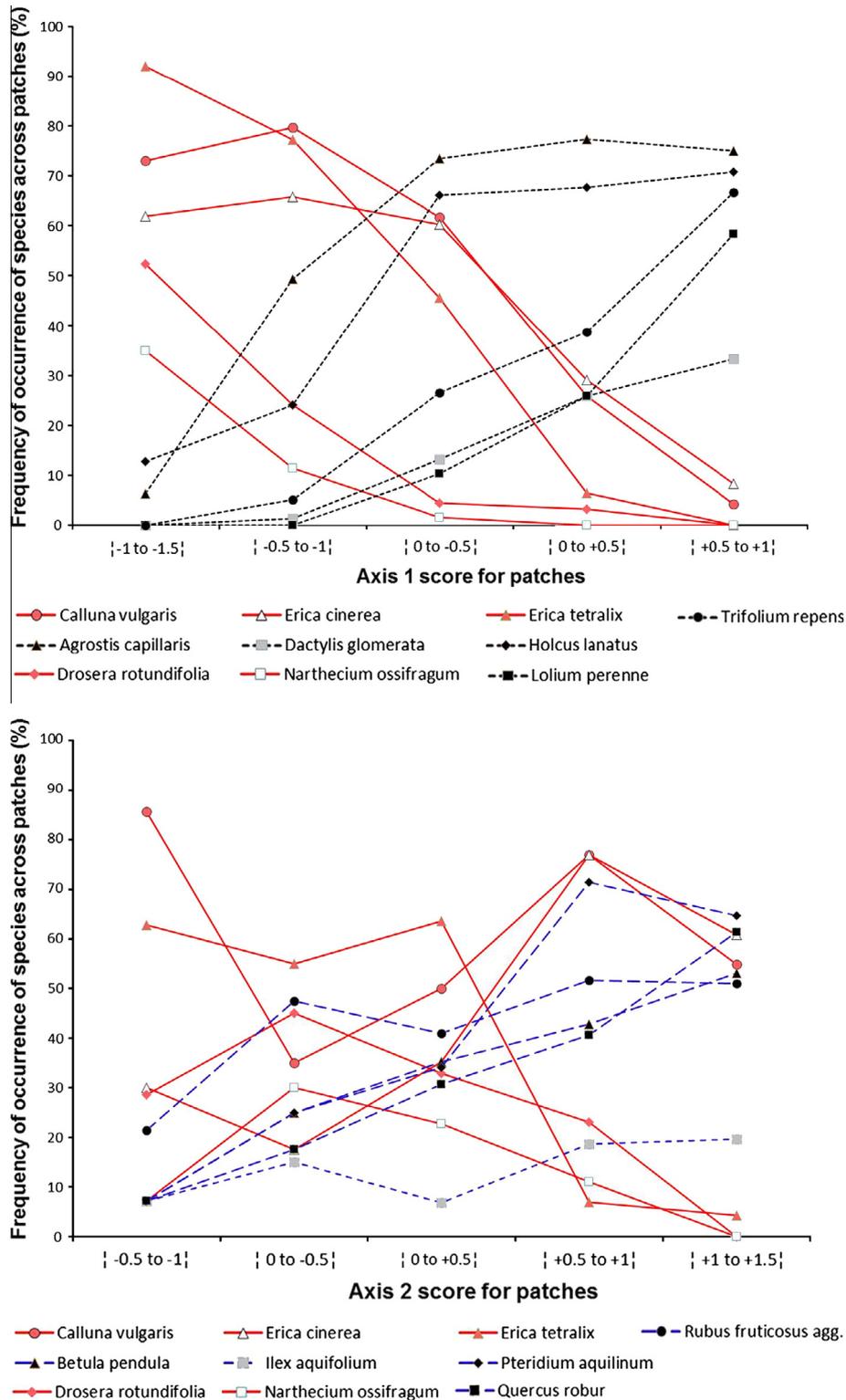


Fig. 1 (continued)

(Keith et al., 2009) calcareous grasslands (Newton et al., 2012) and hedgerows (Staley et al., in press). At the patch scale, mean α -diversity increased in calcareous grasslands and hedgerows and remained unchanged in woodlands. However, all four habitats showed similar sharp declines in specialist species, and spread of generalist species. These trends were associated with differences in γ - and β -diversity recorded in these studies. The γ -diversity decreased for heaths, woods and for the herbaceous component of

the hedgerow but increased over time for calcareous grasslands and the woody species component of the hedgerows. This appeared to be due to increased incidence of mesotrophic grassland and woodland species. By contrast, β -diversity was unchanged in the AP heaths and calcareous grasslands but decreased in IP heaths, woodlands and hedgerows. The current analyses therefore indicates that results are case specific and dependent on the extent to which homogenisation due to loss of rare species can be

Table 1
Contribution of species to similarity of communities within the 1930s and 2010 surveys for the AP and IP sets. Results are from SIMPER analysis with a cut-off of 50% contribution.

Species	Contrib(%)	Cum. contrib (%)	Broad habitat association
All Patches set 1930s			
Average similarity: 24.35			
<i>Calluna vulgaris</i>	11.2	11.2	Dwarf shrub heath; Bog
<i>Erica tetralix</i>	9.9	21.1	Dwarf shrub heath; Bog
<i>Erica cinerea</i>	9.3	30.4	Dwarf shrub heath
<i>Molinia caerulea</i>	7.9	38.3	Bog
<i>Agrostis curtisii</i>	7.1	45.4	Acid grassland; dwarf shrub heath
<i>Potentilla erecta</i>	5.6	51.0	Acid grassland
All Patches set 2010			
Average similarity: 23.96			
<i>Agrostis capillaris</i>	11.1	11.1	Acid grassland
<i>Holcus lanatus</i>	8.2	19.3	Improved grassland; neutral grassland
<i>Lolium perenne</i>	7.0	26.3	Improved grassland; neutral grassland
<i>Rubus fruticosus agg.</i>	6.6	32.9	Broadleaved, mixed and yew woodland; boundary and linear features
<i>Trifolium repens</i>	5.6	38.5	Improved grassland; neutral grassland
<i>Pteridium aquilinum</i>	5.4	44.0	Broadleaved, mixed and yew woodland; Bracken
<i>Pinus sylvestris</i>	5.0	49.0	Coniferous woodland
<i>Ulex europaeus</i>	4.9	53.9	Dwarf shrub heath
Intact Patches set 1930s			
Average similarity: 23.10			
<i>Erica tetralix</i>	13.0	13.0	Dwarf shrub heath; Bog
<i>Molinia caerulea</i>	11.0	24.0	Bog
<i>Calluna vulgaris</i>	9.2	33.2	Dwarf shrub heath; Bog
<i>Erica cinerea</i>	7.0	40.2	Dwarf shrub heath
<i>Pteridium aquilinum</i>	5.1	45.3	Broadleaved, mixed and yew woodland; Bracken
<i>Juncus acutiflorus</i>	5.0	50.3	Fen, mar sh and swamp
Intact Patches set 2010			
Average similarity: 31.78			
<i>Molinia caerulea</i>	9.0	9.0	Bog
<i>Ulex europaeus</i>	8.5	17.5	Dwarf shrub heath
<i>Pteridium aquilinum</i>	8.4	25.9	Broadleaved, mixed and yew woodland; Bracken
<i>Erica tetralix</i>	7.8	33.7	Dwarf shrub heath; Bog
<i>Quercus robur</i>	7.2	40.9	Broadleaved, mixed and yew woodland; boundary and linear features
<i>Betula pendula</i>	6.8	47.6	Broadleaved, mixed and yew woodland
<i>Calluna vulgaris</i>	6.3	53.9	Dwarf shrub heath; Bog

Table 2
Metacommunity structure of unconverted heathlands and all sites, indicated by elements of metacommunity structure analysis (EA = embedded absences; SR = species replacements; MI = Morisita's index). Significant values are in bold. EA, SR and MI comprise the three structural elements, which together, indicate the idealised structure.

Set	AP	AP	AP	AP	IP	IP	IP	IP
Year	1930s	1930s	2010	2010	1930s	1930s	2010	2010
Axis	1	2	1	2	1	2	1	2
Actual EA	26,142	32,433	19,701	25,141	7814	8594	5425	6225
Mean null model EA	37,949	37,590	24,882	24,569	11,801	11,696	6630	6490
<i>p</i> EA	<0.001	<0.001	<0.001	0.646	<0.001	<0.001	0.001	0.486
S.D. EA	1491	1510	1203	1246	637	648	377	381
Actual SR	19,012,350	13,840,554	9,987,630	5,309,417	2,744,584	1,397,803	858,707	563,783
Mean null model SR	17,143,000	20,355,000	8,709,977	6,280,822	1,637,465	1,419,029	802,375	503,464
<i>p</i> SR	0.021	<0.001	0.023	0.061	<0.001	0.773	0.314	0.144
S.D. SR	811,190	1,047,700	559,956	519,146	102,723	73,702	55,956	41,329
Actual MI	3.7	3.61	2.43	2.33	2.97	3.06	2.33	2.83
<i>p</i> MI	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Idealised structure	Clementsian	Nested with clumped species loss	Clementsian	Random	Clementsian	Quasi-Clementsian	Quasi-Clementsian	Random

mitigated by gain of common species, but provides some further evidence for the loss of β -diversity (i.e. biotic homogenisation) that has been recorded in studies of other plant assemblages (Castro and Jaksic, 2008; Rooney et al., 2007). Different results for different systems may also be attributable to the operation of a combination of different factors such as the well-established relationship between habitat fragmentation and increasing beta diversity, caused either directly through fragmentation effects or by underlying spatial heterogeneity (Tschardt et al., 2012).

The community composition of both APs and IPs shifted from characteristic heath and mire communities in the 1930s towards woodland and acid and mesotrophic grassland communities in 2010. It seems probable that shifts towards woodland communities are attributable to successional change following a decline in management intensity (Mitchell et al., 1997), whilst shifts towards grasslands may be attributable to an increase in grazing pressure (Celaya et al., 2007; Bullock and Pakeman, 1997; Newton et al., 2009). The shifts to grassland may also be in part driven by

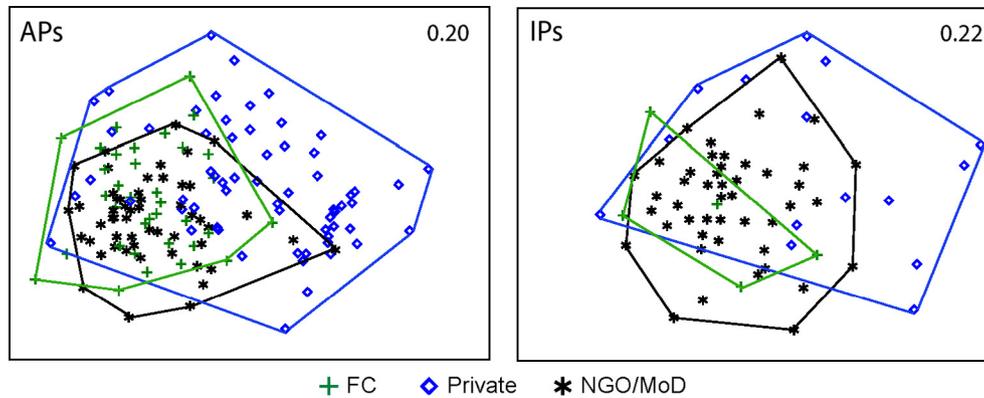


Fig. 2. Differences in community composition between patches grouped by 2010 owner type. The plot was generated with non-metric multidimensional scaling (NMSD).

eutrophication owing to atmospheric N deposition, as has been found on other heaths both in the UK and in continental Europe (Bobbink et al., 2010; Fagúndez, 2013), or by an interaction of N deposition and grazing effects (Alonso et al., 2009).

Patch occupation for individual species decreased, particularly for characteristic heathland, acid grassland, mire and marsh species. Some of these species are of conservation importance because they are nationally rare, and others (such as the ericaceous taxa) play important roles in providing habitat for threatened animal species (Webb, 1998). Conservation value of the grassy heaths found in 2010 was relatively low, because these communities lacked the rarer species typical of open ground habitats traditionally created via turf cutting, cattle poaching or burning (Byfield and Pearman, 1996; Webb, 1998). Loss of plant species can also contribute to declines in diversity at higher trophic levels, for example, invertebrate pollinators (Ebeling et al., 2008) and herbivores (Zurbrügg and Frank, 2006). Many of the forb species that decreased were species of pioneer heaths and open, short acid grasslands but some were calcareous grassland and wetland species. These may have been associated with now destroyed calcareous springs and with the edges of paths that used to be surfaced with limestone chippings, a practise that has now ceased on Dorset Heaths. Most species that significantly increased in occupancy are common components of native woodland and mesotrophic grassland plant communities (Rodwell et al., 1991a,b, 1992), supporting the broad shift in assemblage type observed at the community level. Only one non-native species, *Rhododendron ponticum*, increased significantly in patch occupation. Its increase reflects its behaviour as a highly invasive species, and it may have contributed to some losses of rare species in our study through competitive exclusion (Tyler et al., 2006). Our finding that species and community level analyses showed differences between APs and IPs that were not apparent from the diversity data alone, supports the suggestion that diversity metrics are not robust indicators of ecological degradation, and that evaluation of species composition can provide valuable added insights (Devictor and Robert, 2008).

Metacommunity structure changed over time both for APs and IPs, but the specific nature of change differed between patch sets. The APs maintained a Clementsian structure along the predominant axis, suggesting that the historical 1930s communities exhibited assemblage types within which species occurred together with high fidelity. This result suggests that habitat patches were heterogeneous throughout the landscape, and each type of habitat patch was associated with a specific assemblage (Leibold et al., 2004). However, the second axis indicated a structural change, from a situation where species were lost from communities in a predictable sequence as richness decreased, to a situation of random species loss. This may indicate change in the processes structuring communities over time. Potentially, a change in land use or

management practices may have resulted in a reduction in habitat quality or area and generated an extinction debt (Kuussaari et al., 2009). Alternatively, Clementsian structure in the 1930s may have been driven by species interactions (Leibold et al., 2004) that were absent by 2010. The shift from a Clementsian to a quasi-Clementsian structure recorded in IPs could similarly reflect altered intraspecific interactions over time. It may be that metacommunity structure in the 1930s was dependent on a competitive hierarchy of species, which has dissipated owing to the loss of relatively uncompetitive, heathland specialist species. Comparison of these results with those obtained for Dorset woodlands (Keith et al., 2009) and calcareous grassland (Newton et al., 2012), where no change in metacommunity structure was observed over this same time interval, suggests that heathland metacommunities may be more susceptible to environmental change than those of woodlands and calcareous grasslands. This may be because their structure is particularly dependent on dominant but specialist ericaceous species that are vulnerable to environmental change.

4.2. Effects of local management and large-scale environmental change

Local differences in land ownership had major effects on the floristic composition of patches, irrespective of whether APs or IPs were considered. In both cases, most change occurred in the privately owned patches. Patches managed for conservation by NGOs/MoD changed least between the two surveys in that they retained the highest mean species richness and had the smallest increase in the invasive fern *Pteridium aquilinum*. Nonetheless, shifts towards later successional states were evident, suggesting management success in reversing succession and reducing water drainage was only partial. Land owned by the FC showed the greatest increase in (non-planted) tree and scrub species and, although an understory of *Calluna vulgaris* was present in most patches and of *Erica cinerea* in some, the prevalence of other species characteristic of heathland declined sharply over time. This finding concurs with other research that has found that heathland species are less prevalent in later successional stages, where reduced light availability leads to reduced growth, reproduction and colonisation (Eycott et al., 2006). *Calluna vulgaris* may be less susceptible to such competitive exclusion than other heathland taxa as it is quite long-lived, can be wind pollinated (Hanley et al., 2008) and is able to grow under a wide range of soil moisture conditions and under light shade (Welch and Scott, 1997). However, the extent to which modified heathland plant communities can contribute to metacommunity function whilst under a forest canopy requires further investigation. As found by Scheffer et al. (2006), processes that affect metacommunities at one trophic level may also have important cascading effects on other trophic levels, owing to species

interactions. Furthermore, trophic interactions such as grazing by domestic stock can affect vegetation composition many decades after cessation of grazing, as demonstrated on grassy islands on the Stockholm archipelago (Aggemyr and Cousins, 2012).

Analysis of plant characteristics indicated that climate change may be a significant influence on vegetation change of the Dorset Heaths towards either woodland or mesotrophic grassland. The potential for climate to affect forest dynamics is well recognised (Milad et al., 2011) and changes found in our study may reflect increased rates of woodland succession owing to increased tree growth rates. Vegetation changes towards woodland were related to increased shade, drought, eutrophication, and to less acidic soils. These relationships were correlated, because forest development on heathland leads not only to increased shade but to an increase in soil nutrients and pH (Mitchell et al., 1997). Increased shade and eutrophication were also identified as environmental drivers involved in changes in the Dorset woodlands over 70 years (Keith et al., 2009). Vegetation changes among the APs diverged as some patches moved towards woodland and others towards grassland, but both groups were correlated with increases in N and pH. Eutrophication resulting from atmospheric sources of nitrogen was also identified as a possible factor for community change in the parallel study on Dorset calcareous grasslands (Newton et al., 2012), as well as in a range of habitats types in Finland (von Nümers and Korvenpää, 2007), and in acid grassland across Europe (Duprè et al., 2010). Such environmental factors could have potentially interacted with changes in land use and management on Dorset Heaths, as also suggested for these other habitat types.

4.3. Implications for conservation management of metacommunities

The need for regional-scale approaches to conservation management is now widely recognised but there is currently limited evidence regarding the long-term implications of adopting more traditional, site-based management approaches. Our analyses of metacommunity dynamics provide some insight into the regional-scale consequences of local site-based management approaches. Results indicate that even the lowland heathland patches considered as currently intact have decreased in α -diversity, β -diversity and γ -diversity over the past 70 years, indicating biodiversity loss at both local and regional scales. While analysis of management strategy, associated with land ownership, identified partial success of conservation management actions in reducing these losses on individual sites, they did not prevent diversity-loss at the regional regional scale or an apparent change in the processes structuring the metacommunity. Implications of these combined losses at local and regional scales for long-term viability or resilience of the metacommunity are poorly understood, and require elucidation.

Our results suggest that degraded patches can be considered as an integral part of the metacommunity, and may play an important role in supporting metacommunity resilience to environmental change. Consequently they should be considered in regional-scale conservation management planning. In particular, our results suggest that future conservation action should arguably focus on addressing the observed decline in heathland specialist species, given their key contribution to both biodiversity loss and metacommunity structure. Introduction of a regional-scale conservation approach might usefully prioritize conservation management of sites where management activities are required to maintain, expand or restore populations of such species. Further research in this area would be timely for supporting the development and implementation of policy in relation to metacommunity conservation.

A current focus of environmental policy in the UK (Lawton et al., 2010), and in many other countries (Boitani et al., 2007), is to

create ecological networks of connected patches to support inter-patch species dispersal. While such approaches may have positive impacts on metacommunity resilience, they would not necessarily address some of the threatening processes identified here which appear to be impacting the Dorset heathland metacommunity. Rather, identification of site-level management approaches that would contribute to regional-scale conservation goals may be more appropriate. This implies a need for development of regional-scale conservation strategies and plans, involving coordinated approaches to management across multiple sites. Such regional-scale strategies could be usefully informed by a greater understanding of metacommunity dynamics both in heathland and in other ecological systems.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2013.08.018>.

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