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Can landscape-scale approaches to conservation management resolve biodiversity–ecosystem service trade-offs?

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Running title: Resolving biodiversity–ecosystem service trade-offs

Summary

1. Conservation management is increasingly being required to support both the provision of ecosystem services and maintenance of biodiversity. However, trade-offs can occur between biodiversity and ecosystems services. We examine whether such trade-offs can be resolved through landscape-scale approaches to management.

2. We analysed the biodiversity value and provision of selected ecosystem services (carbon storage, recreation, aesthetic and timber value) on patches of lowland heathland in the southern English county of Dorset. We used transition matrices of vegetation dynamics across 112 heathland patches to forecast biodiversity and ecosystem service provision on patches of different sizes over a 27 year timeline. Management scenarios simulated the removal of scrub and woodland, and compared: (i) no management (NM); (ii) all heaths managed equally (AM); management focused on (iii) small heaths (SM) and (iv) large heaths (LM).

3. Results highlighted a number of trade-offs. Whereas biodiversity values were significantly lower in woodland than in dry and humid heath, timber, carbon storage and aesthetic values were highest in woodland. While recreation value was positively related to dry heath area, it was negatively related to woodland area. Multi-Criteria Analysis ranked NM highest for aesthetic value, carbon storage and timber value. In contrast, SM ranked highest for recreation and LM highest for biodiversity value. In no scenario did the current site-based approach to management (AM) rank highest.

4. *Synthesis and applications*. Biodiversity–ecosystem service trade-offs are reported in lowland heathland, an ecosystem type of high conservation value. Trade-offs can be addressed through a landscape-scale approach to management, by varying interventions according to heathland patch size. Specifically, if management for biodiversity conservation is focused on larger patches, the aesthetic, carbon storage and timber value of smaller patches would increase, as a result of woody succession. In this way, individual heathland patches of either relatively high biodiversity value or high value for provision of ecosystem services could both potentially be delivered at the landscape scale.

Key-words: ecosystem function, fragment, heathland, landscape, natural capital, patch size, protected area

Introduction

In recent years, landscape-scale management approaches have increasingly been adopted for the conservation of biodiversity (Jones 2011). Examples include metapopulation management (Rouquette & Thompson 2007), landscape restoration (Newton *et al.* 2012), ecological networks (Boitani *et al.* 2007) and rewilding (Navarro & Pereira 2012). Such approaches are also being incorporated into environmental policy, for example by the Convention on Biological Diversity (CBD) (Sayer *et al.* 2013) and the European Union (EU) (Jones-Walters 2007). As illustration, the EU Biodiversity Strategy aims to "reconnect fragmented natural areas and improve their functional connectivity within the wider countryside" (European Union 2011). Similarly in the UK, the current national biodiversity strategy is based around a "move away from piecemeal conservation actions towards a more effective, more integrated, landscape-scale approach” (Defra 2011).

Landscape-scale management has potential value for addressing trade-offs between biodiversity conservation and economic development (Sayer *et al.* 2013). In this context, the concept of ecosystem services, or the benefits provided to people by ecosystems, is relevant. It has been suggested that a failure to incorporate the value of ecosystem services in land-use decision making is a widespread cause of biodiversity loss (Carpenter *et al.* 2009; Rands *et al.* 2010; Reyers *et al.* 2012). However, research has documented that trade-offs often occur between biodiversity and ecosystem services, and between different ecosystem services (Howe *et al.* 2014). For example, a trade-off between agricultural production and biodiversity has been widely reported (e.g. Chapin *et al.* 2000; Jiang *et al*. 2013; Macfayden *et al.* 2012; Newton *et al.* 2012), and trade-offs between carbon storage and other ecosystem services have also been identified (Goldstein *et al.* 2012; Nelson *et al.* 2008). Such trade-offs have major implications for environmental management, as they can potentially undermine the case for biodiversity conservation, and hinder the identification of ‘win–win’ solutions to conservation and sustainable development where both goals can be achieved concurrently (Bullock *et al*. 2011; Goldstein *et al.* 2012; Howe *et al.* 2014; McShane *et al.* 2011; Reyers *et al.* 2012).

Conservation and economic development objectives can potentially be reconciled by targeting management interventions on different components of the landscape (Sayer *et al.* 2013). Identification of the optimal allocation of different management options at the landscape scale then becomes a key challenge (de Groot *et al.* 2010). Even in situations where optimal solutions to land management planning are difficult to identify, the explicit consideration of trade-off choices should itself lead to improved conservation outcomes (McShane *et al.* 2011). However, this has rarely been demonstrated in practice. As noted by de Groot *et al.* (2010), improved decision-making in land management relating to such trade-offs requires empirical information on the relationships between ecosystem management and provision of ecosystem services at the landscape scale. This information is currently lacking for most ecosystems.

A limited number of studies have examined the impact of landscape-scale conservation management approaches on trade-offs between biodiversity and ecosystem services (Newton *et al.* 2012; Hodder *et al.* 2014; Birch *et al.* 2010). However, these studies did not identify how such trade-offs might be resolved in practice, and each focused on conservation management interventions distributed across entire landscapes. In practice, management actions may frequently be restricted to sites of relatively high biodiversity value, such as protected areas or designated sites. In such situations, landscape-scale approaches require consideration of how management interventions should be distributed among a network of sites. Analysis of metapopulation and metacommunity dynamics has indicated that traditional site-based approaches to management can fail to conserve biodiversity effectively at the landscape scale (Economo 2011; Siqueira *et al.* 2012). This is illustrated by analysis of long-term change in lowland heathland in the southern English county of Dorset, which found that values of γ and α-diversity of vascular plant communities both decreased over time, despite conservation management being conducted on many individual sites (Diaz *et al.* 2013).

As noted by Economo (2011), the effective allocation of scarce conservation resources remains an important theoretical and applied problem. Here we consider the position of a conservation practitioner who is responsible for managing multiple sites of high biodiversity value, as might be encountered in a protected area network. Increasingly, such managers will be required to deliver enhanced provision of ecosystem services as well as biodiversity (Goldman & Tallis 2009; Macfayden *et al.* 2012; Whittingham 2011), in a situation where financial resources are likely to be limited. In such circumstances, how might a landscape-scale approach to management deliver a 'win-win' solution in terms of biodiversity conservation and provision of ecosystem services? To address this question, we compare a management approach focused on larger habitat patches with an alternative strategy focusing preferentially on smaller patches. The size of individual patches has been identified as a key factor influencing the persistence of both metapopulations (Hanski 1999) and metacommunities (Leibold *et al.* 2004), but its impact on provision of ecosystem services has rarely been investigated. According to theory, ecosystem functions and associated services may be influenced by patch size, although the effects may be both complex and non-linear (Wardle *et al.* 2012).

Here we test the hypothesis that contrasting relationships with habitat patch size will lead to trade-offs between biodiversity and ecosystem services, which will be influenced by the management approach adopted. We do so in the lowland heathlands of Dorset, UK. Heathlands are successional plant communities dominated by ericaceous shrubs, and are an international priority for biodiversity conservation, owing to their high value as habitat for vascular plants, reptiles, amphibians, birds and invertebrates (Webb 1986). During the past century, heathlands in Dorset have suffered both a major decline in extent and an increase in fragmentation, as a result of changing patterns of land use (Diaz *et al.* 2013; Rose *et al.* 2000; Hooftman & Bullock 2012). Over the past 30 years, the floristic composition of all remaining heathland patches has been monitored, providing an opportunity to examine trends in both biodiversity and provision of ecosystem services in relation to patch size. Here, scenarios of future change based on trends in these empirical data are used to explore the dynamics of both ecosystem services and biodiversity under different management strategies, to identify both trade-offs and synergies. Further, we examine whether such trade-offs can potentially be resolved through adoption of an appropriate landscape-scale management approach.

Materials and methods

Study area

The Dorset heathlands are situated in southern England (50°39’N 2°5’W), and are generally associated with free-draining and acidic soils overlying Tertiary sands and gravels. The heathlands comprise a mosaic of different vegetation types, characterized by dwarf shrub communities dominated by members of the Ericaceae (e.g. *Calluna vulgaris*, *Erica* spp.), together with areas of mire, grassland, scrub and woodland. If left unmanaged, heathlands undergo succession to scrub (often dominated by *Ulex* spp.) and woodland (characterized by *Betula* spp., *Pinus* spp., *Quercus* spp. and *Salix* spp.). The majority of heathland sites are currently under some form of conservation management, which is implemented to reduce succession to scrub and woodland. Management interventions include cutting and burning of vegetation, and grazing by livestock (Diaz *et al.* 2013; Newton *et al.* 2009). Individual heathland patches are also managed for ecosystem services, such as recreation and timber production, as well as biodiversity conservation (Diaz *et al.* 2013).

The Dorset Heathland Survey (DHS)

In 1978, a comprehensive vegetation survey was conducted on the Dorset heathlands that was subsequently repeated in the years 1987, 1996 and 2005. Detailed methods and results from the first three surveys have been published previously (Rose *et al.* 2000; Webb 1990). Data for 2005 are presented by Rose et al. (2015). For each survey, square plots of 4 ha (200 m x 200 m) were located based on the national Ordnance Survey mapping grid and were surveyed for the cover of all major vegetation types. These included four types associated with relatively dry soils (dry heath, grassland, scrub and woodland) and five additional types associated with relatively wet or poorly draining soils (brackish marsh, carr, humid heath, wet heath and mire). The other seven categories were bare ground, sand dunes, pools and ditches, sand and gravel, arable, urban and other land uses. The first survey in 1978 established 4 ha plots throughout all Dorset heaths, resulting in a total survey area of 3110 plots (12 440 ha). The same set of plots was resurveyed at each subsequent survey date. Within each plot, the cover of each vegetation type was recorded on a 3-point scale (1 = 1-10% cover; 2 = 10-50% cover; 3 = ≥50% cover).

Biodiversity value

Analysis focused on species of conservation concern according to the UK Biodiversity Action Plan (UKBAP; http://jncc.defra.gov.uk). Distribution records of UKBAP mammal, bird, butterfly, reptile, amphibian, vascular plant and bryophyte species (Appendix S1 in Supporting Information) were overlaid on vegetation maps derived from the heathland survey data. Biodiversity value was calculated for each vegetation type as the mean number of species recorded within 4 ha survey squares dominated by the respective cover type (i.e. > 50% cover). Values of the number of species per unit area were normalized on a scale of 0 to 1 using the clusterSim package in R (R Development Core Team 2012).

Ecosystem service assessment

Four ecosystem services were selected for measurement, based on their relatively high importance in heathlands: carbon storage, aesthetic value, recreation value and timber production. A value for each vegetation type was obtained for the provision of each service, using the following methods.

Carbon storage

Carbon storage (t C ha^{-1}) was assessed by directly measuring the amount of carbon in the following carbon pools: vegetation, soil (to 30 cm depth), roots, humus and dead organic matter. Measurements were conducted on ten heathlands on sites that were selected using stratified random sampling methods. Carbon pools were quantified by obtaining vegetation and soil samples from 0.01 ha circular plots in each vegetation type on each heath, which were used to measure biomass and carbon content, with soil sampled from two pits within each plot (see Appendix S1).

Aesthetic value

Aesthetic value was measured by conducting a questionnaire survey of 200 heathland visitors distributed equally across ten randomly selected heaths, and eliciting preference values for each vegetation type that were represented by photo-realistic images. The aesthetic preference values were measured on a Likert scale (1–5), scoring how visually appealing the images were to heathland visitors (see Appendix S1).

Recreational value

The number of visitors to individual heaths was obtained from a questionnaire survey conducted by Liley *et al.* (2008), which was sent to 5000 randomly selected postcodes from across the region. On the basis of the 1632 responses received, the number of visitors for each of 26 heaths was calculated, representing the heaths for which recreational visits were reported. The association between log-transformed values of vegetation cover and visitor number was then examined using Spearman's rank correlation, using the proportion of each vegetation type in each heath calculated from the DHS data. Correlation coefficients for each vegetation cover type were then applied as an indicator of their relative value for recreation.

Timber value

Potential timber value was associated only with woodland. The extent of woodland cover on each heath was determined from the DHS data, supported by interpretation and digitization of high resolution aerial photographs and field observations. Timber value was estimated following Newton *et al.* (2012) using local yield data based on cumulative felling and local timber production values obtained from the Forestry Commission, UK. This takes account of overall extraction throughout the rotation, including the value of timber removed through thinning. For the scenarios, it was assumed that timber would be harvested after a 27 year rotation, following five thinnings in the case of conifers and two thinnings in the case of broadleaved trees.

Analysis of vegetation dynamics

The extent of the current vegetation cover of the Dorset heaths was mapped by digitizing high resolution (25 cm) aerial photographs from 2005 (Bluesky International Limited, Coalville, UK) in ArcGIS 10 (ESRI 2011), used in conjunction with the DHS data. The following vegetation types were mapped: grassland, humid/wet heath, mire, dry heath, scrub and woodland.

To analyse vegetation dynamics, state transition matrices were developed using the DHS data, across the time steps of successive surveys (1978–1987, 1987–1996 and 1996–2005, labelled t78-87, t87-96 and t96-05 respectively). Transition matrices were developed by quantifying the probability of change between all vegetation cover types, across all the heaths surveyed. Individual transition matrices were created for each of the 112 heathland patches and validated using the DHS data collected at subsequent survey dates (see Appendix S2).

Scenario development

Future vegetation cover change under different management scenarios was modelled by multiplying the current area of each vegetation type in each heath (derived from the land cover map) by transition matrices, using the R 2.15 statistical package (R Development Core Team 2012). For this purpose, the transition matrices were modified to include only the following cover types: grassland, humid/wet heath, mire, dry heath, scrub and woodland. Separate transition matrices were developed for small (< 40 ha), medium (≥ 40 and < 150 ha) and large (≥ 150 ha) heaths, and represented vegetation cover change over nine years, which was the interval between the surveys from which the matrices were derived (see Appendix S2). A 27 year scenario projection time was chosen (three time steps), representing 2005 until 2032, to provide a policy-relevant timeline.

Four scenarios were developed (Table 1), reflecting different management approaches. These were: (i) no management (NM); (ii) all heaths managed equally, mimicking a site-scale approach to management (AM); and two landscape-scale approaches to management, respectively focusing only on

(iii) small heaths (SM) and (iv) large heaths (LM). Management in all scenarios focused on the removal of woodland and scrub and was designed such that an equal area of these vegetation types was removed in AM, SM and LM (see Appendix S1).

Analysis of trade-offs and synergies

To compare scenarios for their relative effectiveness at providing biodiversity benefits and ecosystem services, a multi-criteria analysis (MCA) was performed (see Appendix S1) using DEFINITE 3.1.1.7 (DEFINITE 2006). The MCA was conducted by applying different preference weights: (i) equal weighting of all services and biodiversity; (ii) market services (carbon and timber) weighted equally, and non-market services (aesthetic, recreation) and biodiversity given zero weight; (iii) biodiversity only, with all ecosystem services given a zero weight; (iv) recreation and aesthetic services given equal weight, and all other services and biodiversity given zero weight. Scenarios were then ranked using the output of the MCA, based on the weighted sum of the criteria scores, which were also inspected to identify synergies and trade-offs.

Results

Analysis of woody succession

Regression analysis of the heathland survey data indicated that the percentage increase in area of scrub and woodland was significantly and negatively related to heathland patch size between all survey years (1978–1987, r^2 = 0.623; 1987–1996, r^2 = 0.549; 1996–2005, r^2 = 0.583; P < 0.001 in each case). This indicates a higher rate of succession from heathland to scrub and woodland on smaller than on larger heaths. This result was illustrated by the transition matrices, which generally indicated a higher proportion of heath vegetation types transitioning to woodland or scrub on smaller heaths, regardless of the year of survey (Table 2).

Management scenarios

Apart from the areas of grassland and of mire, all vegetation types displayed contrasting responses between management scenarios (Fig. 1). Areas of dry and humid/wet heath declined in all scenarios, but particularly in NM, and least in LM. Areas of scrub and woodland increased in all scenarios, particularly in NM, and least in LM (Figure 1; Appendix S1).

Biodiversity and ecosystem service values

The total number of UKBAP species differed between vegetation types, ranging from 20 in mire to 58 in dry heath. Biodiversity values per unit area were significantly higher in dry and humid/wet heath than in woodland (Table 3). Carbon storage value was highest for woodland and lowest for humid/wet heath (Table 4; see Appendix S3). Potential timber value was only associated with woodland. Highest aesthetic values were recorded for woodland and lowest for mire, with significantly lower values recorded for dry or humid heath than either scrub or woodland (Table 4). Conversely, recreational value was significantly and positively related to proportion of dry heath, but negatively related to both humid/wet heath and woodland (Table 4).

Analysis of trade-offs

The biodiversity and ecosystem service values associated with different vegetation types highlighted a number of trade-offs. Whereas biodiversity values were significantly lower in woodland than in dry and humid heath, timber, carbon storage and aesthetic values were highest in woodland. Further, while recreation value was positively related to dry heath, it was negatively related to woodland area.

MCA analysis evaluated the impact of management approach on these trade-offs. The normalized scores for each ecosystem service and biodiversity were summed across all vegetation cover types and heathland patches at the completion of the management scenarios, to provide values aggregated at the landscape-scale. Results indicated that NM ranked highest for aesthetic value, carbon storage and timber value, whereas SM ranked highest for recreation and LM highest for biodiversity (Figure 2). This reflects the relatively large area of scrub and woodland in the NM scenario resulting from woody succession.

Results of the MCA varied markedly depending on which weights were selected. If each ecosystem service and biodiversity were equally weighted, NM ranked highest and LM lowest (Figure 3a), reflecting the relatively large number of services that were positively associated with woodland and scrub. Higher weighting of services with a market value, namely carbon and timber, accentuated this result (Figure 3b). However, if biodiversity was weighted preferentially, NM ranked lowest of the four management options, and LM the highest, reflecting the lower woodland area associated with the latter scenario. In no scenario did the current site-based approach to management, which approximates AM, rank highest out of the management options considered.

Discussion

Our study indicates that in the case of lowland heathland, trade-offs can occur between different ecosystem services, and between ecosystem services and biodiversity. Specifically, a trade-off was identified between carbon storage, timber and aesthetic value on the one hand, versus biodiversity and recreational value on the other. The higher biodiversity value associated with heath vegetation and the lower value associated with woodland supports the current approach to conservation management of lowland heathland sites, which is primarily aimed at reducing encroachment of woody plants (Diaz *et al.* 2013; Newton *et al.* 2009). However, according our results, the provision of carbon storage, timber and aesthetic value would be reduced by such a management approach compared to alternative approaches.

Our results also indicate that these trade-offs might be addressed through appropriate landscape-scale management. Both biodiversity value and the provision of ecosystem services were related to the size of heathland patches. This reflects an underlying negative relationship between heathland patch size and the rate of woody plant succession. Therefore, targeting management interventions to heathland patches of different sizes could reduce conflicts in biodiversity conservation and delivery of particular ecosystem services, based on priority setting. For example, if biodiversity conservation was the principal goal, management would be most effective if focused preferentially on larger heathland patches. Under this approach, the aesthetic, carbon storage and timber value of smaller patches would increase. In this way, individual heathland patches of either relatively high biodiversity value or high value for provision of ecosystem services could both be delivered at the landscape scale.

Although ecosystem service trade-offs have been widely reported in the literature, few previous studies have indicated they might be resolved in practice. In the context of agricultural land, Goldman *et al.* (2007) suggested that individual sites should be managed in a coordinated way across landscapes, without defining how this might be achieved practically. Other authors have highlighted the potential of spatially separating different land uses to avoid management conflicts, for example by differentiating between production and conservation areas, leading to the concept of multifunctional landscapes (Moilanen *et al.* 2011; Schneiders *et al.* 2012). Recognition of trade-offs can potentially be incorporated into land-use planning processes, including target setting, design and negotiation, to optimize multi-functional use (De Groot *et al.* 2010; Wainger *et al.* 2010).

Following Yapp *et al.* (2010), we suggest that the balance of ecosystem service provision and biodiversity at the landscape scale can be manipulated through distribution of vegetation management across different sites. Specifically, we suggest that in the current example, biodiversity–ecosystem service trade-offs can potentially be addressed by targeting management interventions at different locations within a landscape based on consideration of patch size. It is pertinent to consider whether such an approach is relevant to other ecological contexts. A trade-off between carbon storage and biodiversity value is likely wherever early successional habitats are associated with relatively high biodiversity value, which is the case for a number of other plant communities in north-western Europe, including semi-natural grasslands and shrublands (Sutherland 2000). Similarly in New Zealand, Dickie *et al.* (2011) reported an increase in carbon pools with woody succession, but found negative impacts on species richness of selected taxonomic groups. Other studies have also reported a negative relationship between patch size and rate of wood plant succession, as recorded here. For example, Wardle *et al.* (2012) found that small islands in a Swedish archipelago were likely to undergo succession more rapidly, owing to increased incidence of fire on larger islands. However, converse results have also been reported, for example by Cook *et al.* (2005) in experimentally fragmented agricultural fields. Such contrasting results highlight the difficulty of generalizing about the impact of patch size on successional trajectories, reflecting the potential influence of many other factors and stochastic events on the successional process (Matthews 2014).

If biodiversity–ecosystem trade-offs can potentially be addressed by appropriate landscape-scale management, the question remains: should they be? This question is relevant to a major current debate in conservation science. The concept of ecosystem services was originally developed to promote the protection of natural ecosystems, and many authors have subsequently suggested that increased recognition of the value of ecosystem services to human society will strengthen the conservation of biodiversity (e.g. Bayon & Jenkins 2010; Ghazoul 2007). However, management for provision of ecosystem services has increasingly become a goal in its own right (Soulé 2013). It has been suggested that management strategies “must be promoted that simultaneously maximize the preservation of biodiversity and the improvement of human well-being” (Kareiva & Marvier 2012). Such suggestions have sparked an acrimonious debate, which is still ongoing (Soulé 2013; Tallis & Lubchenko and 238 cosignatories 2014). If ‘win-win’ outcomes can be identified, then there is no conflict between these two management goals. However, identification of trade-offs indicates that conflict exists between these goals, representing a ‘win-lose’ situation. Kareiva & Marvier (2012) suggest that in such circumstances, trade-offs should be minimized by “actively seeking to optimize both conservation and economic goals”. Here we demonstrate that this can potentially be achieved by implementing contrasting management approaches on heathland patches of different sizes. However, if management interventions were reduced on smaller heathland patches, this would result in biodiversity loss, which would undermine the viability of the overall heathland metacommunity (Diaz *et al.* 2013). Our results therefore suggest that “optimization” of both conservation and economic goals will inevitably result in some losses, either of biodiversity and/or of ecosystem service provision.

In the context of lowland heathland, we therefore support the suggestion of McShane *et al.* (2011) that rather than attempting to identify ‘win-win’ solutions for biodiversity conservation and economic development, it would be more appropriate to focus on identifying and explicitly acknowledging the trade-offs that exist. Hard choices will need to be made in implementing management for biodiversity conservation, because even “optimal” solutions will involve some form of losses (McShane *et al.* 2011), as demonstrated here. We suggest that management choices will become harder if practitioners are tasked with enhancing provision of ecosystem services, as well as conservation of biodiversity, as required by current policy (e.g. European Union (2011)). In the case of lowland heathland, we suggest that future management strategies should be developed at the landscape scale, based on explicit consideration of trade-offs associated with different management options. This will require coordination of planning and management across multiple sites, which represents a significant departure from the traditional management approach focusing on single sites in isolation (Heller & Zavaleta 2009). In addition, approaches will be required to enable the identification, analysis and communication of trade-offs, to support management decision-making. In this context, the guiding principles for analysing trade-offs presented by McShane *et al.* (2011) provide a valuable first step. As demonstrated here, tools such as MCA can also be of value in this context.

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Data accessibility

The Dorset Heathland Survey data used in the analyses have been assigned a Digital Object Identifier (Rose *et al* 2015). The other data used in the analyses presented here are uploaded as online supporting information.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Additional details of methods.

Appendix S2. Details of transition matrices.

Appendix S3. Additional results: carbon stocks.

Table 1. Details of management scenarios. Heaths were managed according to their size: small (< 40 ha), medium (≥ 40 and < 150 ha) and large (≥ 150 ha)

Scenario name		Management summary	Management interventions in each time step
No management	NM	No heaths managed	None
All heaths managed	AM	All heaths subjected to management, mimicking a 'site' scale approach to management	Equal amounts of scrub and woodland as removed in the SM scenario were removed from small, medium and large heaths. The area removed in each heathland size category was proportional to the area of scrub and woodland in each size category.
Small heaths managed	SM	Small (< 40 ha) heaths only managed.	All woodland and most scrub (leaving 10% on each heath) removed in each time step.
Large heaths managed	LM	Large (≥ 150 ha) heaths only managed.	The same total amount of scrub and woodland that was removed in the SM scenario was removed, and divided equally between all large heaths.

Table 2. Summary of transition matrices of heathland dynamics across all years in small (< 40 ha), medium (> 40 and < 150 ha) and large (> 150 ha) heaths (full matrices in Appendix S2). Vegetation types: G - grassland; M - mire; HH/WH -humid/wet heath; D - dry heath; S - scrub; W – woodland

Vegetation cover type	Small	Medium	Large	Vegetation cover type		Small	Medium	Large
Proportion of area staying the same				Proportion of area transitioning				
a) t78-87				a) t78-87				
				From	*To*			
G	0.46	0.54	0.81	M	SC	0.06	0.04	0.02
M	0.64	0.77	0.94	HH/WH	SC	0.11	0.04	0.02
HH/WH	0.72	0.82	0.94	DH	SC	0.12	0.07	0.05
DH	0.65	0.76	0.80	M	WO	0.08	0.06	0.01
SC	0.9	0.93	0.98	HH/WH	WO	0.07	0.06	0.01
WO	0.9	0.97	0.96	DH	WO	0.09	0.07	0.04
b) t87-96				b) t87-96				
G	0.58	0.68	0.86	M	SC	0.07	0.13	0.04
M	0.46	0.48	0.57	HH/WH	SC	0.11	0.03	0.02
HH/WH	0.44	0.69	0.80	DH	SC	0.08	0.04	0.01
DH	0.57	0.76	0.87	M	WO	0.21	0.07	0.11
SC	0.70	0.88	0.94	HH/WH	WO	0.15	0.11	0.04
WO	0.90	0.93	0.99	DH	WO	0.17	0.07	0.04
c) t96-05				c) t96-05				
G	0.42	0.7	1.00	M	SC	0.16	0.07	0.02
M	0.32	0.59	0.70	HH/WH	SC	0.11	0.13	0.04
HH/WH	0.35	0.44	0.55	DH	SC	0.10	0.11	0.01
DH	0.36	0.69	0.85	M	WO	0.22	0.08	0.09
SC	0.57	0.81	0.92	HH/WH	WO	0.31	0.05	0.11
WO	0.92	0.87	0.98	DH	WO	0.31	0.04	0.06

Table 3. Relative value of each vegetation cover type for biodiversity (number of UKBAP species). Values grouped by the same letter are not significantly different (Mann-Whitney U test $P > 0.05$, conducted on medians)

Vegetation cover type	Total number of survey squares	Total number of species recorded	Biodiversity value (mean number of species per 4 ha survey square)
Grassland	46	37	$2.76 \pm 0.60^{a,b}$
Dry heath	220	58	2.50 ± 0.13^{a}
Humid/wet heath	112	42	2.42 ± 0.18^{a}
Mire	18	20	$1.67 \pm 0.21^{a,b}$
Scrub	60	48	$2.52 \pm 0.39^{a,b}$
Woodland	170	53	1.95 ± 0.10^{b}

Table 4. Ecosystem service values for vegetation cover types found on heathlands. Carbon storage values (t C ha^{-1}) were measured directly, except for mire, where the value was obtained from Alonso *et al.* (2012). Values grouped by the same letter are not significantly different (Mann-Whitney U test $P > 0.05$, conducted on medians). Potential timber value refers to volume of timber (m^3 ha^{-1}). Aesthetic values were mean public preference values rated on a scale of 1–5 (with 5 meaning most appealing). Values grouped by the same letter are not significantly different (Wilcoxon Signed Ranks Test $P > 0.05$). Recreational values were coefficients of correlations between visitor numbers and proportion of area comprised by vegetation cover types in an individual heath. Significance of Spearman rank correlation indicated by: * $P \leq 0.05$; *** $P \leq 0.001$

Vegetation cover type	Carbon storage t C ha^{-1}	Timber value m^3 ha^{-1}		Aesthetic value	Recreational value
		Coniferous	Broadleaf		
Grassland	137[a,c]	0	0	3.4[a,d]	-0.33
Dry heath	159[a,b,c]	0	0	3.1[c]	0.61***
Humid/wet heath	125[a]	0	0	3.1[a,c]	-0.41*
Mire	138	0	0	2.7[b]	-0.17
Scrub	181[a,b,c]	0	0	3.4[d]	0.01
Woodland	244[b]	710	60	4.2[e]	-0.39*

Figure 1. Areas (ha) of cover types across all heaths for each scenario projection over 27 years (2005–2032), based on application of transition matrices. NM, black continuous line; SM, dashed line; LM, grey continuous line; AM dotted line.

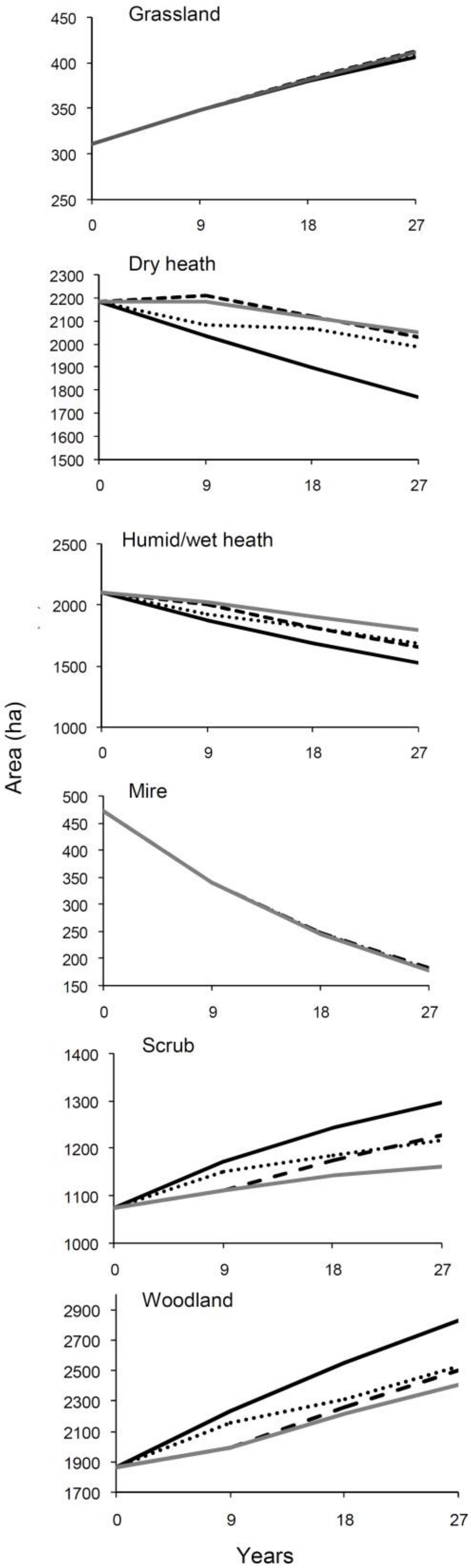

Figure 2. Ranking of scenarios based on the standardized scores for criteria. Values presented (‘MCA scores’) represent the normalized score for each ecosystem service and biodiversity, summed across all vegetation cover types and heathland patches, using the vegetation areas at the termination of the scenarios: (a) aesthetic value, (b) carbon storage, (c) recreation, (d) timber, (e) biodiversity. For details of scenarios, see Table 1.

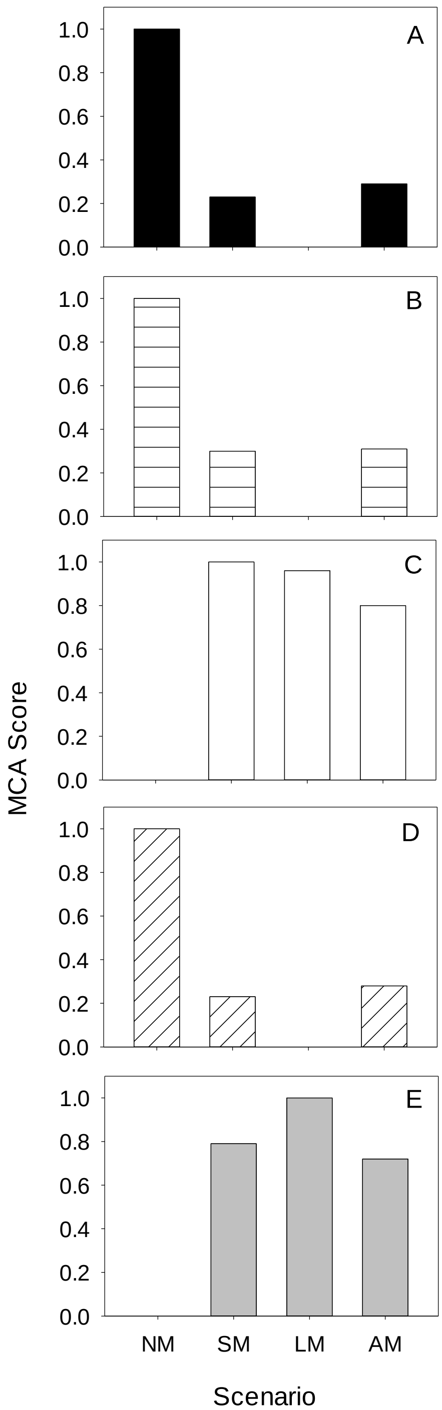

Figure 3. Ranking of scenarios based on MCA results attributable to combined ecosystem services and biodiversity, according to four different weighting methods: (a) equal weighting of all services and biodiversity; (b) market services (carbon and timber) weighted equally, and non-market services (aesthetic, recreation) and biodiversity given zero weight; (c) biodiversity only, with all ecosystem services given a zero weight; (d) recreation and aesthetic services given equal weight, and all other services and biodiversity given zero weight. The scores represent the outputs of the MCA, based on the weighted sum of the criteria scores. For details of scenarios, see Table 1.