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

4

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17

18 Running title: Resolving biodiversity–ecosystem service trade-offs

19

20 **Summary**

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

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

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

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

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

55 **Introduction**

56 In recent years, landscape-scale management approaches have increasingly
57 been adopted for the conservation of biodiversity (Jones 2011). Examples
58 include metapopulation management (Rouquette & Thompson 2007),
59 landscape restoration (Newton *et al.* 2012), ecological networks (Boitani *et al.*
60 2007) and rewilding (Navarro & Pereira 2012). Such approaches are also
61 being incorporated into environmental policy, for example by the Convention
62 on Biological Diversity (CBD) (Sayer *et al.* 2013) and the European Union
63 (EU) (Jones-Walters 2007). As illustration, the EU Biodiversity Strategy aims
64 to “reconnect fragmented natural areas and improve their functional
65 connectivity within the wider countryside” (European Union 2011). Similarly in
66 the UK, the current national biodiversity strategy is based around a “move

67 away from piecemeal conservation actions towards a more effective, more
68 integrated, landscape-scale approach” (Defra 2011).

69

70 Landscape-scale management has potential value for addressing trade-offs
71 between biodiversity conservation and economic development (Sayer *et al.*
72 2013). In this context, the concept of ecosystem services, or the benefits
73 provided to people by ecosystems, is relevant. It has been suggested that a
74 failure to incorporate the value of ecosystem services in land-use decision
75 making is a widespread cause of biodiversity loss (Carpenter *et al.* 2009;
76 Rands *et al.* 2010; Reyers *et al.* 2012). However, research has documented
77 that trade-offs often occur between biodiversity and ecosystem services, and
78 between different ecosystem services (Howe *et al.* 2014). For example, a
79 trade-off between agricultural production and biodiversity has been widely
80 reported (e.g. Chapin *et al.* 2000; Jiang *et al.* 2013; Macfayden *et al.* 2012;
81 Newton *et al.* 2012), and trade-offs between carbon storage and other
82 ecosystem services have also been identified (Goldstein *et al.* 2012; Nelson *et*
83 *al.* 2008). Such trade-offs have major implications for environmental
84 management, as they can potentially undermine the case for biodiversity
85 conservation, and hinder the identification of ‘win–win’ solutions to
86 conservation and sustainable development where both goals can be achieved
87 concurrently (Bullock *et al.* 2011; Goldstein *et al.* 2012; Howe *et al.* 2014;
88 McShane *et al.* 2011; Reyers *et al.* 2012).

89

90 Conservation and economic development objectives can potentially be
91 reconciled by targeting management interventions on different components of

92 the landscape (Sayer *et al.* 2013). Identification of the optimal allocation of
93 different management options at the landscape scale then becomes a key
94 challenge (de Groot *et al.* 2010). Even in situations where optimal solutions to
95 land management planning are difficult to identify, the explicit consideration of
96 trade-off choices should itself lead to improved conservation outcomes
97 (McShane *et al.* 2011). However, this has rarely been demonstrated in
98 practice. As noted by de Groot *et al.* (2010), improved decision-making in land
99 management relating to such trade-offs requires empirical information on the
100 relationships between ecosystem management and provision of ecosystem
101 services at the landscape scale. This information is currently lacking for most
102 ecosystems.

103

104 A limited number of studies have examined the impact of landscape-scale
105 conservation management approaches on trade-offs between biodiversity and
106 ecosystem services (Newton *et al.* 2012; Hodder *et al.* 2014; Birch *et al.*
107 2010). However, these studies did not identify how such trade-offs might be
108 resolved in practice, and each focused on conservation management
109 interventions distributed across entire landscapes. In practice, management
110 actions may frequently be restricted to sites of relatively high biodiversity
111 value, such as protected areas or designated sites. In such situations,
112 landscape-scale approaches require consideration of how management
113 interventions should be distributed among a network of sites. Analysis of
114 metapopulation and metacommunity dynamics has indicated that traditional
115 site-based approaches to management can fail to conserve biodiversity
116 effectively at the landscape scale (Economio 2011; Siqueira *et al.* 2012). This

117 is illustrated by analysis of long-term change in lowland heathland in the
118 southern English county of Dorset, which found that values of γ and α -
119 diversity of vascular plant communities both decreased over time, despite
120 conservation management being conducted on many individual sites (Diaz *et*
121 *al.* 2013).

122

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

142

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

162

163 **Materials and methods**

164 *Study area*

165 The Dorset heathlands are situated in southern England (50°39'N 2°5'W), and
166 are generally associated with free-draining and acidic soils overlying Tertiary

167 sands and gravels. The heathlands comprise a mosaic of different vegetation
168 types, characterized by dwarf shrub communities dominated by members of
169 the Ericaceae (e.g. *Calluna vulgaris*, *Erica* spp.), together with areas of mire,
170 grassland, scrub and woodland. If left unmanaged, heathlands undergo
171 succession to scrub (often dominated by *Ulex* spp.) and woodland
172 (characterized by *Betula* spp., *Pinus* spp., *Quercus* spp. and *Salix* spp.). The
173 majority of heathland sites are currently under some form of conservation
174 management, which is implemented to reduce succession to scrub and
175 woodland. Management interventions include cutting and burning of
176 vegetation, and grazing by livestock (Diaz *et al.* 2013; Newton *et al.* 2009).
177 Individual heathland patches are also managed for ecosystem services, such
178 as recreation and timber production, as well as biodiversity conservation (Diaz
179 *et al.* 2013).

180

181 *The Dorset Heathland Survey (DHS)*

182 In 1978, a comprehensive vegetation survey was conducted on the Dorset
183 heathlands that was subsequently repeated in the years 1987, 1996 and
184 2005. Detailed methods and results from the first three surveys have been
185 published previously (Rose *et al.* 2000; Webb 1990). Data for 2005 are
186 presented by Rose *et al.* (2015). For each survey, square plots of 4 ha (200 m
187 x 200 m) were located based on the national Ordnance Survey mapping grid
188 and were surveyed for the cover of all major vegetation types. These included
189 four types associated with relatively dry soils (dry heath, grassland, scrub and
190 woodland) and five additional types associated with relatively wet or poorly
191 draining soils (brackish marsh, carr, humid heath, wet heath and mire). The

192 other seven categories were bare ground, sand dunes, pools and ditches,
193 sand and gravel, arable, urban and other land uses. The first survey in 1978
194 established 4 ha plots throughout all Dorset heaths, resulting in a total survey
195 area of 3110 plots (12 440 ha). The same set of plots was resurveyed at each
196 subsequent survey date. Within each plot, the cover of each vegetation type
197 was recorded on a 3-point scale (1 = 1-10% cover; 2 = 10-50% cover; 3 =
198 \geq 50% cover).

199

200 *Biodiversity value*

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

211

212 *Ecosystem service assessment*

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

217

218 *Carbon storage*

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

227

228 *Aesthetic value*

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

235

236 *Recreational value*

237 The number of visitors to individual heaths was obtained from a questionnaire
238 survey conducted by Liley *et al.* (2008), which was sent to 5000 randomly
239 selected postcodes from across the region. On the basis of the 1632
240 responses received, the number of visitors for each of 26 heaths was
241 calculated, representing the heaths for which recreational visits were reported.

242 The association between log-transformed values of vegetation cover and

243 visitor number was then examined using Spearman's rank correlation, using
244 the proportion of each vegetation type in each heath calculated from the DHS
245 data. Correlation coefficients for each vegetation cover type were then applied
246 as an indicator of their relative value for recreation.

247

248 *Timber value*

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

259

260 *Analysis of vegetation dynamics*

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

266

267 To analyse vegetation dynamics, state transition matrices were developed
268 using the DHS data, across the time steps of successive surveys (1978–1987,

269 1987–1996 and 1996–2005, labelled t78-87, t87-96 and t96-05 respectively).
270 Transition matrices were developed by quantifying the probability of change
271 between all vegetation cover types, across all the heaths surveyed. Individual
272 transition matrices were created for each of the 112 heathland patches and
273 validated using the DHS data collected at subsequent survey dates (see
274 Appendix S2).

275

276 *Scenario development*

277 Future vegetation cover change under different management scenarios was
278 modelled by multiplying the current area of each vegetation type in each heath
279 (derived from the land cover map) by transition matrices, using the R 2.15
280 statistical package (R Development Core Team 2012). For this purpose, the
281 transition matrices were modified to include only the following cover types:
282 grassland, humid/wet heath, mire, dry heath, scrub and woodland. Separate
283 transition matrices were developed for small (< 40 ha), medium (≥ 40 and <
284 150 ha) and large (≥ 150 ha) heaths, and represented vegetation cover
285 change over nine years, which was the interval between the surveys from
286 which the matrices were derived (see Appendix S2). A 27 year scenario
287 projection time was chosen (three time steps), representing 2005 until 2032,
288 to provide a policy-relevant timeline.

289

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

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

298

299 *Analysis of trade-offs and synergies*

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

312

313 **Results**

314 *Analysis of woody succession*

315 Regression analysis of the heathland survey data indicated that the
316 percentage increase in area of scrub and woodland was significantly and
317 negatively related to heathland patch size between all survey years (1978–
318 1987, $r^2 = 0.623$; 1987–1996, $r^2 = 0.549$; 1996–2005, $r^2 = 0.583$; $P < 0.001$ in

319 each case). This indicates a higher rate of succession from heathland to scrub
320 and woodland on smaller than on larger heaths. This result was illustrated by
321 the transition matrices, which generally indicated a higher proportion of heath
322 vegetation types transitioning to woodland or scrub on smaller heaths,
323 regardless of the year of survey (Table 2).

324

325 *Management scenarios*

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

331

332 *Biodiversity and ecosystem service values*

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

343

344 *Analysis of trade-offs*

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

351

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

361

362 Results of the MCA varied markedly depending on which weights were
363 selected. If each ecosystem service and biodiversity were equally weighted,
364 NM ranked highest and LM lowest (Figure 3a), reflecting the relatively large
365 number of services that were positively associated with woodland and scrub.
366 Higher weighting of services with a market value, namely carbon and timber,
367 accentuated this result (Figure 3b). However, if biodiversity was weighted
368 preferentially, NM ranked lowest of the four management options, and LM the

369 highest, reflecting the lower woodland area associated with the latter scenario.
370 In no scenario did the current site-based approach to management, which
371 approximates AM, rank highest out of the management options considered.

372

373 **Discussion**

374 Our study indicates that in the case of lowland heathland, trade-offs can occur
375 between different ecosystem services, and between ecosystem services and
376 biodiversity. Specifically, a trade-off was identified between carbon storage,
377 timber and aesthetic value on the one hand, versus biodiversity and
378 recreational value on the other. The higher biodiversity value associated with
379 heath vegetation and the lower value associated with woodland supports the
380 current approach to conservation management of lowland heathland sites,
381 which is primarily aimed at reducing encroachment of woody plants (Diaz *et al.*
382 *2013*; Newton *et al.* 2009). However, according our results, the provision of
383 carbon storage, timber and aesthetic value would be reduced by such a
384 management approach compared to alternative approaches.

385

386 Our results also indicate that these trade-offs might be addressed through
387 appropriate landscape-scale management. Both biodiversity value and the
388 provision of ecosystem services were related to the size of heathland patches.
389 This reflects an underlying negative relationship between heathland patch size
390 and the rate of woody plant succession. Therefore, targeting management
391 interventions to heathland patches of different sizes could reduce conflicts in
392 biodiversity conservation and delivery of particular ecosystem services, based
393 on priority setting. For example, if biodiversity conservation was the principal

394 goal, management would be most effective if focused preferentially on larger
395 heathland patches. Under this approach, the aesthetic, carbon storage and
396 timber value of smaller patches would increase. In this way, individual
397 heathland patches of either relatively high biodiversity value or high value for
398 provision of ecosystem services could both be delivered at the landscape
399 scale.

400

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

413

414 Following Yapp *et al.* (2010), we suggest that the balance of ecosystem
415 service provision and biodiversity at the landscape scale can be manipulated
416 through distribution of vegetation management across different sites.
417 Specifically, we suggest that in the current example, biodiversity–ecosystem
418 service trade-offs can potentially be addressed by targeting management

419 interventions at different locations within a landscape based on consideration
420 of patch size. It is pertinent to consider whether such an approach is relevant
421 to other ecological contexts. A trade-off between carbon storage and
422 biodiversity value is likely wherever early successional habitats are associated
423 with relatively high biodiversity value, which is the case for a number of other
424 plant communities in north-western Europe, including semi-natural grasslands
425 and shrublands (Sutherland 2000). Similarly in New Zealand, Dickie *et al.*
426 (2011) reported an increase in carbon pools with woody succession, but found
427 negative impacts on species richness of selected taxonomic groups. Other
428 studies have also reported a negative relationship between patch size and
429 rate of wood plant succession, as recorded here. For example, Wardle *et al.*
430 (2012) found that small islands in a Swedish archipelago were likely to
431 undergo succession more rapidly, owing to increased incidence of fire on
432 larger islands. However, converse results have also been reported, for
433 example by Cook *et al.* (2005) in experimentally fragmented agricultural fields.
434 Such contrasting results highlight the difficulty of generalizing about the
435 impact of patch size on successional trajectories, reflecting the potential
436 influence of many other factors and stochastic events on the successional
437 process (Matthews 2014).

438

439 If biodiversity–ecosystem trade-offs can potentially be addressed by
440 appropriate landscape-scale management, the question remains: should they
441 be? This question is relevant to a major current debate in conservation
442 science. The concept of ecosystem services was originally developed to
443 promote the protection of natural ecosystems, and many authors have

444 subsequently suggested that increased recognition of the value of ecosystem
445 services to human society will strengthen the conservation of biodiversity (e.g.
446 Bayon & Jenkins 2010; Ghazoul 2007). However, management for provision
447 of ecosystem services has increasingly become a goal in its own right (Soulé
448 2013). It has been suggested that management strategies “must be promoted
449 that simultaneously maximize the preservation of biodiversity and the
450 improvement of human well-being” (Kareiva & Marvier 2012). Such
451 suggestions have sparked an acrimonious debate, which is still ongoing
452 (Soulé 2013; Tallis & Lubchenko and 238 cosignatories 2014). If ‘win-win’
453 outcomes can be identified, then there is no conflict between these two
454 management goals. However, identification of trade-offs indicates that conflict
455 exists between these goals, representing a ‘win-lose’ situation. Kareiva &
456 Marvier (2012) suggest that in such circumstances, trade-offs should be
457 minimized by “actively seeking to optimize both conservation and economic
458 goals”. Here we demonstrate that this can potentially be achieved by
459 implementing contrasting management approaches on heathland patches of
460 different sizes. However, if management interventions were reduced on
461 smaller heathland patches, this would result in biodiversity loss, which would
462 undermine the viability of the overall heathland metacommunity (Diaz *et al.*
463 2013). Our results therefore suggest that “optimization” of both conservation
464 and economic goals will inevitably result in some losses, either of biodiversity
465 and/or of ecosystem service provision.

466

467 In the context of lowland heathland, we therefore support the suggestion of
468 McShane *et al.* (2011) that rather than attempting to identify ‘win-win’

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

489

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494 studentship.

495

496 **Data accessibility**

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

500

501 **References**

502 Bayon, R. & Jenkins, M. (2010) The business of biodiversity. *Nature*, **466**,
503 184–185.

504 Birch, J., Newton, A.C., Alvarez Aquino, C., Cantarello, E., Echeverría, C.,
505 Kitzberger, T., Schiappacasse, I. & Tejedor Garavito, N. (2010) Cost-
506 effectiveness of dryland forest restoration evaluated by spatial analysis
507 of ecosystem services. *Proceedings of the National Academy of*
508 *Sciences USA*, **107(50)**, 21925-21930.

509 Boitani, L., Falcucci, A., Maiorano, L. & Rondinini, C. (2007) Ecological
510 networks as conceptual frameworks or operational tools in
511 conservation. *Conservation Biology*, **21(6)**, 1414–1422.

512 Bullock, J.M., Aronson, J., Newton, A.C., Pywell, R.F. & Rey Benayas, J.M.
513 (2011) Restoration of ecosystem services and biodiversity: conflicts
514 and opportunities. *Trends in Ecology and Evolution*, **26**, 541-549.

515 Carpenter, S.R., Mooney, H.A., Agard, J., Capistrano, D., DeFries, R.S., Diaz,
516 S., Dietz, T., Duraiappah, A.K., Oteng-Yeboah, A., Pereira, H.M.,
517 Perrings, C., Reid, W.V., Sarukhan, J., Scholes, R.J. & Whyte, A.
518 (2009) Science for managing ecosystem services: Beyond the

519 Millennium Ecosystem Assessment. *Proceedings of the National*
520 *Academy of Sciences USA*, **106**, 1305-1312.

521 Chapin, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M.,
522 Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E.,
523 Mack, M.C. & Diaz, S. (2000) Consequences of changing biodiversity.
524 *Nature*, **405**, 234-242.

525 Cook, W.M., Yao, J., Foster, B.L., Holt, R.D. & Patrick, L.B. (2005) Secondary
526 succession in an experimentally fragmented landscape: community
527 patterns across space and time. *Ecology*, **86(5)**, 1267-1279.

528 DEFINITE. (2006) *DEFINITE*. Institute for Environmental Studies, Amsterdam,
529 the Netherlands.

530 Defra (2011) *Biodiversity 2020: a strategy for England's Wildlife and*
531 *Ecosystem Services*. Department for Environment, Food and Rural
532 Affairs, London.

533 De Groot, R.S., Alkemade, R., Braat, L., Hein, L. & Willemsen, L. (2010)
534 Challenges in integrating the concept of ecosystem services and
535 values in landscape planning, management and decision making.
536 *Ecological Complexity*, **7(3)**, 260–272.

537 Diaz, A., Keith, S.A., Bullock, J.M., Hooftman, D.A.P. & Newton, A.C. (2013)
538 Conservation implications of long-term changes detected in a lowland
539 heath metacommunity. *Biological Conservation*, **167**, 325-333.

540 Dickie, I.A., Yeates, G.W., St John, M.G., Stevenson, B.A., Scott, J.T., Rillig,
541 M.C., Peltzer, D.A., Orwin, K.H., Kirschbaum, M.U.F., Hunt, J.E.,
542 Burrows, J.E., Barbour, M.M. & Aislabie, J. (2011) Ecosystem service

543 and biodiversity trade-offs in two woody successions. *Journal of*
544 *Applied Ecology*, **48(4)**, 926-934.

545 Economo, E.P. (2011) Biodiversity conservation in metacommunity networks:
546 linking pattern and persistence. *American Naturalist*, **177(6)**, E167-80.
547 doi: 10.1086/659946.

548 ESRI. (2011) *ArcGIS Desktop: Release 10*. Environmental Systems Research
549 Institute, Redlands, CA.

550 European Union. (2011) *The EU Biodiversity Strategy to 2020*. European
551 Union publications office, Luxembourg.

552 Ghazoul, J. (2007) Recognising the complexities of ecosystem management
553 and the ecosystem service concept. *Gaia*, **16**, 215–221.

554 Goldman, R.L. & Tallis, H. (2009) A critical analysis of ecosystem services as
555 a tool in conservation projects: The possible perils, the promises, and
556 the partnerships. *Annals of the New York Academy of Science*, **1162**,
557 63-78.

558 Goldstein, J.H., Caldarone, G., Duarte, T.K., Ennaanay, D., Hannahs, N.,
559 Mendoza, G., Polasky, S., Wolny, S. & Daily, G.C. (2012) Integrating
560 ecosystem-service tradeoffs into land-use decisions. *Proceedings of*
561 *the National Academy of Sciences USA*, **109(19)**, 7565-7570.

562 Hanski, I. (1999) *Metapopulation ecology*. Oxford University Press, Oxford.

563 Heller, N.E., & Zavaleta, E.S. (2009) Biodiversity management in the face of
564 climate change: a review of 22 years of recommendations. *Biological*
565 *Conservation*, **142(1)**, 14–32.

566 Hodder, K.H., Newton, A.C., Cantarello, E. & Perrella, L. (2014) Does
567 landscape-scale conservation management enhance the provision of

568 ecosystem services? *International Journal of Biodiversity Science,*
569 *Ecosystem Services and Management*, **10(1)**. 71-83.

570 Hooftman, D.A.P. & Bullock, J.M. (2012) Mapping to inform conservation: A
571 case study of changes in semi-natural habitats and their connectivity
572 over 70 years. *Biological Conservation*, **145(1)**, 30-38.

573 Howe, C., Suich, H., Vira, B. & Mace, G.M. (2014) Creating win-wins from
574 tradeoffs? Ecosystem services for human well-being: a meta-analysis
575 of ecosystem service tradeoffs and synergies in the real world. *Global*
576 *Environmental Change*, **28**, 263-275.

577 Jiang, M., Bullock, J.M. & Hooftman, D.A.P. (2013) Mapping ecosystem
578 services and biodiversity changes over 70 years in a rural English
579 county. *Journal of Applied Ecology*, **50**, 841-850.

580 Jones, J.P. (2011) Monitoring species abundance and distribution at the
581 landscape scale. *Journal of Applied Ecology*, **48(1)**, 9-13.

582 Jones-Walters, L. (2007) Pan-European Ecological Networks. *Journal for*
583 *Nature Conservation*, **15**, 262—264.

584 Kareiva, P. & Marvier, M. (2012) What is conservation science? *BioScience*,
585 **62(11)**, 962-969.

586 Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M.,
587 Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M.,
588 & Gonzalez, A. (2004) The metacommunity concept: a framework for
589 multi-scale community ecology. *Ecology Letters*, **7(7)**, 601-613.

590 Liley, D., Sharp, J. & Clarke, R.T. (2008) *Access patterns in South-east*
591 *Dorset. Dorset household survey and predictions of visitor use of*
592 *potential greenspace sites*. Footprint Ecology, Wareham, Dorset.

593 Macfayden, S., Cunningham, S.A., Costamanga, A.C. & Schellhorn, N.A.
594 (2012) Managing ecosystem services and biodiversity conservation in
595 agricultural landscapes: are the solutions the same? *Journal of Applied*
596 *Ecology*, **49**, 690-694.

597 Matthews, J.W. (2014) Group-based modeling of ecological trajectories in
598 restored wetlands. *Ecological Applications* doi:10.1890/14-0390.1

599 McShane, T.O., Hirsch, P.D., Trung, T.C., Songorwa, A.N., Kinzig, A.,
600 Monteferri, B., Mutekanga, D., Van Thang, H., Dammert, J.L., Pulgar-
601 Vidal, M., Welch-Devine, M., Brosius, J.P., Coppolillo, P. & O'Connor,
602 S. (2011) Hard choices: making tradeoffs between biodiversity and
603 human well-being. *Biological Conservation*, **144**, 966-972.

604 Moilanen, A., Anderson, B.J., Eigenbrod, F., Heinemeyer, A., Roy, D.B.,
605 Gillings, S., Armsworth, P.R., Gaston, K.J. & Thomas, C.D. (2011)
606 Balancing alternative land uses in conservation prioritization. *Ecological*
607 *Applications*, **21(5)**, 1419–1426.

608 Navarro, L.M. & Pereira, H.M. (2012) Rewilding abandoned landscapes in
609 Europe. *Ecosystems*, **15(6)**, 900-912.

610 Nelson, E., Polasky, S., Lewis, D.J., Plantinga, A.J., Lonsdorf, E., White, D.,
611 Bael, D. & Lawler, J.J. (2008) Efficiency of incentives to jointly increase
612 carbon sequestration and species conservation on a landscape.
613 *Proceedings of the National Academy of Sciences USA*, **105(28)**,
614 9471–9476.

615 Newton, A.C., Hodder, K., Cantarello, E., Perrella, L., Birch, J.C., Robins, J.,
616 Douglas, S., Moody, C., & Cordingley, J. (2012) Cost–benefit analysis

617 of ecological networks assessed through spatial analysis of ecosystem
618 services. *Journal of Applied Ecology*, **49(3)**, 571–580.

619 Newton, A.C., Stewart, G.B., Myers, G., Diaz, A., Lake, S., Bullock, J.M. &
620 Pullin, A.S. (2009) Impacts of grazing on lowland heathland in north-
621 west Europe. *Biological Conservation*, **142(5)**, 935–947.

622 R Development Core Team. (2012) *R: a language and environment for*
623 *statistical computing*. R Foundation for Statistical Computing, Vienna,
624 Austria. Available at: <http://www.R-project.org/>.

625 Rands, M.R.W., Adams, W.M., Bennun, L., Butchart, S.H.M., Clements, A.,
626 Coomes, D., Entwistle, A., Hodge, I., Kapos, V., Scharlemann, J.P.W.,
627 Sutherland, W.J. & Vira, B. (2010) Biodiversity conservation:
628 challenges beyond 2010. *Science*, **329(5997)**, 1298–1303.

629 Reyers, B., Polasky, S., Tallis, H., Mooney, H.A., Larigauderie, A. (2012)
630 Finding common ground for biodiversity and ecosystem services.
631 *Bioscience*, **62**, 503-507.

632 Rose, R. J., Bullock, J. M., Clarke, R. T., Cordingley, J. E. & Newton, A. C.
633 (2015) Individual heath area estimates for land cover types in Dorset:
634 1978-2005. NERC-Environmental Information Data Centre doi:
635 10.5285/[4c347ec4-0beb-4355-9780-89dad718b2f3](https://doi.org/10.5285/4c347ec4-0beb-4355-9780-89dad718b2f3)

636 Rose, R.J., Webb, N.R., Clarke, R.T., & Traynor, C.H. (2000) Changes on the
637 heathlands in Dorset, England, between 1987 and 1996. *Biological*
638 *Conservation*, **93(1)**, 117–125.

639 Rouquette, J.R. & Thompson, D.J. (2007) Patterns of movement and
640 dispersal in an endangered damselfly and the consequences for its
641 management. *Journal of Applied Ecology*, **44(30)**, 692–701.

642 Sayer, J., Sunderland, T., Ghazoul, J., Pfund, J.-L., Sheil, D., Meijaard, E.,
643 Venter, M., Boedihartono, A.K., Day, M., Garcia, C., van Oosten, C. &
644 Buck, L.E. (2013) Ten principles for a landscape approach to
645 reconciling agriculture, conservation, and other competing land uses
646 *Proceedings of the National Academy of Sciences USA*,
647 **110 (21)**, 8349-8356.

648 Schneiders, A., Van Daele, T., Van Landuyt, W., Van Reeth, W. (2012)
649 Biodiversity and ecosystem services: Complementary approaches for
650 ecosystem management? *Ecological Indicators*, **21**, 123-133.

651 Siqueira, T., Bini, L.M., Roque, F.O. & Cottenie, K. (2012) A metacommunity
652 framework for enhancing the effectiveness of biological monitoring
653 strategies. *PloS One*, **7(8)**, e43626.

654 Soulé, M. (2013) The “New Conservation”. *Conservation Biology*, **27(5)**, 895-
655 897.

656 Sutherland, W.J. (2000) *The Conservation Handbook. Research,*
657 *Management and Policy*. Blackwell Science, Oxford. UK.

658 Tallis, H., Lubchenko, J. & 238 cosignatories (2014) A call for inclusive
659 conservation. *Nature*, **515**, 27-28.

660 Wainger, L.A., King, D.M., Mack, R.N., Price, E.W., Maslin, T. (2010) Can the
661 concept of ecosystem services be practically applied to improve natural
662 resource management decisions? *Ecological Economics*, **69**, 978-987.

663 Wardle, D.A., Jonsson, M., Bansal, S., Bardgett, R.D., Gundale, M.J. &
664 Metcalfe, D.B. (2012) Linking vegetation change, carbon sequestration
665 and biodiversity: insights from island ecosystems in a long-term natural
666 experiment. *Journal of Ecology*, **100**, 16-30.

667 Webb, N.R. (1990) Changes on the heathlands of Dorset, England, between
668 1978 and 1987. *Biological Conservation*, 51(4), 273–286.

669 Webb, N.R. (1986) *Heathlands*. Collins, New Naturalist Series, London.

670 Whittingham, M.J. (2011) The future of agri-environment schemes:
671 biodiversity gains and ecosystem service delivery? *Journal of Applied*
672 *Ecology*, **48**, 509–513.

673 Yapp, G., Walker, J., Thackway, R. (2010) Linking vegetation type and
674 condition to ecosystem goods and services. *Ecological Complexity*, **7**,
675 292-301.

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678 **Supporting Information**

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

680 article:

681 **Appendix S1.** Additional details of methods.

682 **Appendix S2.** Details of transition matrices.

683 **Appendix S3.** Additional results: carbon stocks.

684

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686 Table 1. Details of management scenarios. Heaths were managed according
 687 to their size: small (< 40 ha), medium (≥ 40 and < 150 ha) and large (≥ 150
 688 ha)
 689

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.

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692 Table 2. Summary of transition matrices of heathland dynamics across all
 693 years in small (< 40 ha), medium (> 40 and < 150 ha) and large (> 150 ha)
 694 heaths (full matrices in Appendix S2). Vegetation types: G - grassland; M -
 695 mire; HH/WH -humid/wet heath; D - dry heath; S - scrub; W – woodland
 696

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			
				<i>From</i>	<i>To</i>		
G	0.46	0.54	0.81	M	SC	0.06	0.04
M	0.64	0.77	0.94	HH/WH	SC	0.11	0.04
HH/WH	0.72	0.82	0.94	DH	SC	0.12	0.07
DH	0.65	0.76	0.80	M	WO	0.08	0.06
SC	0.9	0.93	0.98	HH/WH	WO	0.07	0.06
WO	0.9	0.97	0.96	DH	WO	0.09	0.07
b) t87-96				b) t87-96			
G	0.58	0.68	0.86	M	SC	0.07	0.13
M	0.46	0.48	0.57	HH/WH	SC	0.11	0.03
HH/WH	0.44	0.69	0.80	DH	SC	0.08	0.04
DH	0.57	0.76	0.87	M	WO	0.21	0.07
SC	0.70	0.88	0.94	HH/WH	WO	0.15	0.11
WO	0.90	0.93	0.99	DH	WO	0.17	0.07
c) t96-05				c) t96-05			
G	0.42	0.7	1.00	M	SC	0.16	0.07
M	0.32	0.59	0.70	HH/WH	SC	0.11	0.13
HH/WH	0.35	0.44	0.55	DH	SC	0.10	0.11
DH	0.36	0.69	0.85	M	WO	0.22	0.08
SC	0.57	0.81	0.92	HH/WH	WO	0.31	0.05
WO	0.92	0.87	0.98	DH	WO	0.31	0.04

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

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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 ± 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 ± 0.21 ^{a,b}
Scrub	60	48	2.52 ± 0.39 ^{a,b}
Woodland	170	53	1.95 ± 0.10 ^b

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707 Table 4. Ecosystem service values for vegetation cover types found on
 708 heathlands. Carbon storage values (t C ha⁻¹) were measured directly, except
 709 for mire, where the value was obtained from Alonso *et al.* (2012). Values
 710 grouped by the same letter are not significantly different (Mann-Whitney U test
 711 $P > 0.05$, conducted on medians). Potential timber value refers to volume of
 712 timber (m³ ha⁻¹). Aesthetic values were mean public preference values rated
 713 on a scale of 1–5 (with 5 meaning most appealing). Values grouped by the
 714 same letter are not significantly different (Wilcoxon Signed Ranks Test $P >$
 715 0.05). Recreational values were coefficients of correlations between visitor
 716 numbers and proportion of area comprised by vegetation cover types in an
 717 individual heath. Significance of Spearman rank correlation indicated by: * $P \leq$
 718 0.05; *** $P \leq 0.001$
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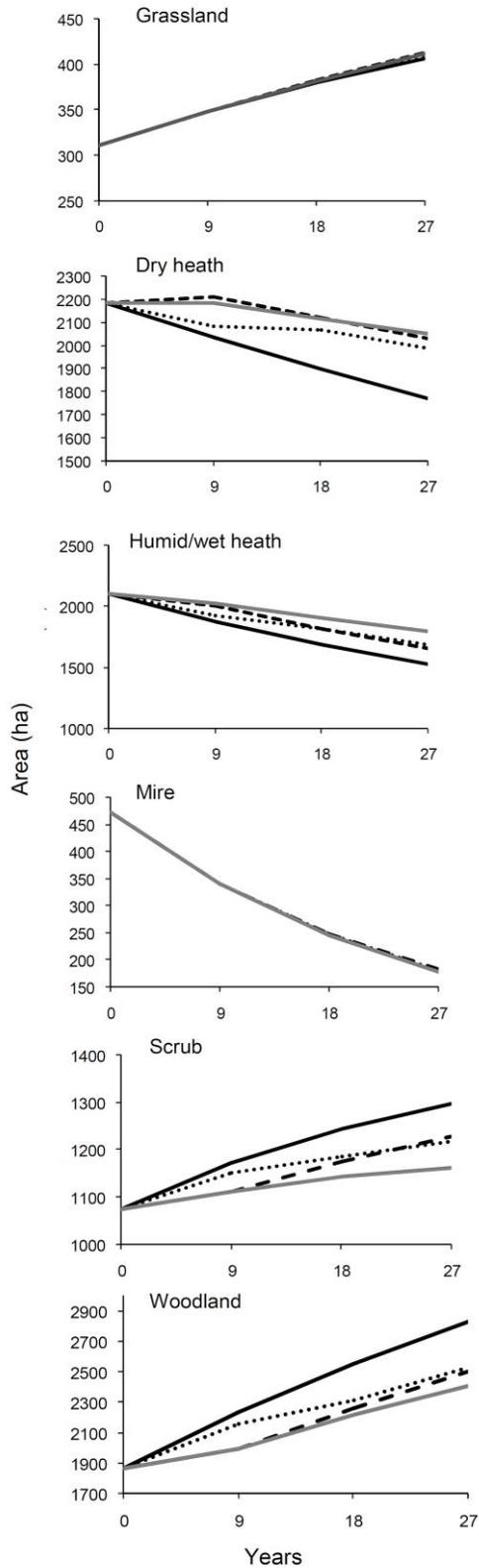
Vegetation cover type	Carbon storage t C ha ⁻¹	Timber value m ³ ha ⁻¹		Aesthetic value	Recreational value
		Coniferous	Broadleaf		
Grassland	137 ^{a,c}	0	0	3.4 ^{a,d}	-0.33
Dry heath	159 ^{a,b,c}	0	0	3.1 ^c	0.61 ^{***}
Humid/wet heath	125 ^a	0	0	3.1 ^{a,c}	-0.41 [*]
Mire	138	0	0	2.7 ^b	-0.17
Scrub	181 ^{a,b,c}	0	0	3.4 ^d	0.01
Woodland	244 ^b	710	60	4.2 ^e	-0.39 [*]

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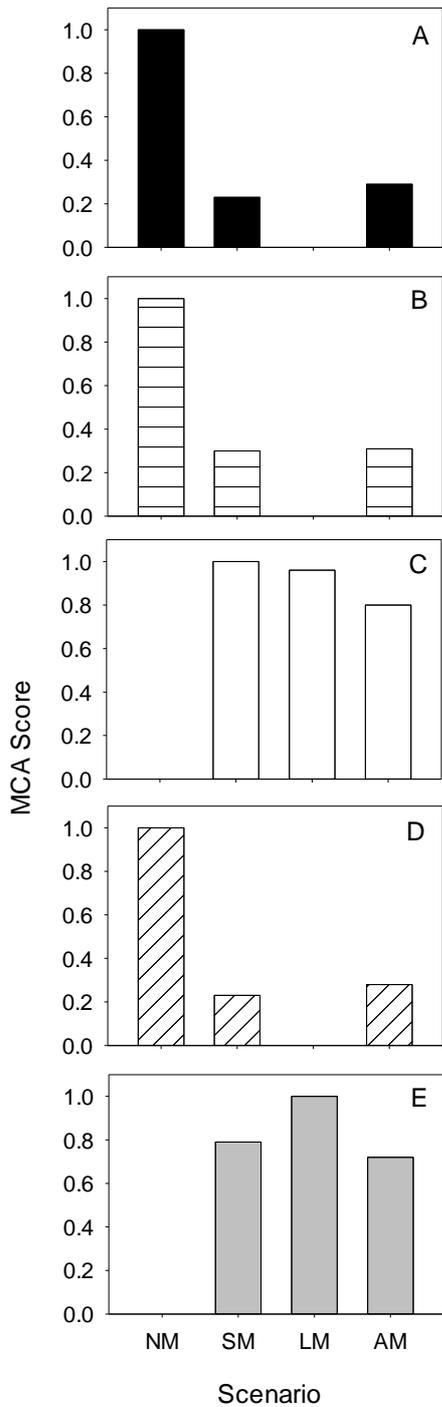
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723 Figure 1. Areas (ha) of cover types across all heaths for each scenario
 724 projection over 27 years (2005–2032), based on application of transition
 725 matrices. NM, black continuous line; SM, dashed line; LM, grey continuous
 726 line; AM dotted line.
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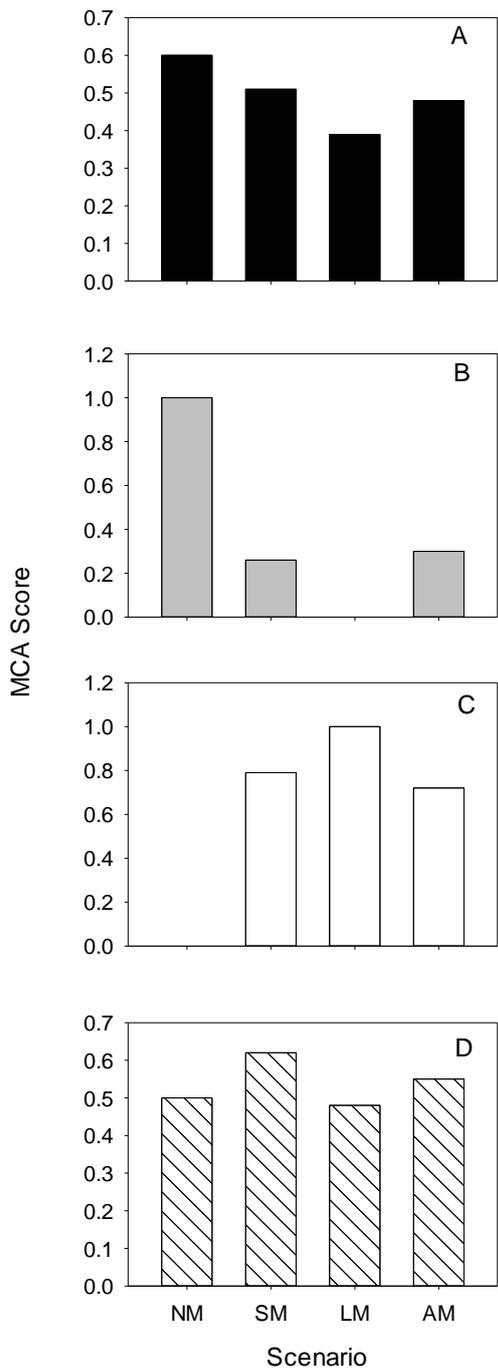
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731 Figure 2. Ranking of scenarios based on the standardized scores for criteria.
 732 Values presented ('MCA scores') represent the normalized score for each
 733 ecosystem service and biodiversity, summed across all vegetation cover types
 734 and heathland patches, using the vegetation areas at the termination of the
 735 scenarios: (a) aesthetic value, (b) carbon storage, (c) recreation, (d) timber,
 736 (e) biodiversity. For details of scenarios, see Table 1.
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739 Figure 3. Ranking of scenarios based on MCA results attributable to combined
 740 ecosystem services and biodiversity, according to four different weighting
 741 methods: (a) equal weighting of all services and biodiversity; (b) market
 742 services (carbon and timber) weighted equally, and non-market services
 743 (aesthetic, recreation) and biodiversity given zero weight; (c) biodiversity only,
 744 with all ecosystem services given a zero weight; (d) recreation and aesthetic
 745 services given equal weight, and all other services and biodiversity given zero
 746 weight. The scores represent the outputs of the MCA, based on the weighted
 747 sum of the criteria scores. For details of scenarios, see Table 1.
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