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REVIEW

Human activities and biodiversity opportunities in pre-industrial cultural landscapes: relevance to conservation

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Summary

1. Conservation practices in Europe frequently attempt to perpetuate or mimic the 'traditional' forms of management of semi-natural habitats, but with a limited understanding of what these entailed.

2. We review the emerging understanding of ecological processes, structures and management interventions that enhance biodiversity (wildlife) at diverse scales. These are then examined in the context of pre-industrial (*c*. 1200–1750) land management systems in lowland England, in order to identify historic practices which are likely to have provided important wildlife resources, but which are relatively neglected in current conservation management.

3. Principles enhancing alpha and beta diversity and the conservation status of threatened species include structural complexity and heterogeneity at nested spatial scales; physical disturbance and exposure of mineral substrate; nutrient removal; lengthened successional rotations; and spatial variation in grazing regimes.

4. The available evidence suggests that pre-industrial land management was generally characterized by intense resource exploitation and significant levels of biomass harvest; complex nested structural heterogeneity both between and within landscape elements; overlaying of multiple land uses; and spatial and temporal variability in management, rendering the concept of long-lived 'traditional' practice problematic. Grazing patterns are poorly understood, but intensive grazing was probably the norm in most contexts, potentially resulting in simplified sward structures and suppressed ecotonal vegetation.

5. In much of the pre-industrial period, early-successional and disturbed microhabitats were widespread, but ungrazed or lightly grazed herb-rich vegetation may have been limited, the converse of current conservation management. The key change since then has been homogenization at multiple scales, coupled with reduction of specific niches and conditions.

6. *Synthesis and applications*. In adopting perceived 'traditional' management practices, modern conservation rarely achieves the range and complexity of conditions that were present in the past. A better understanding of past practices allows more favourable management of those surviving semi-natural habitats where historic assemblages persist – with greater emphasis on physical disturbance and variability in prescriptions both temporally and spatially. When creating or restoring habitats, after interruption of management sufficiently long for dependent assemblages to be lost, better appreciation of historic management encourages novel forms of intervention to enhance biodiversity, with emphasis on complex structural and spatial heterogeneity at nested scales, biomass removal and nutrient reduction. These strongly management-based approaches are complementary to the use of large herbivores to create and maintain dynamic ecotonal mosaics in the manner advocated by some proponents of 'rewilding'.

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Introduction

An appreciation of the long-term interactions of human societies and wildlife has long formed a cornerstone of conservation philosophy across much of western Europe (Martin *et al.* 2012) and remains central to species conservation in anthropogenic landscapes elsewhere (Fischer, Hartel & Kuemmerle 2012). However, biodiversity conservation within cultural landscapes is at a crossroads, with the paradigm (Wright, Lake & Dolman 2012) of semi-natural habitat management through mimicking 'traditional' land-use patterns being increasingly challenged by a vogue for the restoration of natural processes or 'rewilding' (Linnell *et al.* 2015). For both camps, knowledge of past land-use systems has often been limited or simplistic. In the future, biodiversity conservation faces significant challenges from accelerating climatic change, increasing agricultural demands and changing economies. A perspective from historic ecology focusing on resource and process requirements can offer valuable insights for conservation strategies.

Information on the long-term development of habitats and environments has so far been insufficiently utilized in developing conservation solutions and insights (Willis *et al.* 2007; Hanley *et al.* 2008). Here, we link current understanding of resource needs in the maintenance of biodiversity (i.e. the multiplicity of scale dependencies and niches of species) to recent knowledge about the variability and range of historic land management systems. Our aim is to identify historic practices that appear to have been important in providing past opportunities for biodiversity, but which are neglected or insufficiently promoted in current conservation management. This knowledge can potentially inform current attempts to create opportunities for wildlife within changing anthropogenic landscapes.

Since the mid-20th century, four tenets have commonly influenced conservation in regions, such as western Europe, that have been heavily populated by humans over extended periods of time. The first is that virtually all original natural vegetation has long since been destroyed or substantially modified. Whilst broadly true, elements of former naturalness are retained in various ecosystems including coasts, mountains and woodland. Secondly, destruction and fragmentation of the original natural vegetation, especially in productive lowland regions, has filtered biodiversity through an 'ecological bottleneck', exemplified by the loss of Urwald fauna (Buckland & Dinnin 1993). The rich assemblages that developed in the resulting semi-natural landscapes comprised a subset of the original biodiversity, with an increased abundance of open-habitat and thermophilous species (Buckland & Dinnin 1993), supplemented by arriving pseudo-steppe species. The third concerns surviving patches of semi-natural vegetation (*sensu* Tansley 1939), that is, ancient but anthropogenic ecosystems comprising native vegetation with substantially modified composition and structure. As these systems support rich (albeit filtered) biodiversity, including many species that are now scarce or threatened, it is generally accepted that they should be managed in ways that mimic the largely obsolete land-use practices that created and maintained them, practices which typically involved repeatedly interrupting ecological succession (Westhoff 1971; Duffey *et al.* 1974). During the last century, successional change following abandonment of 'traditional' practices led to population declines and extirpations within these remaining habitat fragments, and widespread loss of ecological richness and distinctiveness (e.g. Fojt & Harding 1995; Spitzer *et al.* 2008) – strengthening the belief that replicating historic management should be fundamental to conservation. A fourth tenet is that some historic management practices sustain species because they provide important natural ecological processes that have otherwise been lost from modified, fragmented landscapes (Wright, Lake & Dolman 2012).

This semi-natural management paradigm can lead to questionable assumptions. In particular, it is sometimes thought that past human activities were generally benign and that mimicking 'traditional' practices, rather than exploring novel forms of management, will of necessity optimize biodiversity (Morris 1991). Moreover, a focus on semi-natural habitats *per se*, rather than on the specific resources which these provide, can obscure what should be the main aim of conservation activity – the maintenance of biodiversity (Dolman, Panter & Mossman 2012). It also serves to downplay the potential value to biodiversity of novel vegetation structures and management interventions. This approach is further limited, moreover, by a simplified understanding of historic management, with an emphasis on some practices but an almost complete neglect of others, and further presupposes that a stable period of 'tradition' can be identified as a reference or baseline.

Cooperation between landscape historians and ecologists means that we can begin to use our knowledge of land-use systems and landscape structures in pre-industrial England to assess the likely patterns, habitat extents, structures and resources available to wildlife in the past. Our chosen period of study is *c.* 1200 to *c.* 1750, after which point complex technological, social and economic developments introduced fundamental and accelerating changes in land use and management, changes that resulted in a massive reduction in the extent, and quality, of habitats (Ratcliffe 1984; Moore 1987). Although historic management is often discussed as if it was unchanging and 'traditional', these five and a half centuries were characterized by major shifts in land exploitation driven by demographic, social and technical change (Williamson 2013a). Management systems over this long period of time have been particularly well studied in lowland England, because of an abundance of documentary evidence and the survival in the modern landscape of fragments of past environments, which can be studied archaeologically.

Resource-based perspectives of species conservation

European conservation habitats are frequently classified with reference to their past exploitation, which – together with hydrology, soil type and climate – determine their plant composition and vegetation structure (e.g. Tansley 1939; Ratcliffe 1977). Examples include chalk 'downland', heathland, reed- and sedge beds, litter fen, meadows, moorland, coppiced woodland and wood pasture. Such attention to historic land-use patterns underpins much statutory designation under both UK (Ratcliffe 1977) and European (EC 1992) conservation legislation and shapes key management objectives. Where conservation seeks to maintain or restore these anthropogenic habitats, however, there is often insufficient consideration of the particular vegetation structures and ecological processes that provide the niches and resources required by their associated species (Dolman, Panter & Mossman 2012), to such an extent that resulting interventions may in fact be detrimental to priority biodiversity (Dolman *et al.* 2011). Considering the microhabitat, autecological and resource requirements of multiple species provides a stronger basis for conservation prescriptions. Below we outline the management principles that appear, on current evidence, to be critical in delivering biodiversity at diverse scales in cultural landscapes.

NESTED HETEROGENEITY AND STRUCTURAL COMPLEXITY

One emerging conservation paradigm is the importance of structural complexity and the juxtaposition of structures and successional stages at nested spatial scales: microhabitat, vegetation patch and landscape. Land-use mosaics allow farmland birds, for example, to exploit complementary landscape elements (Vickery & Arlettaz 2012). The nested juxtaposition of landscape elements and microhabitats is important to many invertebrates with complex life histories, and with resource requirements that differ between oviposition, foraging or diapause stages (Alexander, Colenutt & Denton 2005; Dolman, Panter & Mossman 2012). Ecotonal vegetation frequently provides this structural complexity for many invertebrates (Kirby 1992, 2001; Alexander, Colenutt & Denton 2005). Fine-scale topographic variation is important to terrestrial species with semi-aquatic larvae, and to many littoral species (McBride *et al.* 2011; Mossman, Panter & Dolman 2012). Within grassland or heath, the juxtaposition of exposed mineral soil, short swards, ungrazed nectar resources and well-vegetated overwintering sites is vital to many beetles, lepidoptera and hymenoptera. Scattered scrub is significant in both grass-heath and fen contexts (Dolman, Panter & Mossman 2010; McBride *et al.* 2011). The adults of many beetle and fly species, whose larvae develop in dead wood, require the nectar sources provided by scrub or herbaceous vegetation (Warren & Key 1991; Alexander, Colenutt & Denton 2005).

GRAZING

Restoring 'traditional management' to abandoned semi-natural vegetation by reintroducing livestock, often traditional breeds, has become widespread, but its results have been controversial (Newton *et al.* 2009; Denton 2013). Evaluation of its impact as 'positive' or 'detrimental' is often subjective, involving the adoption of arbitrary baselines and reference conditions for plant community composition (e.g. Lake, Bullock & Hartley 2001; Newton *et al.* 2009), but with biodiversity objectives poorly defined. Multitaxa responses remain poorly assessed. Large herbivores can disperse a considerable proportion of regional vascular flora including many species with no apparent dispersal adaptation (Eycott *et al.* 2007); thus, livestock movement among landscape elements may have sustained recolonization dynamics. We consider the regular and commonplace (daily or seasonal) movements of livestock at local scales to have been more significant in this regard than long-distance droving between regions. Grazing can maintain early-successional habitats, but it can also remove seed heads, flowering herbs and potential invertebrate overwintering sites such as dead stems and tussocks (Fry & Lonsdale 1991) and without other disturbance may fail to arrest the development of scrub (Bokdam & Gleichman 2000; Lake, Bullock & Hartley 2001). Intensive grazing is seen as detrimental to many (Lake, Bullock & Hartley 2001; Alexander, Colenutt & Denton 2005; McBride *et al.* 2011; Denton 2013) although not all (Dolman *et al.* 2011) invertebrate habitats. Lower stocking densities, variable timing (e.g. rotational autumn/winter, summer, fallow) or large extensive grazing units may all provide greater diversity of vegetation structures and thus better quality invertebrate habitat (Wells 1969; Fry & Lonsdale 1991; Alexander, Colenutt & Denton 2005), but a concentration of grazing in the summer months – damaging to some invertebrate interest – may be required to control coarse grasses (Wells 1969; Fry & Lonsdale 1991; Hawes 2015). Infrequent bursts of hard grazing may remove substantial biomass, with fewer species impacts, than sustained low-intensity grazing (Offer, Edwards & Edgar 2003). However, impacts on flora and fauna of grazing by different livestock species, and different breeds, remain poorly evaluated and context specific (Lake, Bullock & Hartley 2001).

PHYSICAL DISTURBANCE

Physical (including mechanical) disturbance creates the early-successional habitats required by many scarce and threatened species, including ruderal plants and invertebrates associated with exposed soil (Key 2000; Dolman, Panter & Mossman 2012; Pedley *et al.* 2013). In fen, reedswamp and aquatic ditches, many species of conservation importance require either the earliest stages of succession or the later and heavily vegetated stages achieved through extended rotations (Mossman, Panter & Dolman 2012). In grassland, after removal of biomass and topsoil, complex microhabitats, such as isolated tussocks in a matrix of exposed mineral substrate, can develop which are difficult to replicate where consistent grazing alone is employed to arrest succession (Dolman, Panter & Mossman 2010).

BIOMASS REMOVAL AND NUTRIENT DEPLETION

Within a particular ecosystem, areas of lowest nutrient status are generally those of greatest conservation value. Eutrophication reduces alpha diversity, with the loss of specialist and characteristic species (Smart *et al.* 2005; McBride *et al.* 2011). In grassland (Stevens *et al.* 2011), heathland (Diemont 1994; Bokdam & Gleichman 2000) and fen (McBride *et al.* 2011; van Diggelen *et al.* 2015), the removal of vegetation biomass and upper substrate layers can mitigate the detrimental effects of nutrient enrichment. Slower rates of vegetation development following nutrient depletion provide greater temporal habitat continuity for stenotopic species with limited dispersal ability.

VARIABILITY AND CONTINUITY

An overemphasis on facilitating range shift by enhancing habitat connectivity, in order to mitigate climate change, can overlook the limited dispersal ability of many invertebrates, such as molluscs or brachypterous insects (Mossman, Franco & Dolman 2015). Counter-intuitively, many species dependent on physically disturbed, early-successional microhabitats lack dispersal ability (Warren & Key 1991; Pedley *et al.* 2013); their sedentary populations thus require continuity of small-scale disturbance less than one generation's dispersal distance from refugia. The very persistence of a diverse fauna of poor-dispersing species implies that continuity of even ephemeral habitats has been maintained at local (within-patch) scales; small-scale heterogeneity may well explain this paradox. Dynamic mosaics of successional stages recovering from episodic localized disturbances increase beta diversity and provide local temporal continuity of particular successional microhabitats. Many macrofungi, and some dung beetles associated with old grassland or wood pasture, do not tolerate (or take decades to recover from) episodes of ploughing (Buckland & Dinnin 1993; Griffith, Bratton & Easton 2004). Saproxylic and other species associated with veteran trees require continuity of old growth structures (Warren & Key 1991; Kirby & Drake 1993; Siitonen & Ranius 2015). In general, local continuity of habitat availability is critical for population persistence in species with specialized resource needs in the early and the very late stages of succession (Warren & Key 1991). This is partly due to limitations on dispersal, but is also a consequence of the fact that the required resources are themselves scarce.

Historic perspectives to inform species conservation

Research over several decades has thus highlighted a number of broad principles of intervention which serve, in many different contexts, to maintain or enhance biodiversity. While some of these mimic wholly natural processes others do not, yet what is striking is the extent to which many appear to parallel forms of management common in the pre-industrial world (Williamson 2013a).

Evidence from pollen and insect assemblages indicates that pre-agricultural England, like other parts of western Europe, was largely dominated by closed-canopy forest albeit with open areas presumably created and maintained by localized disturbance such as landslips, floods, anthropogenic burning and possibly grazing (Warren & Key 1991; Groves *et al.* 2012; Kirby & Watkins 2015). There were thus relatively limited opportunities for open-habitat species before forest clearance for agriculture and livestock began in the Neolithic (*c.* 7000 BP). By late prehistoric times (*c.* 3000 BP), a range of open anthropogenic habitat types had emerged, and by the thirteenth century, when documentary sources become abundant, it is evident that these were being managed in diverse and sophisticated ways. Such habitats are often considered to have changed little in the period up to industrialization and are frequently discussed in terms of a relatively limited number of homogeneous 'types'. In reality, patterns of exploitation changed over time in response to an interconnected raft of economic, social, tenurial, technological and demographic drivers; what we tend to think of as a single habitat type often displayed considerable variation from place to place. The forces shaping land exploitation in lowland England before the industrial revolution cannot be discussed in detail, but are summarized in Fig. 1. The period before *c.* 1300 saw rising population and the steady contraction of wooded 'wastes' and a concomitant expansion of arable land and other open environments. The medieval economy was characterized by small mixed farms and relatively low levels of regional specialization, although there were considerable (and largely environmentally determined) variations in settlement, field systems and land-use patterns (Williamson 2013b). Close integration of arable and livestock farming was a key feature, with sheep in particular being employed as 'mobile muck-spreaders' in order to transfer nutrients from perennial pasture to cropland. The later fifteenth, sixteenth and seventeenth centuries saw a continuation of these broad themes but also significant changes, especially the development of larger farming units, increasing levels of national market integration and a greater degree of regional specialization, leading to the emergence of a complex mosaic of interdependent farming systems (Thirsk 1987). Although mixed farming generally continued, in some districts, large areas were now laid to grass, for sheep or cattle. Patterns of specialization are often surprising to the modern eye – the now intensely arable claylands of East Anglia were then a dairying and bullock-rearing region – and were determined by both economic factors, especially market access, and environmental ones, particularly soil type.

HEATHS AND COMMON LAND: GRAZING, FUEL, MINERALS

Until the eighteenth century, most 'semi-natural habitats' were common land. Concentrated in the places less suitable for arable farming, their character was shaped by often high intensities of grazing, as well as by high levels of extraction and disturbance, for commons were a major source of raw materials (including sand, clay and gravel) and, above all, of fuel. Heaths for example developed from grazed woodland, often as early as the Bronze Age or Neolithic (Groves *et al.* 2012), but sometimes as late as the eighteenth century, and they rapidly returned to secondary woodland if the intensity of management declined. Pollards cut for fuel and fodder regenerated above the reach of browsing livestock, with long-lived trunks giving continuity of dead heartwood. The line between wood and heath was blurred both spatially and chronologically, with wood pasture heaths forming an intermediate and ecotonally complex landscape type now largely lost, but once common [as late as 1748 one visitor described heaths in south Hertfordshire 'covered with tufts of ling, between which bracken flourished' but on which 'in places hornbeam grew fairly densely to a height of six feet . . . the tops cut for fuel' (Mead 2003; Barnes *et al.* 2007)].

Current conservation policy emphasizes the role of grazing in heathland management, while physical disturbance and biomass removal are relatively neglected (Webb 1998; Denton 2013). Many heaths were indeed intensively grazed in the past, especially where they formed part of 'sheep-corn' systems in which the sheep were taken to the arable fields at night, and close-folded on the fallows, ensuring a regular depletion and transfer of nutrients (Kerridge 1993). From the fourteenth century, moreover, some were used as commercial rabbit warrens (Sheail 1971). But in addition, bracken *Pteridium aquilinum*, heather *Calluna vulgaris* and *Erica* spp., and gorse *Ulex* spp. were regularly cut, partly for thatch, fodder and animal bedding but mainly as fuel (Webb 1998; Albery 2011). Heather was harvested as turves dug to a depth of at least 2·5 cm, which thus included both the vegetation and a square of combustible roots. In the early seventeenth century, Thomas Blenerhasset memorably described how Horsford Heath in Norfolk was 'to Norwich and the Countrye heare as Newcastle coales are to London' (Barrett-Lennard 1921). On some heaths, particular areas were set aside for extraction, distinct from but often intermingled with those exploited by grazing alone.

The burrowing of rabbits, intense grazing, and the extraction of fuel, sand and gravel ensured that heaths often boasted much disturbed ground, especially at times of rapid population growth. In the late sixteenth century, Cawston Heath in Norfolk was described as having 'Sand and gravell . . . cast upp in such great heapes uppon the playne grownd by reason of the digging therof that ther will noe grasse growe upon the said grownde in a verie long tyme' (Whyte 2009). But the character (and intensity) of exploitation varied over space, as well as over time. In Lincolnshire and East Anglia, heaths often lay remote from settlements and were intensively grazed by folding flocks. In southern England, they were more likely to be encircled by houses, like other commons, and grazed (sometimes at lower levels of intensity) by a wider range of livestock, including donkeys, horses and cattle (Lake, Bullock & Hartley 2001) – a diversity probably ensuring a complexity of sward structures rarely matched in conservation management. While most heaths were permanent habitats, some were sporadically ploughed up, either on a casual basis or on a long rotation, fluctuating with population pressure and grain prices (Bailey 1989).

Heaths exemplify the management of common land more generally in terms of intensity and complexity of use, change over time and spatial diversity, combined in some cases with the intermingling of different forms of exploitation in close proximity. Similar characteristics were evident in, for example, the management of common fens and mires formed in valley peats.

WOODLAND

Not all 'semi-natural' environments were common land, subject to frequent or continuous grazing, although all were intensively and rigorously exploited. Woods managed as coppice-with-standards were invariably private property. Most were enclosed by manorial lords from wider areas of grazed woodland during the twelfth and thirteenth centuries, although a minority were established later at the expense of other land-use types. Surviving examples are valued for their plant species diversity (Buckley 1992; Rackham 2003). It is sometimes assumed that this is largely a consequence of continuity with the 'wildwood', but long histories of rotational cutting, maintaining diverse successional stages and niches, were also important. Coppicing encouraged particular herb species,

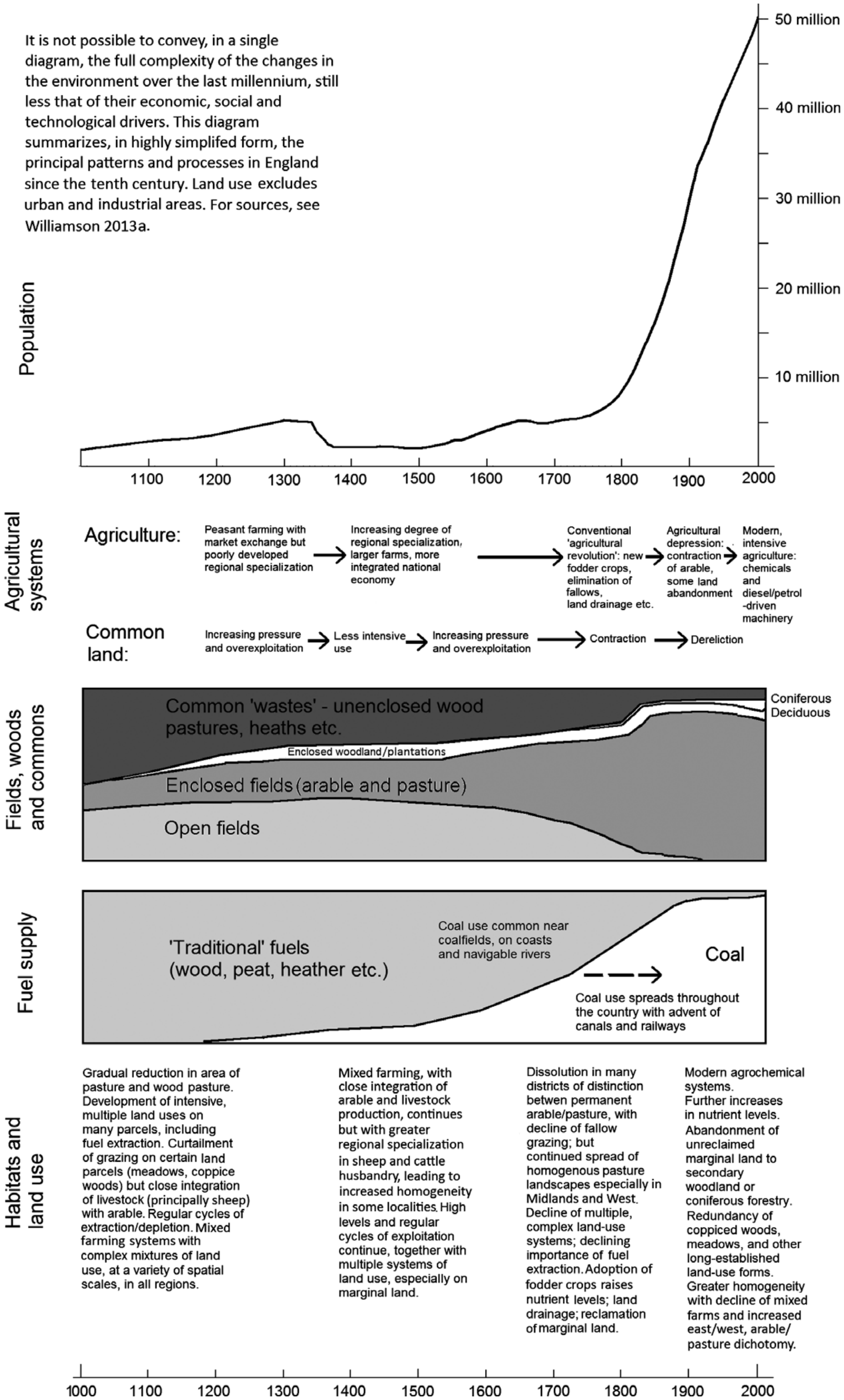

Fig. 1. Summary of major changes in land management in lowland England from *c.* 1100 to the present day.

through the creation of regular cycles of light and dark, varied across the area of an individual wood by its division into separate 'fells', cut on a rotation of 7–15 years (Rackham 2003). Despite the loss of extensive forest landscapes and persistence of remaining woodland in relatively small fragments, this management maintained both structural and species diversity within limited areas.

Coppices were also amongst the few areas in the pre-industrial countryside not subject to any significant degree of grazing, stock being admitted, if at all, only late in the rotation. Some post-medieval leases stipulated the use of muzzles during forestry operations to preserve 'the shoots and slopps of such wood from being bitt by the horses fetching the same' (Barnes & Williamson 2015). Many plants characteristic of coppiced woods have poor resistance to grazing and were thus probably uncommon in the *grazed* woodlands from which most were enclosed (Rotherham 2012). The dominance of oak *Quercus* spp. as a timber tree was the consequence of deliberate selection or planting, and there is evidence that the composition of the understorey was also modified (Barnes & Williamson 2015). Once again, there were temporal changes in management systems, tied to wider patterns of economic (and technological) change. Variations in demand for timber and bark (for tanning) led to fluctuations in the density of standard trees, and thus the extent of canopy shade, but their harvest at 80–150 years prevented development of dead heartwood habitats (Warren & Key 1991).

MEADOWS AND ARABLE

Other types of 'traditional' habitat were similarly exploited by single occupiers and were not subject, in the way that commons were, to frequent and intensive grazing. Almost all, however, were open to domestic livestock for some of the year. Hay meadows, for example, were closed off during late spring and summer, but grazed (often in common) after the farmer had removed his hay. As in coppiced woods, limiting livestock access shaped botanical character, allowing tall, bulky species and other plants intolerant of grazing and trampling to flower and set seed. Mowing regimes displayed considerable variation over time and space, moreover, leading to significant variety in species composition (Peterken 2013). Parcels of arable land were similarly exploited on an individual basis and were of necessity protected from stock for much of the time, although they were invariably grazed, and therefore dunged, after the harvest or during the fallow year. Much arable was farmed as *open fields*, containing the intermingled and unhedged strips of many proprietors, subject to varying degrees of communal regulation, and to common grazing in season. Open fields took a bewildering range of forms (Hall 2014). In Midland districts, they usually constituted all the arable land of a community but elsewhere they were mixed to varying degrees with fields in the modern sense, enclosed by walls and hedges.

The area covered by enclosed fields increased steadily from the fourteenth century, as open fields were enclosed in a variety of ways (Yelling 1977). Enclosure was often associated with a change from arable to pasture, but also with the general growth in farm size, and the adoption of more intensive forms of cultivation. It might be thought that the proliferation of hedges represented a clear environmental gain, but open fields provided important heterogeneity and juxtaposition at both landscape and microhabitat scales. Individual strips were usually separated by narrow unploughed 'balks'; even where they were not, open fields often included ribbons of unploughed ground, managed as pasture or meadow (Williamson, Liddiard & Partida 2013). This juxtaposition of perennial and ruderal elements echoes current management for scarce invertebrates that require ruderal seed resources close to undisturbed overwintering sites (Dolman, Panter & Mossman 2010), and prescriptions of beetle banks that aim to provide refugia for predatory invertebrates (Frampton *et al*. 1995). Balks would have been subject to episodic grazing through cycles of fallowing and cultivation, providing temporal refuge for stress-tolerant grassland perennials excluded by competition from ungrazed closed swards, but unable to persist under constant grazing (e.g. Watt 1971). The importance of unploughed ground in open fields is clear from the writings of early botanists. Babbington (1860) bemoaned how, as a consequence of enclosure in west Cambridgeshire 'the "balks", with the various plants which grew upon them' had been 'destroyed by the plough. Thus the native plants have suffered . . . Where they were once abundant they are now rarely to be found'.

The hedges that enclosed both arable and pasture fields and which increased in numbers over time, were – like everything else in the pre-industrial landscape – managed with an intensity which modern observers would find remarkable. Systematic management and maintenance of hedges ensured they remained stock-proof and provided an abundance of fuel wood. Some hedges were *plashed* or *laid* every ten to fifteen years, while others were simply coppiced on rotation, and most contained numerous mature trees including managed pollards (Warren & Key 1991; Barnes, Pillat & Williamson 2016). Hedges were thus subjected to regular and repeated cycles of change, with different examples on a property at different points on the management successional cycle at any one time, again providing ecological heterogeneity and local continuity of habitat availability for species associated with different growth stages.

THE DEMISE OF 'TRADITIONAL' LANDSCAPES

Conservation has tended to emphasize the scale of semi-natural habitat loss, together with land-use homogenization and intensification, from the mid-twentieth century, but this represented merely an acceleration following a long period of change (Ratcliffe 1984). From the mid eighteenth century, England industrialized and experienced unprecedented levels of population growth (Fig. 1). The late eighteenth and early nineteenth centuries brought a major intensification of farming: the adoption of new fodder crops and rotations increased livestock numbers and thus nutrient levels; open fields and much common land were enclosed and the latter extensively reclaimed, in part because progressive improvements in transport allowed the spread of coal use throughout the country, lessening their significance as a fuel source (Warde & Williamson 2014). Coppiced woods survived and, for the time being, continued to be managed, although now in part to maintain game cover for the large estates that usually owned them (Barnes & Williamson 2015). The same period saw increasing levels of regional specialization in agriculture. As arable land-use intensified in the south and east, large areas in the Midlands, north and west of England were laid to permanent pasture (Williamson 2002). Next, in the 'high farming' period of the mid-nineteenth century, imported or manufactured fertilizers were employed, industrial products in general were more extensively used (particularly animal feeds), and mechanization increased (Harvey 1980). The adoption of industrialized methods was retarded to some extent by the advent of the great depression in farming, caused by agricultural globalization and large-scale imports of grain and frozen meat, which began in the late 1870s and continued, on and off, until the outbreak of the Second World War (Perren 1995). More land was laid to grass; some marginal land (much of it recently reclaimed) went out of cultivation; and surviving commons, now economically redundant, reverted to scrub and secondary woodland. Large areas of both derelict arable and common land were afforested by the Forestry Commission. Large estates, their rental incomes plummeting, were financially challenged, and this, among other things, finally brought coppicing to an end. Hence, the kinds of complex 'traditional' land management systems discussed above had largely disappeared in England before the adoption of modern, chemical-based farming systems in the middle decades of the twentieth century.

Box 1. Attributes of pre-industrial land uses with particular relevance to habitat opportunities for biodiversity

1. High levels of resource exploitation and extraction often involving repeated cycles of extraction or harvesting causing frequent disturbance and dynamic vegetation change, rather than long-term stability.
2. A fine spatial scale of exploitation, for example (i) intermixtures of ploughed and unploughed ground (both fallow and permanent grassy balks) in open fields, (ii) a dense mesh of hedges at varying stages of regrowth, (iii) allocation of turf cutting rights in fens leading to a patchwork of plots.
3. Resource exploitation was based on immediate local need; hence, wood and timber would be extracted piecemeal when needed, not as part of a formal forest management system.
4. Nested heterogeneity in vegetation and physical structures.
5. A degree of local self-sufficiency existed in a mixed agricultural economy, resulting in a diversity of land use and 'habitat' within local landscapes. Hence, many parishes supported fens, downs, commons, wastes, woods and fields.
6. Spatial variation in some management practices among and within regions.
7. Temporal flux in exact management systems (e.g. grazing intensity, coppice cycles, enclosure patterns).
8. The transfer of nutrients from heath, common and downland to cropland, achieved through systematic movement of animals.
9. Intensive but intermittent extraction of raw materials (e.g. sand, gravel, stone, peat) based on local need; an area could be cleared and dug intensively for a decade, then abandoned for several decades allowing episodes of disturbance and successional recovery.
10. Active interventions which either prevented, or encouraged, the movement of livestock (e.g. exclusion of animals from coppices or sheep moved daily from heaths to arable).

Discussion

Land management in pre-industrial England was almost invariably complex and rigorous (Box 1). In many contexts, it was organized around extended rotations, something which served to maintain early stages of succession. It was characterized by high levels of extraction and disturbance (often involving exposure of substrates) and, in many contexts, by high intensities of livestock grazing. Where grazing was limited or curtailed, as in coppices or meadows, this had its own particular effects, creating distinctive suites of species which are now regarded as being of high conservation value. In many cases, individual parcels of land were used in diverse ways, either at the same time, or according to a regular cycle. Heterogeneity existed at numerous scales, from farming regions down to individual farms and land parcels, the latter sometimes involving the close and intimate intermingling of different kinds of land use (as in open fields), and sometimes the creation of diverse successional stages in close proximity within the same land-use type (as in coppices). Local movement of livestock between pastures and fallows added further dynamism.

Some aspects of traditional management served to mimic natural processes which had been lost in the transition from 'wildscape' to landscape. In medieval woodland, for example, the ground disturbance resulting from the cutting, felling and processing of wood and timber, in the absence of defined rides, mimicked to some extent the effects of the wild boar *Sus scrofa*, by this stage rare. But management also created habitats which, while biologically diverse, had almost certainly been infrequent or even non-existent before the development of farming.

Many pre-industrial management practices were strikingly different to those currently adopted, both within and outside conservation land; yet they appear to have embodied many of the key processes and principles for enhancing biodiversity outlined above. But as we have emphasized, practices changed significantly over time, because they were inextricably linked to social and economic systems that were themselves in a constant state of flux. Periodic or temporary physical disturbance, such as occasional cultivation of heaths or episodic mineral extraction, would have created transitional microhabitats that do not occur under consistent management prescriptions. Even where particular forms of land use (woodland, arable, pasture) continued in the same places for centuries, the degree of stability can be exaggerated, and there appears to have been much variation, in space as in time, in the details of mowing, grazing and coppicing – that is, in the key practices now used by conservationists to retain the open habitats upon which so many species depend.

The most important change affecting biodiversity over the last two or three centuries may not have been an intensification of land use *per* se. Indeed, land use was arguably more intensive and complex in the past in many contexts, and high priority 'conservation habitats' such as coppiced woodland, fen and heathland usually experienced far greater levels of resource extraction and disturbance than is the case today. At least as detrimental to biodiversity has been homogenization, at multiple spatial scales. What we now label as a single 'habitat type' displayed much variation from district to district, and intimately complex patterns of structural heterogeneity, at nested spatial scales, were a feature of many lowland landscapes. All these, in addition to the more familiar loss of specific niches and conditions (ancient trees, wet areas, species-rich grassland, etc.), have led to markedly lower levels of beta diversity across most of lowland England.

'Traditional' forms of management were not universally benign. In perennial pastures, the high intensity of grazing will frequently have reduced complexity of vegetation structure and inhibited woody regeneration. Demand for fuel was often so high that dead wood in the form of branches must have been rare, though large trees with dead heartwood may have been widespread in wood pasture and also hedgerows (Warren & Key 1991). The density of people working in the countryside was far higher than today, rendering many areas unsuitable for those mammals and birds unable to withstand exploitation. Nevertheless, a better understanding of past management practices, how they changed and developed over time, and what they actually achieved in terms of maintaining biodiversity, is essential for framing future conservation practices.

Conclusions

We agree with Marrs (2008) that there is considerable potential for combining elements of past land management methods with modern science in order to develop effective conservation management for the future. Synergy between ecologists and historians can help create a better understanding of past environmental heterogeneity – its causes and how it scaled across time and space – which can assist the development of future resilience for biodiversity. Ecologists should work with practitioners to understand how best to implement fine-scale environmental complexity within realistic analogues of human-induced disturbance regimes that may have been widespread for many centuries.

The overriding message is that simplistic, generalized notions of 'traditional management' practices are meaningless because land-use systems displayed a high degree of spatial and temporal variation. This leads to several conclusions about how relationships between pre-industrial human activities and biodiversity can be relevant to modern conservation:

1. The selection of a historic baseline for conservation in cultural landscapes is arbitrary, subjective and rarely useful.

2. Heavily prescriptive approaches to conservation management (e.g. recommended generic 'habitat' based treatments) applied widely on conservation land risk creating excessive uniformity and stability, likely to diminish rather than enhance diversity of vegetation structure and niches.

3. While the maintenance or resurrection of perceived past management systems is appropriate in many contexts (particularly where continuity of management has sustained associated assemblages: Warren & Key 1991), greater consideration should be given to specific practices that mimic or replicate their essential characteristics (Box 1). The complexity of management within individual land parcels should encourage a focus on the various ecological processes rather than simplified 'habitat types'.

4. The absence of historic stability erodes the distinction between the replication of 'tradition' or the adoption of new practices and interventions, so that conservation has greater freedom to innovate in cultural landscapes through, for example, the creation of novel anthropogenic sites with low nutrient status by the addition of mineral or industrial spoil, or the adoption of more diverse physical disturbance practices.

Perhaps the greatest uncertainty about pre-industrial landscapes concerns grazing, specifically the densities of livestock at different times and in different places (e.g. pasture, fallow), often difficult to reconstruct from documentary evidence. Where grazing pressure was high, which it undoubtedly was in many contexts, simplified sward structures and limited ecotonal vegetation would have been typical, of less conservation value than the more varied vegetation structures favoured by much current conservation management.

While the above discussion has focused on the more intensively managed, less obviously 'natural' elements of the pre-industrial landscape, and their implications for future conservation, some past land-use types were closer in character to the natural woodlands. Private wood pastures and wooded commons were important components of the landscape in most districts well into the post-medieval period and will have ensured relatively high availability of niches for saproxylic and other late successional species. Natural processes – and in particular the use of large herbivores to create and maintain dynamic ecotonal mosaics – clearly have an important role to play in some contexts. Nonetheless, the maintenance of the high levels of habitat complexity and of complementary vegetation structures, which appears to be one of the best strategies available for coping with the uncertainties of future environmental change (Fuller 2012), may be best achieved through planned interventions. In some cases, these might involve a more accurate replication of ancient practices (particularly where there has been long continuity of such practices); but in others it could be more appropriate to adopt new approaches informed by an understanding of biodiversity requirements. The key point is that no single conservation approach can deliver all the resources required to maintain high alpha and beta biological diversity.

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Data accessibility

Data have not been archived as this article does not contain data.

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