Conserving threatened Lepidoptera: Towards an effective woodland management policy in landscapes under intense human land-use

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ABSTRACT

Although intensive forestry practices have greatly reduced the biodiversity of native woodland, sympathetic management offers much potential to reverse these negative trends. We tested, using a species-rich group, whether woodland conservation management practices could be of overall benefit, for threatened generalists and specialists alike. Our landscape-scale light-trap experiment compared presence/absence, abundance and species richness of macro-moths at 36 repeatedly sampled sites from six experimental 'woodland management' treatments. We recorded 11,670 individuals from 265 species.

Our results show that the sheltered, dark, humid, late-successional, high deciduous forest biotope is characterised by high numbers of both individuals and species of moth, and is especially important for some scarce and specialist species of conservation concern.

Coppicing and ride widening, which open up dense forest structures, are also valuable woodland conservation tools for macro-moths. Specifically, we show that the mechanism behind the pattern of increased species richness at the woodland-scale involved an increased structural and hence increased micro-climatic and resource diversity for species with an affinity for more open biotopes. This benefits generalist species of conservation concern. Additionally, we show that woodland area is an important factor affecting both moth abundance and species richness in coppiced plots, especially so for nationally declining and severely declining species, suggesting that larger woodlands offer the best opportunities to increase biodiversity through active coppice management.

Based on these complementary findings we recommend zoning woodland conservation management practices to take into account the differential value of successional stages for different ecological groups of Lepidoptera.

1. Introduction

It has become clear in a range of taxa that it is not only rare, localised, and specialist species that require conservation action, but (formerly) common, widespread, and generalist species too (e.g. Van Dyck et al., 2009; Desender et al., 2010; Elliott et al., 2010; Lindenmayer et al., 2011). Population declines for the latter group have hitherto been largely unnoticed (Cowley et al., 1999; Ceballos and Ehrlich, 2002; Pereira and Cooper, 2006; Van Dyck et al., 2009). However, more recent species-level monitoring of population trends have shown severe declines for large proportions of species in a range of taxa – even for those that are still widespread – in line with significant changes in human land-use over recent decades (Conrad et al., 2006; Gaston and Fuller, 2007; Van Dyck et al., 2009). Because of their generalist character and often broader resource requirements, these widespread but declining species need a different conservation approach to the one required for specialist species (Merckx et al., 2009a), which generally have highly specific resource requirements, demanding targeted conservation management strategies. Precisely what this approach should consist of is not yet clear. Moreover, both conservation practitioners and scientists have been slow to tackle this problem, perhaps because of the notion that specialist species are somehow more valuable, despite their relatively low overall biomass, and that an added focus on declining generalist species would necessarily distract from, or even conflict with, efforts to

conserve specialist species. But what is clear is that it is timely for landscape-scale conservation projects to take up the challenge and cater simultaneously for both threatened specialists and generalists alike (e.g. Lawton et al., 2010), and for conservation biologists to provide evidence on how best to do so.

Macro-moths are a very suitable group to help provide such evidence. The group is highly species-rich (e.g. c.900 species in the UK) and many specialist species are currently under threat (e.g. 81 species listed as UK Biodiversity Action Plan (BAP) Priority species). At the same time, it has recently been demonstrated that the majority of common, widespread macro-moth species have declined during the last few decades (Britain: Conrad et al., 2006; The Netherlands: Groenendijk and Ellis, 2011). In Britain, 71 species (i.e. 21% of common species) declined severely (i.e. national decline >69% over 35 years) and as a result were listed in 2007 as 'widespread but rapidly declining' BAP Priority species. As moths are a species-rich group occupying a wide range of terrestrial biotopes and ecological niches, patterns in their abundance and distribution may also be indicative for other types of terrestrial invertebrates.

Recent conservation science on macro-moths has mainly focused on farmed landscapes and the design of agri-environment schemes to reverse these declining trends. The uptake of certain management options (for example, wide, nectar-rich field margins and hedgerow trees) and the landscape-scale implementation of these schemes have been shown to be important factors, beneficial both for widespread moth species (Merckx et al., 2009a,b, 2010a; Fuentes-Montemayor et al., 2011) and possibly more localised species as well (Merckx et al., 2010b).

However, the cause of population declines in widespread macro-moth species is only partly understood, and factors other than management of farmland are also likely to be important. Work on other Lepidoptera (butterflies) has demonstrated that woodlands have lost a significant proportion of their original butterfly fauna during the second half of the last century (van Swaay et al., 2006). As well as specialised woodland species having been lost, so too have been species that make use of open areas (e.g. rides, heaths and glades) within woodlands (Gorissen et al., 2004). The main reason for this loss is afforestation of open areas and intensive, high forest management practices that have almost completely replaced traditional coppicing practices (Gorissen et al., 2004), particularly since the Second World War. It seems likely that it is a decline in habitat quality, associated with the loss of this more open and light woodland biotope, that has caused the decline in butterflies associated with woodland, as the total area of woodland has often remained stable or has even increased in western Europe (Sparks et al., 1996; Gorissen et al., 2004; van Swaay et al., 2006; Van Dyck et al., 2009). Additionally, woodland habitat quality may also have declined as a result of increased atmospheric nitrogen deposition (Öckinger et al., 2006; Feest and Spanos, 2009).

Native woodland used to be the dominant, climax biotope over large parts of Europe. It is hence likely to offer great potential to reverse a large proportion of declining species trends through sympathetic management. Semi-natural, broad-leaved, lowland woodland is an extremely important habitat for widespread moth species, with an estimated 60% of them being highly or partly dependent on this biotope. However, while the impacts of contrasting woodland management have been relatively well studied, and are well understood for butterflies (Warren and Thomas, 1992; Feber et al., 2001; Benes et al., 2006; Konvicka et al., 2008; Spitzer et al., 2008; Hodgson et al., 2009), this is not the case for moths, with the few existing studies characterised by sampling limited to single woodlands, with a restricted number of sites and treatments, and with limited re-sampling (Sterling and Hambler, 1988; Waring, 1988; Broome et al., 2011). Studies largely relate to the effects of large-scale timber harvesting in boreal or tropical forests, with moth communities found to respond predictably to management practices, driven by changes in plant communities (e.g. Fiedler and Schulze, 2004; Summerville and Crist, 2008).

In England, broad-leaved, semi-natural woodlands are embedded within agricultural landscapes, and these sheltered biotopes contrast strongly with the highly exposed agricultural landscape. Semi-natural woodland provides habitat resources (e.g. food plants, nectar sources and shelter) for large suites of moth species (Usher and Keiller, 1998; Summerville and Crist, 2004). Some species are believed to be restricted exclusively to rather dense woodland, while others are also found within open woodland complexes as they provide resources to a greater or lesser degree (Waring and Townsend, 2009). However, no work has been done to quantify these associations.

Here, by focusing on macro-moths within the woodland biotope, we carried out a landscape-scale experiment to explore whether woodland conservation management can potentially cater for both rare and localised species of traditional conservation concern as well as widespread but nonetheless declining species. Our aims were to test how woodland conservation management practices affect macro-moth abundance and species richness, to test whether species groups of different conservation status react differently to these practices and to explain such differences based on ecological differences, and to suggest clear recommendations on woodland conservation management, taking into account the differential value of management practices for different ecological and conservation status groups of Lepidoptera.

2. Methods

The Tytherley woodland landscape (east of Salisbury, UK) contains 98 woodland patches totalling 2500 ha of ancient semi-natural woodland within a landscape of about 17,000 ha (Fig. 1). It has Bentley Wood 'Site of Special Scientific Interest' at its center, and was chosen for the study as it has a relatively diverse Lepidoptera fauna and has been the focus of long-term and ongoing woodland conservation management within Butterfly Conservation's South East England Woodlands Project. Data on presence/absence, abundance and species richness of macro-moths were collected from early-July until mid-October 2010 at 36 sites during a total of 27 trap nights, with 12 sites sampled on any one night. Each of the sites was sampled on nine different occasions (i.e. 324 single trap events), never on consecutive nights.

We sampled six experimental 'woodland management' treatments, each replicated by six trap sites: (i) young (1–2 years) hazel coppice, (ii) medium (3–6 years) hazel coppice, (iii) old (7–9 years) hazel coppice, (iv) wide (>20 m) rides, (v) standard (<10 m) rides and (vi) non-coppiced, high deciduous oak forest 'standard woodland'. All 36 trap sites were in ancient woodland or plantations on ancient woodland, defined as being continuously wooded since 1600. Deciduous woodland in the 'standard woodland' class was at least 60 years old, with some individual trees being up to 300 years old. All coppice sites had a history of coppice stretching back several centuries, and although undergoing some periods of inactivity since 1939, all have had a cycle of active coppicing for at least 20 years. Inter-trap distances were invariably larger than 50 m, which avoids possible light trap interference due to the light traps' small radius of attraction by moths (typically only up to 10–15 m in both open and sheltered conditions; Slade and Merckx, pers. obs.). In order to make sure that the sample was as much as possible representative of the management treatment, trap sites in coppice were located at the center of a 'coupe' and at least 25 m away from any other management type, trap sites in standard woodland were at least 25 m away from any ride or edge, and trap sites in rides were always placed 1–2 m away from the woodland edge, and at least 25 m away from crossings with other rides. Trap
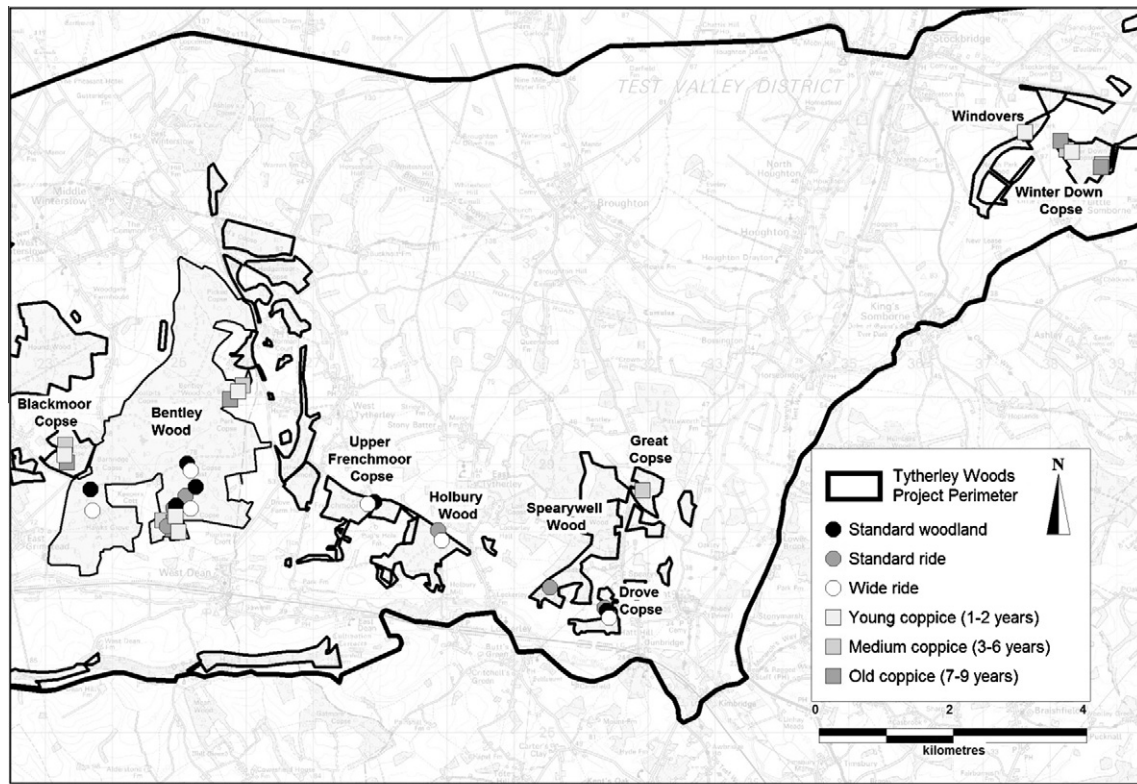
Fig. 1. Location of all 36 fixed trap sites (six from six experimental treatments each) and woodlands (blank polygons) within the Tytherley woodland landscape. Trap sites encompass a total of six woodlands: Bentley, including Blackmoor copse (711 ha); Frenchmoor (36 ha); Holbury (64 ha); Mottisfont woods (122 ha); Windovers (8 ha); Winterdown (40 ha).

sites of the same experimental group were as much as possible located in different woods and invariably more than 100 m apart in order to avoid spatial auto-correlation. These measures favour the statistical independence of each of the six replicates for each treatment. Note also that nearby trap sites were not necessarily being sampled during the same nights, and that the large majority of inter-trap distances were considerably larger than these minimum values (Fig. 1). We further avoided bias by sampling all treatments every trap night, in equal numbers, and only under suitable weather conditions (i.e. minimum night temperature >10 °C; maximum wind speed <20 km/h; no persistent rain).

Light trapping is a passive method proven to be highly suitable for sampling moth communities (Young, 1997). Macro-moths were sampled using Heath pattern actinic light traps (6 W), which operate on the 'lobster-pot principle', whereby individuals are drawn to an actinic tube secured vertically between baffles, fall unharmed down a funnel, and rest inside the trap (Merckx et al., 2009a). Although this battery-run trap type does not result in samples as large as those from generator-run traps, the advantage is that a larger number of identical traps can be deployed simultaneously, which is preferable when comparing relative abundances among sites. Their small attraction radius (see above) results in a good representation of local abundance. Light traps were placed during late afternoon and checked early next morning when we recorded the abundance of each macro-moth species.

Prior to analyses, all species were classified in terms of conservation status and woodland affinity. We distinguished between (i) nationally scarce and Red Data Book ('Scarce/RDB') species (Waring and Townsend, 2009), (ii) severely declining common and widespread species (i.e. Rothamsted Research (RR) national abundance trends over 35 years >69% decline: Conrad et al., 2006) ('Common Severely Declining'), (iii) declining common and widespread

species (i.e. RR national abundance trends 0–69% decline) ('Common Declining'), (iv) increasing common and widespread species (i.e. RR national abundance >0% increase) ('Common Increasing'), and (v) 'Unknown Status'. With regard to woodland affinity we distinguished between (i) 'ubiquitous' species, (ii) 'non-woodland': species whose main biotope is not woodland, (iii) 'broad-woodland': woodland species which main biotope is woodland but which also occur in other biotopes and (iv) 'strict-woodland': woodland species whose only known biotope is woodland (Waring and Townsend, 2009).

Generalised Linear Mixed Model (GLMM) regression analyses, with normal (Gaussian) error distribution, were carried out to test whether, and to what extent, the two woodland management practices (coppicing and ride management) differentially affected species richness and abundance of the species groups [conservation status, a 5-level class variable (see above), was included within models], and to test differences between coppiced woodland of the three different age-classes. The treatment factor contained six levels: standard woodland, standard ride, wide ride, young coppice, medium coppice and old coppice. The regression analyses were performed with log-transformed (to improve normality) average values for abundance and species richness for each of the species groups (i.e. conservation status), calculated over the nine periods for each of the 36 sites, as same-site events were not statistically independent. Woodland patch size (log-transformed) was included as a continuous variable within all models. Model selection started with testing all three- and two-way interactions, and by performing backward selection of non-significant factors ($p > 0.2$) to select final models. All GLMMs included trap site nested within woodland as a random factor, which accounted for the variation merely due to macro-moth abundance and species composition being more similar among trap sites within the same

woodland than among woodlands. Since conservation status and woodland affinity variables were significantly associated ($\chi^2_{12} = 44.53$, $p < 0.0001$, $N = 265$; e.g. strict-woodland species accounted for 60% of 'Scarce/RDB' species, whereas only for ca. 5% of both 'Common Severely Declining' and 'Common Declining' species), we did not include woodland affinity as a parameter within the models.

3. Results

The landscape-scale light-trap experiment recorded a total of 11,670 individuals from 265 macro-moth species (including 4 aggregates, each comprising two essentially cryptic species that could not be distinguished in the available time: i.e. Acronicta, Hoplodrina, Mesapamea and Oligia spp.): 15 'Scarce/RDB' species (249 individuals) (Table A1), 38 'Common Severely Declining' species (891 individuals) (Table A2), 90 'Common Declining' species (3564 individuals), 73 'Common Increasing' species (5986 individuals), and 49 'Unknown Status' species (980 individuals).

Overall, macro-moth abundance was highest in standard rides and standard woodland and lowest in coppice and wide rides (without significant differences neither between coppice age classes, nor between coppice and wide rides; N_{total}: standard woodland: 2479; standard ride: 2513; young coppice: 1248; medium coppice: 1433; old coppice: 2071; wide ride: 1926) (treatment: $F_{5,24} = 8.70$; $p < 0.0001$) (Fig. 2). Overall species richness was highest in standard woodland and both wide and standard rides and lowest in coppice (S_{total}: standard woodland: 180; standard ride: 176; wide ride: 175; young coppice: 160; medium coppice: 167; old coppice: 162) (treatment: $F_{5, 24} = 7.39$; $p = 0.0003$) (Fig. 2).

While this overall pattern applied to all macro-moth species groups, irrespective of their scarcity or national trend status, the 'Common Severely Declining' species showed the smallest difference in abundance between the woodland management treatments. In particular, wide woodland rides were characterised by relatively high abundance of this group (N_{total}: standard woodland: 224; standard ride: 141; young coppice: 82; medium coppice: 131; old coppice: 145; wide ride: 168) (treatment x status: $F_{20, 96} = 2.05$; $p = 0.011$) (Fig. 3).

Another key finding was that the total area of the woodland patch surrounding coppiced plots (all ages) had a strong positive effect on the abundance of 'Common Severely Declining' species, an effect absent for the other species groups ($N_{trap\ average\ 'Common\ Severely\ Declining'\ species} \pm$ SE: young coppice: 1.3 ± 0.5 versus 1.6 ± 0.4; medium coppice: 1.5 ± 0.5 versus 3.4 ± 0.8; old coppice: 0.4 ± 0 versus 3.8 ± 1.2; wide ride: 4.1 ± 0.7 versus 2.1 ± 0.2; standard ride: 2.2 ± 0.4 versus 3.0 ± 0.8; standard woodland: 7.9 ± 5.0 versus
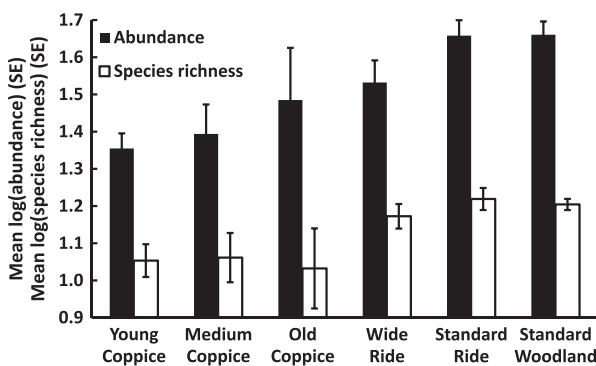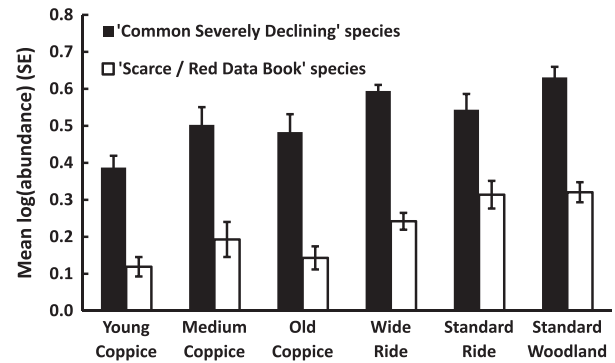

Fig. 3. Abundance ($\log_{10}$-transformed mean(SE)) of two high profile conservation status species groups for six experimental woodland management treatments. Whereas the 'Scarce /RDB' species followed the overall trend depicted in Fig. 2 with overall macro-moth abundance highest in standard rides and standard woodland and lowest in coppice and wide rides, the 'Common Severely Declining' species, by contrast, were relatively abundant at wide woodland rides, whilst showing the smallest difference in abundance between the woodland management treatments.

2.3 ± 0.4; small versus large surrounding patch, but treated as continuous variable within analyses, respectively) (treatment x status x area: $F_{20, 96} = 2.21$; $p = 0.0056$). Larger surrounding woodland area also significantly increased overall macro-moth species richness at medium/old coppice (treatment x area: $F_{5, 24} = 5.70$; $p = 0.0013$), particularly through its effect on the group of 'Common Declining' species which was more pronounced than for the other species groups ($S_{trap\ average} \pm$ SE: 'Common Declining': 4.0 ± 0.4 versus 6.0 ± 0.3; 'Common Severely Declining': 1.1 ± 0.1 versus 1.2 ± 0.1; 'Common Increasing': 5.0 ± 0.5 versus 6.0 ± 0.3; 'Scarce/RDB': 0.3 ± 0.1 versus 0.5 ± 0.05; 'Unknown Status': 1.3 ± 0.2 versus 1.9 ± 0.1; small ($N = 15$) versus large ($N = 21$) surrounding patch, respectively) (status x area: $F_{4, 136} = 3.63$; $p = 0.0077$).

Although standard rides and standard woodland (i.e. sheltered sites) were characterised by high overall macro-moth abundance and species richness, with the occurrence of 22 species (i.e. 8% of the total of 265 species) completely restricted to these sheltered sites, 124 species (i.e. 47% of the total) actually occurred in lower numbers at sheltered sites than at coppice and wide rides (i.e. more open, exposed sites), corrected for the difference in sample size between sheltered and more exposed sites. Moreover, these open sites held 49 species (i.e. 18% of the total) not found elsewhere, including 10 'Common Severely Declining' species and 5 'Scarce/RDB' species, though species numbers are not corrected for the sample size difference. The pattern of lower abundance at sheltered sites than at open sites, corrected for the difference in sample size, was strongest for the 'Common Severely Declining' species, with 22 of the 38 recorded species (i.e. 58%) occurring in equal or higher numbers at open compared to sheltered sites. In this respect, they differed from the 'Common Increasing' and 'Scarce/RDB' species groups where only 38% ($N = 28$) and 40% ($N = 6$) of species, respectively, occurred in equal or higher numbers at open sites ($\chi^2_1 = 3.85$, $p = 0.05$; trend only; respectively). Moreover, and although overall abundance within the 'Common Severely Declining' species group increased from young ($N = 82$), over medium ($N = 131$), to old coppice ($N = 145$), species richness decreased (young: $S = 22$; medium: $S = 18$; old: $S = 15$).

4. Discussion

Overall macro-moth abundance was lower at coppiced sites and wide rides than at standard woodland and standard rides. Similarly, overall species richness was lowest in coppice and highest

Fig. 2. Overall macro-moth abundance (number of individuals) and species richness (number of species) ($\log_{10}$-transformed mean(SE)) for six experimental woodland management treatments.

at standard rides and standard woodland, but was high at wide rides too. Although the difference in visibility and hence light trap efficiency in open versus sheltered sites is likely to be small (Slade and Merckx, *pers. obs.*: similar attraction radii of moths to light traps in woodland versus fields), such an effect would only make these key observations conservative. The results may be linked to the amount of shelter and bare ground associated with the woodland management treatments. Central areas of coppiced plots, in particular, are relatively exposed, whereas at least some shelter is provided by the adjacent woodland edges for wide rides, and both standard ride and within-woodland environments are characterised by high levels of shelter. Young coppice, and also to some extent medium and old coppice, is characterised by plenty of bare ground, which when not irradiated by the sun, lowers the temperature of the air layer directly above it. Such factors impact on levels of convective cooling (Merckx et al., 2008), and are likely to have significant impacts on the activity levels and occurrence of these night-flying endothermic insects. Climate change, paradoxically, can lead to further microclimatic cooling of open sites in spring by advancing plant growth, an effect worsened by excess atmospheric nitrogen (Feest and Spanos, 2009), with spring-developing, thermophilous organisms such as butterflies and moths being particularly sensitive (Wallis de Vries and van Swaay, 2006). Differences in plant species richness and structural heterogeneity – in terms of niche availability – among experimental groups are also likely to be important factors explaining differences in macro-moth abundance and species richness (Broome et al., 2011). In this respect, the relatively exposed conditions of wide rides and resulting low overall macro-moth abundance may have been countered by the relatively high plant species richness and more diverse structure resulting in the observed high macro-moth species richness at wide woodland rides. Also, the high levels of abundance and species richness at standard rides and standard woodland may not all have been due to beneficial flight conditions in terms of convective cooling (i.e. shelter and temperature effects), but partly due to the larger structural heterogeneity compared to coppiced sites. Although vegetation diversity is a potentially important factor (Broome et al., 2011), differences in vegetation diversity levels on their own are probably not able to explain the differences in moth abundance and richness levels observed here. For instance, high plant species diversity typically establishes itself in recently coppiced areas (Barkham, 1992), which is where we observed the lowest numbers of moth individuals and moth species. Since our observations were made during summer conditions only, it would be worthwhile to run a similar experiment to test whether our results on the relative contribution of coppiced areas and wide rides hold true during the typically colder spring conditions, and with the typically different, though less diverse adult moth species composition.

The overall picture for moths, of lowest abundance in coppice and wide rides and lowest species richness in coppice, contrasts with that for most day-flying Lepidoptera (i.e. butterflies and day-flying moths). We explain this contrast by the fact that butterflies are typically heliothermic, deriving their body heat almost exclusively from the sun, whereas nocturnal moths are myothermic, their major heat source being muscular energy (Clench, 1966). Woodland conservation management targeted at extended-width rides and coppiced areas creates and maintains early-successional biotopes, providing sunny areas of host plants and nectar sources, which is particularly suitable for many butterfly species within woodland (Warren and Thomas, 1992; Young, 1992; Sparks et al., 1996; Smallidge and Leopold, 1997). As coppicing is carried out rotationally (e.g. cycles of 7–10 years through most recorded history for Hazel *Corylus avellana*), the amount of light and warmth reaching the forest floor in coppiced areas changes through the different successional phases (Barkham, 1992), with many butterfly species strongly favouring the first successional years, while other more shade-tolerant species prefer the later years of the coppice cycle (Warren and Thomas, 1992; Greatorex-Davies et al., 1993).

On top of the overall picture, one group of moths showed differing responses to woodland management. Although abundance of individuals in the 'Common Severely Declining' species group was lower at coppiced sites than at more sheltered sites, differences among woodland management treatments were smaller than for the other species groups. Wide woodland rides in particular were characterised by relatively high abundance of these rapidly declining species, similar to their abundance in standard rides and woodland. Moreover, just under half of all species recorded (i.e. 124 of 265 species) occurred in equal or higher numbers at open than at more sheltered sites (coppice/wide rides versus standard rides/woodland), with 18% of species (i.e. 49 of 265 species) fully restricted to these open areas. Again, this pattern was strongest for the 'Common Severely Declining' species, which had the largest proportion of species (i.e. 58%; 22 of 38 species) occurring in equal or higher numbers at open sites compared to sheltered sites, with their species richness declining from young, over medium to old coppice. Only 5% of recorded species within this group (i.e. 2 of 38 species) were indeed categorised as 'strict-woodland' species, whereas the woodland biotope is for 45% of them (i.e. 17 of 38 species) only one of several possible biotopes. For 16% of these species (i.e. 6 of 38 species) woodland is not mentioned as their biotope at all, while the remaining 34% of species within this group (i.e. 13 of 38 species) are ubiquitous species.

Results of the species-specific analyses also show that the sheltered, dark, humid, late-successional, high deciduous forest biotope is characterised by high numbers of both individuals and species, and is especially important for scarce and RDB species. Of the 15 observed species in this group, 9 appear to be 'strict-woodland' species (i.e. 60%), and the woodland biotope is one of the main biotopes for the other 6 species too. In accordance with the overall analyses, these findings demonstrate the value of the woodland biotope and that the final successional stage clearly needs to be accounted for within woodland management. This recommendation is in line with the findings of Broome et al. (2011) who found mature, closed canopy coppice (11–20 years) both to contain a distinctive range of scarce and threatened, specialist species as well as to be characterised by a higher species richness and abundance of both micro and macro-moths than medium-aged and young coppice in a Sweet Chestnut (*Castanea sativa*) woodland. Similarly, abundance and species richness of both leaf-miner micro-moths and macro-moths have been shown to be higher in abandoned than in young Hazel coppice (leaf-miner micro-moths: Sterling and Hambler, 1988; macro-moths: Waring, 1988). In general, work on moth communities in North American deciduous forests has shown that species richness gradually increases after felling while reaching almost original levels within 25 years (Summerville et al., 2009), with essentially rare species taking decades to recolonize and recover (Summerville and Crist, 2008). However, our work also shows that coppicing and ride widening, which are currently typical woodland conservation management practices for butterflies, can also be valuable conservation tools for macro-moths with an affinity for more open biotopes. We suggest that the mechanism behind the resulting pattern of increased total species richness at the woodland-scale – open sites within woodland held 49 species (i.e. 18% of the total) not found at sheltered sites – involves an increased structural and hence microclimatic diversity of woods and a provision of additional resources for species with an affinity for more open biotopes. Our results show that this especially benefits 'Common Severely Declining' species, with 10 species of this group only found in open sites, and that the benefits of coppicing for 'Common Declining' and

Table A1
List of 15 UK Biodiversity Action Plan (BAP) Priority Species, UK Nationally Scarce and UK Red Data Book species (conservation statuses according to Waring and Townsend, 2009, except Clifden Nonpareil's provisional status as it has only recently recolonized the country) – in the paper referred to as 'Scarce/RDB' – with observed abundance (*N*) and indication of experimental 'woodland management' groups (YC: Young Coppice; MC: Medium Coppice; OC: Old Coppice; WR: Wide Ride; SR: Standard Ride; SW: Standard Woodland) for all observed individuals.

Common name	Genus	Species	Conservation status	*N*	Management group
Festoon	*Apoda*	*limacodes*	Nationally scarce	6	YC/MC/OC/SR
Great oak beauty	*Hypomecis*	*roboraria*	Nationally scarce	46	YC/MC/OC/WR/SR/SW
Kent black arches	*Meganola*	*albula*	Nationally scarce	3	MC/WR
Mere wainscot	*Chortodes*	*fluxa*	Nationally scarce	48	YC/MC/OC/WR/SR/SW
Mocha	*Cyclophora*	*annularia*	Nationally scarce	94	YC/MC/OC/WR/SR/SW
Small black arches	*Meganola*	*strigula*	Nationally scarce	2	MC
White-line snout	*Schrankia*	*taenialis*	Nationally scarce	7	YC/OC/WR/SR/SW
Lunar yellow underwing	*Noctua*	*orbona*	Nationally scarce/BAP	1	WR
Waved black	*Parascotia*	*fuliginaria*	Nationally scarce	8	MC/WR/SR/SW
Double line	*Mythimna*	*turca*	Nationally scarce/former BAP	1	SR
Devon carpet	*Lampropteryx*	*otregiata*	Nationally scarce	21	YC/MC/OC/WR/SR/SW
Dark crimson underwing	*Catocala*	*sponsa*	RDB2 (Vulnerable)/BAP	1	MC
Triangle	*Heterogenea*	*asella*	RDB3 (Rare)	2	OC/SW
Light crimson underwing	*Catocala*	*promissa*	RDB3 (Rare)/BAP	6	MC/SR/SW
Clifden nonpareil	*Catocala*	*fraxini*	Nationally scarce	3	YC/WR

Table A2
List of 38 widespread but rapidly declining UK Biodiversity Action Plan (BAP) Priority Species – in the paper referred to as 'Common Severely Declining' – in alphabetical order, with observed abundance (*N*) and indication of experimental 'woodland management' groups (YC: Young Coppice; MC: Medium Coppice; OC: Old Coppice; WR: Wide Ride; SR: Standard Ride; SW: Standard Woodland) for all observed individuals.

Common name	Genus	Species name	*N*	Management group
August thorn	*Ennomos*	*quercinaria*	1	OC
Autumnal rustic	*Eugnorisma*	*glareosa*	4	MC/WR/SW
Beaded chestnut	*Agrochola*	*lychnidis*	3	YC/WR/SR
Blood-vein	*Timandra*	*comae*	16	YC/MC/WR/SR/SW
Brown-spot pinion	*Agrochola*	*litura*	6	YC/SR/SW
Buff ermine	*Spilosoma*	*luteum*	17	MC/OC/WR/SR/SW
Centre-barred sallow	*Atethmia*	*centrago*	5	MC/OC/WR/SR
Dark-barred twin-spot carpet	*Xanthorhoe*	*ferrugata*	6	MC/WR/SR/SW
Deep-brown dart	*Aporophyla*	*lutulenta*	1	SW
Dusky brocade	*Apamea*	*remissa*	2	OC/WR
Dusky thorn	*Ennomos*	*fuscantaria*	4	YC/MC/WR
Ear moth	*Amphipoea*	*oculea*	2	WR/SR
Feathered gothic	*Tholera*	*decimalis*	25	YC/MC/OC/WR/SR/SW
Figure of eight	*Diloba*	*caeruleocephala*	7	MC
Flounced chestnut	*Agrochola*	*helvola*	1	SR
Garden tiger	*Arctia*	*caja*	3	YC/WR/SR
Ghost moth	*Hepialus*	*humuli*	2	SW
Grass rivulet	*Perizoma*	*albulata*	1	YC
Green-brindled Crescent	*Allophyes*	*oxyacanthae*	130	YC/MC/OC/WR/SR/SW
Hedge rustic	*Tholera*	*cespitis*	2	YC/WR
Knot grass	*Acronicta*	*rumicis*	4	WR/SR/SW
Lackey	*Malacosoma*	*neustria*	1	WR
Large wainscot	*Rhizedra*	*lutosa*	1	YC
Minor shoulder-knot	*Brachylomia*	*viminalis*	267	YC/MC/OC/WR/SR/SW
Mouse moth	*Amphipyra*	*tragopoginis*	6	YC/MC/OC/WR/SR/SW
Oak hook-tip	*Watsonalla*	*binaria*	9	YC/MC/WR/SW
Oak lutestring	*Cymatophorima*	*diluta*	62	MC/WR/SR/SW
Pale eggar	*Trichiura*	*crataegi*	98	YC/MC/OC/WR/SR/SW
Pretty chalk carpet	*Melanthia*	*procellata*	38	YC/MC/OC/WR/SR/SW
Rosy rustic	*Hydraecia*	*micacea*	10	YC/OC/WR/SR
Sallow	*Xanthia*	*icteritia*	47	YC/MC/OC/WR/SR/SW
September thorn	*Ennomos*	*erosaria*	6	WR
Shaded broad-bar	*Scotopteryx*	*chenopodiata*	22	YC/MC/OC/WR/SR/SW
Small emerald	*Hemistola*	*chrysoprasaria*	2	YC
Small phoenix	*Ecliptopera*	*silaceata*	74	YC/MC/OC/WR/SR/SW
Small square-spot	*Diarsia*	*rubi*	2	YC/SR
Sprawler	*Asteroscopus*	*sphinx*	1	SW
White ermine	*Spilosoma*	*lubricipeda*	3	YC/OC/SR

'Common Severely Declining' species are greatest within larger woods. In practical terms, this implies that although coppice management in smaller woods will result in biodiversity gains, larger and hence more cost-effective gains – resulting from a similar management effort – are to be obtained in larger woods.

The community analysis presented here focuses on abundance and species richness, which are two frequently used response variables, whilst paying attention to species-specific conservation status. Additional numerical indices reflecting species group characteristics and functionality could have been generated (e.g.

diversity indices, biomass) (Feest et al., 2010, 2011; Feest and Cardoso, 2012). However, the aim of our experiment was to compare moth abundance and species richness levels among woodland management treatments, and to assess species-specific preferences for treatments, whilst taking into account species-specific conservation profiles, rather than comparing community evenness and diversity levels among woodland management treatments. Biomass is generally considered to be a better indicator of within-community functionality (e.g. insect and moth biomass in terms of bat population viability) than abundance, but correlations between abundance and biomass vary from strong to poor (Saint-Germain et al., 2007). As micro-moths were excluded, we believe that abundance would be a surrogate for biomass in our study since most macro-moth species are similarly sized. Based on the paper's complementary findings our main recommendations are (i) to enlarge existing high forest and create new ones, in order to have a sufficient extent of cores of typical dark woodland biotope, and (ii) to 'buffer' these dark cores from the open 'matrix' by creating, at their edges, lighter woodland zones which can be achieved by implementing coppicing and wide woodland rides. Such zoning will safeguard the dark environment needed by shade- or moisture-loving woodland specialists, whilst at the same time providing accessible woodland habitats for species of mixed and more open biotopes. We show that a conservation focus on either coppicing/ride widening or sheltered woodland will not deliver as much biodiversity value as the combined implementation of both approaches at once. We believe that the two-tier approach we propose here may be vital both for threatened woodland specialists and declining, once-widespread species. Although the exact causes of their declines are still unknown, 'Common Severely Declining' moths are finding it apparently ever more difficult to locate enough resources within current degraded landscapes. For example, eight of the 'Common Severely Declining' species that might have been expected to occur did not and their dramatic national declines (averaging 90% over 35 years) may well explain their absence in our study.

5. Conclusions

By demonstrating clear overall differences in moth abundance and species richness between different woodland management regimes, and different responses by 'Common Severely Declining' (and 'Scarce/RDB' species), we believe that populations of these widespread, but nationally rapidly declining macro-moth species, and indeed most likely other declining moth and invertebrate species too, could be significantly increased by an increased and landscape-scale implementation of coppicing and ride widening within the outer zone of, preferentially, large woodlands, without compromising habitat availability and habitat quality for threatened woodland specialists.

Acknowledgements

Appendix A

Tables 1 and 2

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