Departmental Coversheet

UNIVERSITY OF OXFORD

BIOLOGICAL SCIENCES

Candidate Number	1029326
Supervisor or Advisor	C L I V E H A M B L E R
Title	T H E P O T E N T I A L O F E C O S Y S T E M E N G I N E E R S F O R T H E C O N S E R V A T I O N O F E A R L Y - S U C C E S S I O N A L I N S E C T S
Type of Submission (Project Dissertation, Course Assignment Extended Essay or Course Assignment Abstract for Oral Presentation)	C O U R S E A S S I G N M E N T E X T E N D E D E S S A Y
Word Count (see word limits below)	2 9 9 0

DO NOT ENTER YOUR NAME ANYWHERE IN THIS DOCUMENT.

DO NOT ENTER YOUR CANDIDATE NUMBER ANYWHERE ELSE.

FOR PROJECT DISSERTATIONS AND EXTENDED ESSAYS: YOU MAY ADD AN OPTIONAL PICTURE ON THE FOLLOWING PAGE.

Word limits

Project Dissertation: *Maximum 7,000 words*

Course Assignment Extended Essay: *Maximum 3,000 words*

Course Assignment Abstract for Oral Presentation: *Maximum 500 words*

Abstract

Rewilding is a conservation strategy which is growing in popularity, aiming to produce self-regulating ecosystems by releasing large areas of land from human control, and allowing natural processes, and the species which drive them to return. The removal under rewilding of the human management intervention that is often used to maintain open habitats in the UK means that some conservationists are worried that it may negatively impact species associated with such habitats. In this essay I argue that these species may also stand to benefit, using case studies of three early-successional insect taxa and their conservation, to suggest that the disturbance regimes introduced by 'ecosystem engineers' under rewilding resemble and could even replace traditional conservation *approaches for these species. I then examine a well-known rewilding project in the UK (the Knepp Estate), where early-successional insects appear to be benefitting, and discuss the challenges of understanding the drivers of these benefits that hinder broader application of rewilding. I conclude that conservationists working on species of early-successional habitats that might be concerned about rewilding should look again at its potential.*

Introduction

With the UK among the world's most nature-depleted countries (Hayhow et al. 2016), British conservation is being forced to re-evaluate its priorities and approach. Among its suggested failures is a tendency to be reactive - rushing to protect small remaining areas of habitat, rather than pro-active, in restoring and joining up ecosystems (Lawton et al. 2010), and critics increasingly suggest 'Rewilding' as a more ambitious alternative (Sandom & Macdonald 2015; Sandom & Wynne-Jones 2019). Rewilding definitions are increasingly varied (Jørgensen 2015) but generally focus on releasing large areas of land from human control and allowing the return of missing natural processes (Seddon et al. 2014; Prior & Ward 2016; Corlett 2016), often requiring the reintroduction of species that drive them (so-called ecosystem engineers, which alter their abiotic environment (Jones et al. 1994)). The result, advocates suggest, is a biodiverse, self-regulating ecosystem, rather than one dependent on the human management intervention that often characterises British conservation (Brown et al. 2011). In Europe, where proposals typically focus on the return of the pre-Neolithic megafauna (or proxies) (Hodder et al. 2009), the landscape that would result from rewilding is hotly-debated, with advocates of both savannah-like scrubland (Vera 2000) and closed-canopy woodland (Robinson 2014). With the removal of human intervention though, it is likely to involve at least some loss of early-successional habitats like grassland and heathland that characterise 'cultural landscapes' under low intensity agriculture (Navarro & Pereira 2012). In the UK, conservation often seeks to maintain such habitats by mimicking low-intensity agriculture, and some conservation organisations have voiced concern that rewilding could compound the problems that species dependent on them are already facing due to agricultural intensification (Warren 2016; Barkham 2017).

But perhaps this is a product of shifting baselines – given that most British megafauna were extirpated before the turn of the 19th century(Yalden 1999), when the term 'ecology' was first coined (Haeckel 1866), a view amongst British ecologists and conservationists that many species are dependent on human intervention, rather than natural disturbance from megafauna, seems inevitable. This essay will attempt to demonstrate the value of re-thinking this idea, and in turn the potential benefits of rewilding for early-successional species, by discussing how disturbance from ecosystem engineers that are targets for reintroduction under UK rewilding projects (Rewilding Brtain 2019) resembles current conservation management techniques for three insect taxa of early-successional habitats. Insects are chosen as the focus, as their narrow niches and relatively poor dispersal ability mean they should be among the most sensitive taxa to the removal of management and any loss of required open habitat under rewilding (Thomas 1995).

1. <u>Managing bracken for High Brown Fritillaries</u>

Butterflies (Rhophalocera) are often a conservation priority in early-successional habitats. In the UK, the most threatened of these is the High Brown Fritillary (*Fabriciana adippe*), which has contracted its range by 96% since 1976 (Jones et al. 2015). High Brown Fritillaries require violets (*Viola* spp.) for their larvae, in warm, sheltered micro-climates which were once found in the leaf-litter in the first few years after coppicing in woods (Warren 1995). The widespread decline in coppicing means that the butterfly has been lost from woodland (Thomas et al. 1991), and most if its remaining colonies are now on rough upland grassland with bracken (*Pteridium aquilinum*) communities (Warren & Oates 1995). Here, the bracken acts as a pseudo-woodland canopy, allowing vernal plants (such as Violets) to grow and flower in spring, before shading out more competitive species in summer (Warren & Oates 1995).

The requirements of the High Brown Fritillary in these habitats are complex; if Bracken becomes too dominant, it will overwhelm their violet foodplants, but the warm microclimate that the litter layer creates is also essential to enabling the thermophilous larvae to become active in the spring (Warren 1994). Grazing is generally thought of as the best approach to this difficult balancing act, with heavy ungulates that trample the Bracken, breaking it up, but the expense of fencing and risk of bracken poisoning makes this challenging, while burning and cutting can improve habitat in the short term but also increase the risk of invasion by Rosebay Willowherb (*Chamaenerion angustifolium*) and grasses (*Poa* spp.) in the longer term (Warren & Oates 1995; Joy 1997).

Some managers have even gone as far as using remotely operated ‘flailbots’ to cut bracken stands (National Trust 2019), and while this high-tech approach to might seem a world away from the hands-off approach of rewilding, this conservation problem may benefit from the influence of ecosystem engineers. Wild Boar are one of the few species capable of digesting bracken rhizomes, disturbing the upper layers of the soil with their snouts to access them (Sandom et al. 2013), and through this rooting could prevent bracken stands from becoming too dense and swamping the High Brown Fritillary’s foodplants. Indeed, rooting typically occurs in Bracken stands during the winter, when other food sources are scarce (Sandom et al. 2013) - the same time as grazing is normally recommended for High Brown Fritillaries (Ellis et al. 2019). Rooting may also have the added benefit of creating bare ground germination niches for Violets (Bueno et al. 2011), increasing their cover, while possibly decreasing the vigour of competitors, as it has been shown to reduce the cover of Bluebells (Sims et al. 2014) and Honeysuckle species (Burrascano et al. 2015) in woodland, both negative indicators of habitat quality for High Brown Fritillaries (Ellis et al. 2019). While rooting is more destructive normal management, anecdotal evidence suggests that heavy disturbance may be beneficial for High Brown Fritillaries; Joy (1997) describes, for example, how populations on a site in the Malvern Hills peaked during a period when 4x4 vehicles were being driven through bracken stands during off-road competitions, and the extinction that followed after these ceased.

2. Coppicing for the Small Pearl-Bordered Fritillary

The High Brown Fritillary is one of a guild of violet-feeding fritillaries that has declined in the UK in the past century, another is the Small Pearl-Bordered Fritillary (*Boloria selene*), which has disappeared from 76% of sites since 1976 (Fox et al. 2015). This species has also suffered from the decline in coppicing, though it breeds on Violets in a slightly later successional stage than High Brown Fritillaries; larger, lusher plants surrounded by vegetation in humid situations (Thomas et al. 1991). Recent attempts to restore the butterfly to the woodland habitats from which it has been lost have required the return of coppicing to create suitable clearings (Hulme 2015a), but small markets for coppice products means the expansion of favourable management may be costly (Barnett & Warren 1995), and rewilding may offer a cheaper, lower intervention solution – Beavers.

These highly-specialised herbivores frequently cut down small trees in late summer and autumn to store for winter food in their lodges (Rosell et al. 2005), in a process that strongly resembles the coppicing and scrub clearance work often carried out for Small Pearl-Bordered Fritillaries. Indeed, the felling of Aspen (*Populus tremula*) and Willow (*Salix* spp.), both of which are preferred food sources for beavers (Jones et al. 2009), can produce large flushes of violets favoured by Small Pearl – Bordered Fritillaries, as does Birch (*Betula* spp.) (Barnett & Warren 1995), which was frequently chosen in recent Scottish Beaver releases (Moore et al. 2011). Felling often occurs alongside water bodies, making the stream borders more open and grassy (Macdonald et al. 1995), even appearing ‘clear-felled’ (Naiman et al. 1986), which fits well with observations of Small Pearl-Bordered Fritillaries breeding in clear-felled areas around streams in commercial plantations (Stewart & Bourn 2004). Felled material is also used by Beavers to dam streams and create ponds. When the dam is abandoned and fails, these drain (Rosell et al. 2005), leaving rich alluvial deposits that are soon invaded by plants to form ‘beaver meadows’ (Neff 1957) that are dominated by sedges (*Carex* spp.)

and grasses, with herbs in the understorey (McMaster & McMaster 2008). Sedge cover can be a significant predictor of Small Pearl-Bordered Fritillary patch occupancy in woodland (Stewart et al. 2003), and they often breed in damp grasslands (Barnett & Warren 1995), suggesting that these Beaver meadows may well be highly suitable for them.

While much of the work cited here focuses on North American Beavers (*Castor canadensis*), recent work in eastern Russia where they co-occur with Eurasian Beavers suggests the latter are ecologically similar (Danilov & Fyodorov 2015), and should therefore be able to create the full spectrum of Small Pearl-Bordered Fritillary habitats. They may also be able to do this with sufficient scale and continuity for the poorly-dispersing fritillaries (Thomas et al. 1991), with Coles & Orme (1983) suggesting that beavers may have been second only to humans as drivers of British woodland clearances in the Neolithic, while the meadows they create can persist for as long as a century (Wilde et al. 1950). Furthermore, in the USA, Beavers have been crucial to conserving the endangered St Francis' Satyr (*Neonympha mitchellii francisci)* (Bartel et al. 2010), which, like the Small Pearl-Bordered Fritillary, disperses relatively poorly through woodland, favouring damp openings where its foodplants (sedges) grow (Kuefler et al. 2008). Rather than being dependent on human coppicing though, over 90% of its populations are on abandoned beaver ponds (Kuefler et al. 2008). On top of this, Beaver damming activity raises water levels and is thought to increase the resilience of St Francis' Satyr populations to droughts, as they depend on high water levels that will otherwise be reduced (Aschehoug et al. 2015). Small Pearl-Bordered Fritillaries may also be vulnerable to this threat in the UK, having disappeared from their driest habitats and retreated steadily westwards, to areas of higher rainfall (Hulme & Blencowe 2017).

3. Creating bare ground for heathland Orthoptera

Like Butterflies, many Grasshoppers and Crickets (Orthoptera) are in rapid decline in the UK, and similarly, some of the worst-affected species are those that require the earliest seral stages for their development (Fartmann et al. 2012), with several now heavily dependent on human management (Sutton et al. 2016). For these species, the warm micro-climate created by bare ground is often a vital resource (Weiss et al. 2013). On heathlands, which are among the most important habitats for British Orthoptera (Sutton et al. 2016), conservationists create and maintain this habitat with a combination of sod-cutting and scrape-digging (stripping off the topsoil), grazing, or cutting and burning (to prevent reversion to scrub and woodland) (Sedláková & Chytrý 1999; Britton et al. 2000). This is a labour-intensive process that may need to be scaled up at great cost as increasing atmospheric nitrogen deposition drives the encroachment of grasses into heathland, and the cooling of invertebrate habitat as a result (Barker et al. 2004).

Rooting by Wild Boar, which leaves broken, bare ground as they turn over the upper layers of the soil in search of roots and tubers (Sandom et al. 2013), may offer a pragmatic solution. While this is extremely destructive, the benefits of such intense disturbance for heathland Orthoptera are well-demonstrated by the unlikely refuges to which many are now confined – military training areas. In Germany for example, the nationally red-listed Blue-Winged Grasshopper (*Oedipoda caerulescens*) is largely restricted to military training areas (Warren & Büttner 2008), while in Essex, in the UK, half of the sites for the endangered Mottled Grasshoppers (*Myrmeleotettix maculatus*) are on Ministry of Defence land, the best of which is in the shell craters behind the main targets on a tank range (Gardiner & Benton 2009). On these sites, the passage of heavy armoured vehicles and detonations churn up the ground and constantly re-shape the landscape, providing the bare ground habitat that these species require in abundance (Warren & Büttner 2008; Gardiner & Benton 2009). Wild Boar disturbance may provide similar dynamism, and has already been shown to benefit a threatened heathland butterfly in the Netherlands, the Grizzled Skipper (*Pyrgus malvae*). This species is also highly thermophilous (Brereton 1997) and its oviposition is positively associated with wild boar scrapes, where suitably warm host-plants in bare ground occur (de Schaetzen et al. 2018). Furthermore, in a trial release in the highlands, rooting was most frequent during the summer in grassy areas (Sandom et al. 2013), so Boar may also help to reduce the problem of grass encroachment on heathlands.

Conclusions

The three case studies described here are hypothetical, but not, I believe, implausible, and they highlight the potential for ecosystem engineers to provide for free and in the long term the kind of beneficial disturbance that traditional conservation approaches have produced much more laboriously and, as the declines of the focal species here illustrate, not always successfully. The case studies are drawn from different habitats and focus on taxa that are all currently subjects of conservation action (eg. Gardiner 2010; Butterfly Conservation 2019), highlighting the broad relevance of the potential value of ecosystem engineers to current conservation practice. Furthermore, they are largely drawn from my own specialist interest in butterflies, and it seems likely the disturbance described could benefit a much larger variety of early-successional taxa. As an example, ground disturbance on heathland by ploughing (mimicking Wild Boar) is recommended for threatened species as diverse as the Grey Carpet Moth (*Lithostege griseata*) (Hearle & Ellis 2012) and Woodlark (*Lullula arborea*) (Hawkes et al. 2019).

Actual rewilding projects in the UK are rare, providing scant opportunity to evaluate practically these ideas, but at perhaps the best known example, the Knepp Estate in Sussex, butterflies have been one of the main headlines. Surveys show a steady increase in the number of species recorded each year, particularly of grassland habitats and conservation concern in recent years (Figure 1), suggesting that rewilding at Knepp has been able to create habitat for the rarer species of early-successional habitats that have been discussed here. Evidence that this has resulted from disturbance provided by ecosystem engineers rather than the expected benefits of halting intensive agriculture is however, equivocal, since the time involved in doing butterfly surveys over such the large area at Knepp means that only three can be done at a relatively coarse scale each year. Thus, meaningful trends to evaluate different species' responses to specific changes in the project cannot be produced.

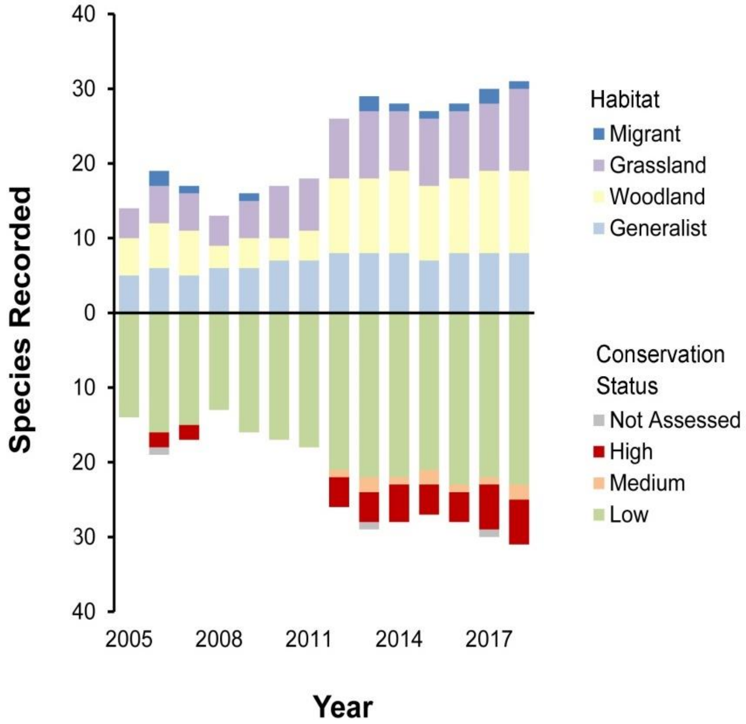

Figure 1: The number of butterfly species recorded each year at Knepp since 2005 from Hulme (2012 - 2018) and Howorth (2008 - 2011). Species are plotted in terms of both habitat associations (following Thomas and Lewington (2014) and conservation status (following BRIG (2007)).

This monitoring challenge is common to all large rewilding projects (Nogués-Bravo et al. 2016), and overcoming it to understand the mechanisms by which ecosystem engineers drive community-level outcomes will be vital to understand their potential effects on targeted conservation efforts, and avoid unexpected impacts. Wild Boar rooting may, for example, create germination niches for Violets in bracken stands, or facilitate their invasion by tree seedlings and ruderal plants (Sondej & Kwiatkowska-Falińska 2017). Other drivers of outcomes in rewilding projects, such as the landscape context also need to be dis-entangled from the effects of ecosystem engineers. This has been important at Knepp, where the lack of sloping ground and heavy clay soil may be limiting nesting opportunities for aculeate hymenoptera and wasps (Wood & Goulson 2016), and the paucity of source colonies in the surrounding landscape is thought to have reduced the colonisation of grassland butterflies (N. Hulme 2019, pers. comm., 4th Feb).

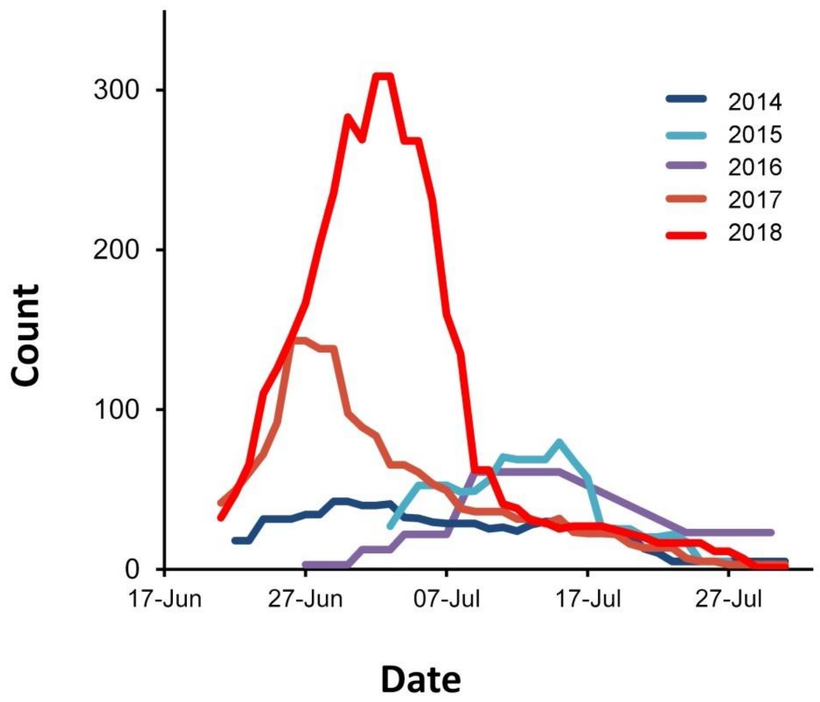

Figure 2: 7 day moving average counts of Purple Emperors at Knepp during June and July from 2014 to 2018 (from Hulme (2014 - 2018)). In 2018, the peak count of nearly 400, was over three times that of the next largest UK site.

Despite the uncertainties in understanding what is driving outcomes at Knepp, its booming populations of the Purple Emperor butterfly (*Apatura iris*) (Figure 2) at least illustrate the surprising benefits of more dynamic landscapes for species of conservation concern, a key theme in this essay. This species is mainly arboreal and has traditionally been associated with large areas of oak woodland (Bourn & Warren 2000), but it owes its abundance at Knepp to ignoring received wisdom and breeding in emerging areas of scrub, rich in the favoured foodplants (broad-leaved Sallow (*Salix*) species) (Oates & Hulme 2013). I believe the case studies described in this essay illustrate the potential of disturbance from ecosystem engineers to benefit species of early-successional habitats, and the potential for more surprises like Knepp's Purple Emperors. This is not however to say that full-scale rewilding projects represent a panacea for the conservation of these species, since they will probably only benefit from such schemes for a short period until, as is likely, heterogeneity declines as woodland forms (Merckx 2015; Van Klink & Wallisdevries 2018). Instead, I suggest that the disturbance regimes restored to British landscapes by rewilding projects may help solve some of the problems traditional conservation faces, and that conservationists that are worried about the impacts of rewilding on target species should look again about its potential.

Bibliography

Aschehoug ET, Sivakoff FS, Clayton HL, Morris WF, Haddad NM. 2015. Habitat restoration affects immature stages of a wetland butterfly through indirect effects on predation. Ecology **96**:1761–1767.

Barker CG, Power SA, Bell JNB, Orme CDL. 2004. Effects of habitat management on heathland response to atmospheric nitrogen deposition. Biological Conservation **120**:41–52.

Barkham P. 2017. "It is strange to see the British struggling with the beaver": why is rewilding so controversial? The Guardian:1–6. Available from https://www.theguardian.com/environment/2017/jul/01/rewilding-conservation-ecology-national-trust.

Barnett LK, Warren MS. 1995. Species Action Plan: Small Pearl - Bordered Fritillary Boloria selene. Butterfly Conservation, Wareham.

Bartel RA, Haddad NM, Wright JP. 2010. Ecosystem engineers maintain a rare species of butterfly and increase plant diversity. Oikos **119**:883–890.

Bourn NAD, Warren MS. 2000. Species Action Plan: Purple Emperor Apatura iris. Butterfly Conservation, Wareham.

Brereton TM. 1997. Ecology and conservation of the butterfly Pyrgus malvae (grizzled skipper) in south-east England. University of East London.

BRIG. 2007. Species and Habitat Review (2007 species status). Available from http://jncc.defra.gov.uk/PDF/UKBAP_Species-HabitatsReview-2007.pdf.

Britton AJ, Marrs RH, Carey PD, Pakeman RJ. 2000. Comparison of techniques to increase Calluna vulgaris cover on heathland invaded by grasses in Breckland, south east England. Biological Conservation **95**:227–232.

Brown C, Mcmorran R, Price MF. 2011. Rewilding – A New Paradigm for Nature Conservation in Scotland? Scottish Geographical Journal **127**:288–314.

Bueno CG, Reiné R, Alados CL, Gómez-García D. 2011. Effects of large wild boar disturbances on alpine soil seed banks. Basic and Applied Ecology **12**:125–133.

Burrascano S, Giarrizzo E, Bonacquisti S, Copiz R, Del Vico E, Fagiani S, Mortelliti A, Blasi C. 2015. Quantifying Sus scrofa rooting effects on the understorey of the deciduous broadleaf forests in Castelporziano Estate (Italy). Rendiconti Lincei **26**:317–324.

Butterfly Conservation. 2019. Conservation projects. Available from https://butterfly-conservation.org/our-work/conservation-projects (accessed April 25, 2019).

Coles JM, Orme BJ. 1983. Homo sapiens or Castor fiber? Antiquity **57**:95–102.

Corlett RT. 2016. Restoration, Reintroduction, and Rewilding in a Changing World. Trends in Ecology & Evolution **31**:453–462.

Danilov PI, Fyodorov F V. 2015. Comparative characterization of the building activity of Canadian and European beavers in northern European Russia. Russian Journal of Ecology **46**:272–278.

de Schaetzen F, van Langevelde F, Wallisdevries M. 2018. The influence of wild boar (Sus scrofa) on microhabitat quality for the endangered butterfly Pyrgus malvae in the Netherlands. Journal of Insect Conservation **22**:51–59.

Ellis S et al. 2019. Are habitat changes driving the decline of the UK's most threatened butterfly: the High Brown Fritillary Argynnis adippe (Lepidoptera: Nymphalidae)? Journal of Insect Conservation:1–17.

Fartmann T, Krämer B, Stelzner F, Poniatowski D. 2012. Orthoptera as ecological indicators for succession in steppe grassland. Ecological Indicators **20**:337–344.

Fox R et al. 2015. The State of the UK ' s Butterflies 2015. Butterfly Conservation and the Centre for Ecology and Hydrology, Wareham.

Gardiner T. 2010. Successful translocation of the locally rare mottled grasshopper Myrmeleotettix maculatus to Jaywick flood defences in Essex, England. Conservation Evidence **7**:106–110.

Gardiner T, Benton T. 2009. Grasshoppers and Bush-Crickets (Orthoptera) of Military Training Grounds Near Colchester. Entomologist's Record and Journal of Variation **121**:167–171.

Haeckel EHPA. 1866. Generelle Morphologie der Organismen. Allgemeine Grundzüge der organischen Formen-Wissenschaft, mechanische Begründet durch die von Charles Darwin reformirte Descendenz-Theorie. Reimer, Berlin, Germany.

Hawkes RW, Smart J, Brown A, Jones H, Dolman PM. 2019. Experimental evidence that ground-disturbance benefits Woodlark *Lullula arborea*. Ibis **161**:447–452. John Wiley & Sons, Ltd (10.1111).

Hayhow DB, Burns F, Eaton MA, Al Fulaij N, August TA, Babey L, Bacon L, Bingham C, Boswell J, Boughey KL, Brereton T, Brookman E, Brooks DR, Bullock DJ, Burke O, Collis M, Corbet L, Cornish N, De Massimi S, Densham J, Dunn E, Elliott S, Gent T, Godber J, Hamilton S, Havery S, Hawkins S, Henney J, Holmes K, Hutchinson N, Isaac NJB, Johns D, Macadam CR, Mathews F, Nicolet P, Noble DG, Outhwaite CL, Powney GD, Richardson P, Roy DB, Sims D, Smart S, Stevenson K, Stroud RA, Walker KJ, Webb JR, Webb TJ, Wynde R and Gregory RD 2016. State of Nature 2016. State of Nature Partnership.

Hearle S, Ellis S. 2012. Specialist Moths in Breckland: Creating Bare Ground on a Landscape Scale. Pages 36–41 in N. A. D. Bourn, C. R. Bulman, and S. Ellis, editors. Landscape Scale Conservation for Butterflies and Moths: Lessons from the UK. Butterfly Conservation, Wareham.

Hodder KH, Buckland PC, Kirby KJ, Bullock JM. 2009. Can the pre-Neolithic provide suitable models for re-wilding the landscape in Britain ? British Wildlife **20**:4–15.

Howorth R. 2008. Timed Butterfly Transect Surveys of the Knepp Estate July 2005 – 2008. Available from https://static1.squarespace.com/static/595ca91bebbd1a1d0aaab285/t/5a36b69a0d92972a198a9f83/1513535131060/Butterfly+survey+report+Knepp+Estate+2005-08.pdf.

Howorth R. 2009. Timed Butterfly Transect Survey of the Knepp Estate 2009. Available from https://static1.squarespace.com/static/595ca91bebbd1a1d0aaab285/t/5a36b872e4966b79a0beba81/1513535603039/Butterfly+survey+report+Knepp+Estate+2009.pdf.

Howorth R. 2010. Timed Butterfly Transect Survey of the Knepp Estate 2010. Available from https://static1.squarespace.com/static/595ca91bebbd1a1d0aaab285/t/5a36bb460d92972a198b3ed4/1513536327186/Butterfly+survey+report+Knepp+Estate+2010.pdf.

Howorth R. 2011. Timed Butterfly Transect Survey of the Knepp Estate 2011. Available from https://static1.squarespace.com/static/595ca91bebbd1a1d0aaab285/t/5a3780a171c10b467b436364/1513586849941/Butterfly+survey+report+Knepp+Estate+2011.pdf.

Hulme N. 2012. Butterfly Surveys, Knepp Castle Estate 2012. Available from https://static1.squarespace.com/static/595ca91bebbd1a1d0aaab285/t/5a378432f9619a424b82c6cb/1513587764251/Butterfly_survey_Knepp_2012.pdf.

Hulme N. 2013. Butterfly Surveys, Knepp Castle Estate 2013. Available from https://static1.squarespace.com/static/595ca91bebbd1a1d0aaab285/t/5a3785ec8165f5e58aaba701/1513588206128/Butterfly+Survey+NH+%282013%29.pdf.

Hulme N. 2014. Butterfly Surveys , Knepp Castle Estate , 2014. Available from https://static1.squarespace.com/static/595ca91bebbd1a1d0aaab285/t/5a37873de4966b79a0d89f98/1513588543149/Butterfly+Survey+NH+%282014%29.pdf.

Hulme N. 2015a. Fritillaries for the Future Project Sussex Fritillaries Action Group Newsletter. Butterfly Conservation, Brighton.

Hulme N. 2015b. Butterfly Surveys , Knepp Castle Estate, 2015. Available from https://static1.squarespace.com/static/595ca91bebbd1a1d0aaab285/t/5aa29902ec212d3b14c7ba84/1520605448410/Knepp+Butterfly+Survey+2015+-+Neil+Hulme.pdf.

Hulme N. 2016. Butterfly Surveys , Knepp Castle Estate 2016. Available from https://static1.squarespace.com/static/595ca91bebbd1a1d0aaab285/t/5aa29c9653450a267ae364ad/1520606360772/Knepp+Butterfly+Surveys+2016+-+Neil+Hulme.pdf.

Hulme N. 2017. Butterfly Surveys , Knepp Castle Estate , 2017. Available from https://static1.squarespace.com/static/595ca91bebbd1a1d0aaab285/t/5a54f0a7c83025ea958275af/1515516083258/Main+Butterfly+report+%282017%29.pdf.

Hulme N. 2018. Butterfly Surveys, Knepp Castle Estate, 2018. Available from https://static1.squarespace.com/static/595ca91bebbd1a1d0aaab285/t/5c9cf9a4fa0d603a9ba6ac4f/1553791397302/Knepp+Butterflies+Neil+Hulme+%282018%29.pdf.

Hulme N, Blencowe M. 2017. The Butterflies of Sussex. Pisces Publications, Newbury.

Jones CG, Lawton JH, Shachak M, Organisms M. 1994. Organisms as Ecosystem Engineers **69**:373–386.

Jones K, Gilvear D, Willby N, Gaywood M. 2009. Willow (Salix spp.) and aspen (Populus tremula) regrowth after felling by the Eurasian beaver (Castor fiber): implications for riparian woodland conservation in Scotland. Aquatic Conservation: Marine and Freshwater Ecosystems **19**:75–87.

Jones R, Martinez A, Plackett J, Wainwright D, Ellis S, Kelly C, Hobson R, Wain M, Bulman CR, Bourn NAD. 2015. The Changing Status of the High Brown Fritillary in the UK (1994-2014). Butterfly Conservation, Wareham.

Jørgensen D. 2015. Rethinking rewilding. Geoforum **65**:482–488.

Joy J. 1997. Bracken management for fritillary butterflies in the West Midlands and Gloucestershire region. Butterfly Conservation, Wareham.

Kuefler D, Haddad NM, Hall S, Hudgens B, Bartel B, Hoffman E. 2008. Distribution, population structure and habitat use of the endangered Saint Francis Satyr butterfly, Neonympha mitchellii francisci. American Midland Naturalist **159**:298–320.

Lawton, J.H., Brotherton, P.N.M., Brown, V.K., Elphick, C., Fitter, A.H., Forshaw, J., Haddow, R.W., Hilborne, S., Leafe, R.N., Mace, G.M., Southgate, M.P., Sutherland, W.J., Tew, T.E., Varley, J., & Wynne, G.R. 2010. Making space for nature: a review of England’s wildlife sites and ecological network. Report to DEFRA.

Macdonald DW, Tattersall FH, Brown ED, Balharry D. 1995. Reintroducing the European beaver to Britain: Nostalgic meddling or restoring biodiversity? Mammal Review **25**:161–200.

McMaster R, McMaster N. 2008. Vascular flora of Beaver wetlands in Western Massachusetts. Rhodora **80**:175–197.

Merckx T. 2015. Rewilding: Pitfalls and Opportunities for Moths and Butterflies. Pages 107–125 in H. M. Pereira and L. M. Navarro, editors. Rewilding European Landscapes.

Moore BD, Sim D, Iason GR. 2011. The Scottish Beaver Trial: Woodland monitoring 2010. Page Scottish Natural Heritage Commissioned Report. Inverness.

Naiman RJ, Melillo JM, Hobbie JE. 1986. Ecosystem Alteration of Boreal Forest Streams by Beaver (Castor Canadensis). Ecology **67**:1254–1269.

National Trust. 2019. Our work in the Heddon Valley | National Trust. Available from https://www.nationaltrust.org.uk/heddon-valley/features/our-work-at-heddon-valley (accessed March 28, 2019).

Navarro LM, Pereira HM. 2012. Rewilding Abandoned Landscapes in Europe. Ecosystems **15**:900–912.

Neff DJ. 1957. Ecological Effects of Beaver Habitat Abandonment in the Colorado Rockies. The Journal of Wildlife Management **21**:80.

Nogués-Bravo D, Simberloff D, Rahbek C, Sanders NJ. 2016. Rewilding is the new Pandora's box in conservation. Current Biology **26**:R87–R91.

Oates M, Hulme N. 2013. Preliminary Report On Purple Emperor Butterfly Surveys , Knepp Castle Estate , July 2013.

Prior J, Ward KJ. 2016. Rethinking rewilding : A response to Jørgensen. Geoforum **69**:132–135.

Rewilding Brtain. 2019. Reintroductions - Rewilding Britain. Available from https://www.rewildingbritain.org.uk/rewilding/reintroductions/ (accessed April 25, 2019).

Robinson M. 2014. The ecodynamics of clearance in the British Neolithic. Environmental Archaeology **19**:291–297.

Rosell F, Bozsér O, Collen P, Parker H. 2005. Ecological impact of beavers Castor fiber and Castor canadensis and their ability to modify ecosystems. Mammal Review **35**:248–276.

Sandom CJ, Hughes J, Macdonald DW. 2013. Rewilding the scottish highlands: Do wild boar, sus scrofa, use a suitable foraging strategy to be effective ecosystem engineers? Restoration Ecology **21**:336–343.

Sandom CJ, Macdonald DW. 2015. What next? Rewilding as a radical future for the British countryside. Page 336 in D. W. Macdonald and R. E. Feber, editors. Wildlife Conservation on Farmland: Managing for nature on lowland farms. Oxford University Press, Oxford.

Sandom CJ, Wynne-Jones S. 2019. Rewilding a country: Britain as a study case. Page 460 in N. Pettorellie, S. M. Durant, and J. T. du Toit, editors. Rewilding. Cambridge University Press, Cambridge.

Seddon PJ, Griffiths CJ, Soorae PS, Armstrong DP. 2014. Reversing defaunation: Restoring species in a changing world. Science **345**:406–412.

Sedláková I, Chytrý M. 1999. Regeneration patterns in a Central European dry heathland: Effects of burning, sod-cutting and cutting. Plant Ecology **143**:77–87.

Sims NK, John EA, Stewart AJA. 2014. Short-term response and recovery of bluebells (Hyacinthoides non-scripta) after rooting by wild boar (Sus scrofa). Plant Ecology **215**:1409–1416.

Sondej I, Kwiatkowska-Falińska AJ. 2017. Effects of Wild Boar (*Sus scrofa* L.) Rooting on Seedling Emergence in Białowieża Forest. Polish Journal of Ecology **65**:380–389.

Stewart KEJ, Bourn NAD. 2004. The Status , Mobility and Habitat Requirements of the Small Pearl-bordered Fritillary (Boloria selene) in Clocaenog Forest An Overview of Three Years Work. Butterfly Conservation, Wareham.

Stewart KEJ, Bourn NAD, Joy J. 2003. The Status , Mobility and Habitat Requirements of the Small Pearl-bordered Fritillary (Boloria selene) in Clocaenog Forest YEAR 2 – Further Study. Butterfly Conservation, Wareham.

Sutton PG, Beckmann BC, Nelson B. 2016. The Current Status of Orthopteroid Insects in Britain and Ireland. Atropos **59**: 6-35

Thomas JA. 1995. Why small cold-blooded insects pose different conservation problems to birds in modern landscapes. Ibis **137**:112–119.

Thomas, JA & Lewington, R. The Butterflies of Britain and Ireland. (British Wildlife Publications, 2014).

Thomas JA, Snazell, R C, Moy IL. 1991. The Conservation of Violet - Feeding Fritillaries in the British Isles. Centre for Ecology and Hydrology, Wareham.

Van Klink R, Wallisdevries M. 2018. Risks and opportunities of trophic rewilding for arthropod communities. Philosophical Transactions of the Royal Society B: Biological Sciences **373**:1–8.

Vera FWM. 2000. Grazing Ecology and Forest History. CABI Publishing, Wallingford.

Warren M. 1995. Managing local microclimates for the High Brown Fritillary, Argynnis adippe. Pages 198–210 in A. S. Pullin, editor. Ecology and Conservation of Butterflies. Springer, Dordrecht.

Warren MS. 1994. Autoecology and Conservation Needs of the High Brown Fritillary. Butterfly Conservation, Wareham.

Warren MS. 2016. Improved green farming schemes are vital to save butterflies when we leave the EU. Available from https://butterfly-conservation.org/news-and-blog/improved-green-farming-schemes-are-vital-to-save-butterflies-when-we-leave-the-eu (accessed April 10, 2019).

Warren MS, Oates MR. 1995. The Importance of Bracken Habitats to Fritillary Butterflies and their Management for Conservation. Pages 178–181 in R. Thornton Smith and J. A. Taylor, editors. Bracken: An Environmental Issue. International Bracken Group.

Warren SD, Büttner R. 2008. Active military training areas as refugia for disturbance-dependent endangered insects. Journal of Insect Conservation **12**:671–676.

Weiss N, Zucchi H, Hochkirch A. 2013. The effects of grassland management and aspect on Orthoptera diversity and abundance: Site conditions are as important as management. Biodiversity and Conservation **22**:2167–2178.

Wilde SA, Youngberg CT, Hovind JH. 1950. Changes in Composition of Ground Water, Soil Fertility, and Forest Growth produced by the Construction and Removal of Beaver Dams. The Journal of Wildlife Management **14**:123–128.

Wood T, Goulson D. 2016. Aculeate bee and wasp survey report 2015/16 for the Knepp Wildland Project. Available from https://knepp.co.uk/s/Knepp-bee-and-wasp-survey-report-2015-2016-Dave-Goulson-and-Tom-Woods.pdf.

Yalden DW. 1999. The history of British mammals. Page T. & A.D. Poyser natural history.