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Effects of clear-felling versus gradual removal of conifer trees on the survival of understorey plants during the restoration of ancient woodlands

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ABSTRACT

Plantations of exotic conifers on ancient woodland sites retain many features of high conservation value and in many countries such sites are being actively restored. Clear-felling of the conifer trees is often a straight-forward first step, but recent guidance on restoration advocates gradual removal of the plantation crop to protect vulnerable woodland specialist plants. To date there has been little empirical evidence to support this policy. One hundred and four stands in 39 woodland sites in the UK owned by the Woodland Trust from Cornwall to Invernesshire were surveyed in 2001 and again in 2009 to assess the survival of woodland flora following restoration by both clear-felling and gradual removal of the plantation crop. On average, there were over seven woodland specialist and ancient woodland indicator species in each of the stands surveyed. Loss of specialist woodland species – the most shade adapted component of the flora – over this time period was strongly correlated with the degree of canopy opening. In contrast, the loss of more light demanding plant species was not related to the intensity of tree removals. This study suggests that a careful assessment and prioritisation of conservation values is needed before restoration. Rapid removal of an exotic species as part of a restoration programme may have an adverse effect on subsequent succession.

1. Introduction

From the nineteenth century extensive exotic conifer plantations were created in many Northern hemisphere countries in order to meet anticipated demand for wood products, many established by clearing less productive natural broadleaved woodland (Zerbe, 2002; Boucher et al., 2009). Conifer plantations are typically monocultural, extensive, created and managed using ploughing, draining and chemical methods, and often are of non-native species (Mason and Quine, 1995; Peterken, 1996; Turner et al., 1999; Buckley et al., 2005; Laarmann et al., 2013). Such plantations are vulnerable to outbreaks of pests and diseases (e.g. Cruickshank et al., 2009) and may be vulnerable to anthropogenic climate change (Felton et al., 2010; Hickler et al., 2012).

In the UK, more than half of all woodland is even-aged conifer plantation whilst only 14% (450,000 ha) of the total forest area is ancient semi-natural woodland (continuous woodland cover for several centuries) (Smith and Gilbert, 2003). A post-war policy of woodland 'rehabilitation' (sensu Garfitt, 1953) resulted in conversion of many ancient woods into plantations, usually of non-native species. By 2002 these plantations occupied 43.5% of the total ancient woodland area in Britain (Pryor and Smith, 2002).

Restoration of forest biodiversity is a focus of the Convention on Biological Diversity (Halme et al., 2013). For both economic (e.g. recreation demands, changes in timber markets) and ecological (e.g. focus on ecosystem functioning) reasons, many countries now have policies aimed at restoring native, semi-natural, broadleaved woodland to conifer plantation sites (Kenk and Guehne, 2001; Zerbe, 2002; Spiecker et al., 2004; Degrave et al., 2006; Yamagawa et al., 2010). Restoration has been shown to have potential benefits for biodiversity (Lust et al., 1998) and carbon storage (Seidl et al., 2008).

In Northern Europe, restoration of exotic conifer plantations has focussed on reintroducing natural forest structures, species and processes (Halme et al., 2013). Since the 1970s, the important role of disturbance in forest ecosystems has been recognised and many

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forest restoration techniques mimic natural disturbances such as fire and wind damage (e.g. Harmer et al., 2011, 2013). In addition, restoration can also retain features such as deadwood (Lindenmayer et al., 2012), rely on natural regeneration from the seedbank (Hirata et al., 2011) or on planting of native deciduous species (Truscott et al., 2004; Madsen and Löf, 2005; Wang et al., 2010). Where wood production remains important, efforts are being made to enhance the biodiversity of exotic conifer plantations, both by recognising their potential as habitat for understory species (e.g. bryophytes, Quine and Humphrey, 2010) and through management to resemble natural forest structure (Aubin et al., 2008).

The restoration of plantations on ancient woodland sites (PAWS) has become enshrined in UK forestry (Forestry Commission, 2011) and conservation policy (UK BAP, 1994) and through independent certification via the UK Woodland Assurance Standard (www.UKWAS.org.uk, §6.3 Conservation of semi-natural woodlands and plantations on ancient woodland sites).

The potential value of restoration is supported by the finding that ancient woodland features remain extant, if in poor condition, within most PAWS (Pryor et al., 2002), and therefore provide a practical basis for restoration (Thompson et al., 2003; Harmer et al., 2011). Several categories of features are recognised; ancient woods have distinctive assemblages of species (Peterken, 1974; Kimberley et al., 2013), habitat characteristics and cultural artefacts (The Woodland Trust, 2009); for example woodland specialist flora, old trees and associated dead wood communities – especially on sites with a history of wood pasture (Hodge and Peterken, 1998), woodland archaeology (Rackham, 2003), and distinctive soil profiles (Ball and Stevens, 1981).

Active restoration is necessary because of the slow rate at which natural succession changes plantation forests. In Spain, Onaindia et al. (2013) have found that natural succession without active silvicultural intervention resulted in very slow convergence in species composition between plantations and natural oak forest. They conclude that active management is needed to achieve ecological restoration objectives.

Any restoration project requires clear management objectives in order that progress can be monitored and lessons learned from successes and failures (Section 7: Society for Ecological Restoration International Science & Policy Working Group, 2004). Broadly speaking these should be twofold:

1. To remove or reduce factors which damage or destroy conservation values.
2. To protect and re-establish, through active management, values associated with an environment which have been damaged or lost.

In UK PAWS the primary factor damaging conservation values is typically the presence of an exotic conifer crop. A prominent strategy adopted in many early attempts at PAWS restoration in the UK is the clear-felling of the plantation crop, often with the objective of stopping its detrimental effects (including natural regeneration) and returning the site to native woodland as quickly as possible. Jonášová et al. (2006) report that the abundance of exotic conifer seedlings was lower, and that of natives species higher where there were gaps in the conifer canopy. In Britain native woodland is considered to be in a 'favourable condition' if the tree canopy comprises around 95% site-native species (JNCC, 2004). Clear-felling of exotic tree species therefore contributes to achieving national Biodiversity Action Plan targets.

However, clear-felling is believed by some to compromise the second important objective of restoration – namely the protection of remnant conservation values. Pryor et al. (2002) list 11 potential adverse effects of clear-felling which may result in the loss of remnant woodland flora of high conservation value. They recommend that rather than focussing on removing exotic tree species and restoring native woodland cover, a better overall aim would be to manipulate the canopy to create the conditions in which the remnant ancient woodland communities can recover. Gradual removal of exotic trees may, they claim, result in better survival and subsequent re-establishment of the woodland flora.

Despite more than a decade elapsing since this recommendation, there is still little detailed analysis of when and where a gradual approach to exotic crop removal might result in better conservation outcomes. In this paper we describe the impacts of clear-felling and gradual approaches on the ground flora of 39 PAW sites undergoing restoration across Britain.

2. Methods

2.1. Field survey

Our analyses are based on data collected during two separate surveys of thirty-nine woodlands situated throughout England, Wales, and Scotland, the first in 2001 and the second eight years later. All of our study sites were owned by the Woodland Trust (www.woodlandtrust.org.uk), a UK-based woodland conservation charity. The Trust does not manage its sites specifically for production but has acquired many woodlands which were managed for production in the past and which contain PAW stands. The Trust is committed to their restoration and has used both clear-felling and more gradual approaches. Our 39 study sites were selected to include the range of altitudes, soil types and plantation crop species found nationally. Eighty-eight PAWS stands were surveyed in total in these sites. Of these, 43 were lowland, and 45 were upland/upland fringe (18 and 27 sites respectively). Thirty-four were recorded as having acid soils and fifty-four base rich or mesotrophic. Fig. 1 shows the breakdown of plantation species found on the stands. Our study sites include all of the common conifer species found on PAWS in the UK (Pryor and Smith, 2002), but not in proportion to their national abundance. Appendix 1 provides a full list of sites and stands, detailing Ordnance Survey Grid References, altitude, crop species, and management status.

A vigorous restoration programme by the Woodland Trust meant that by the time of our second survey in 2009 only three of our original stands retained their complete plantation cover. Twenty-two stands had been clear-felled; three of these after

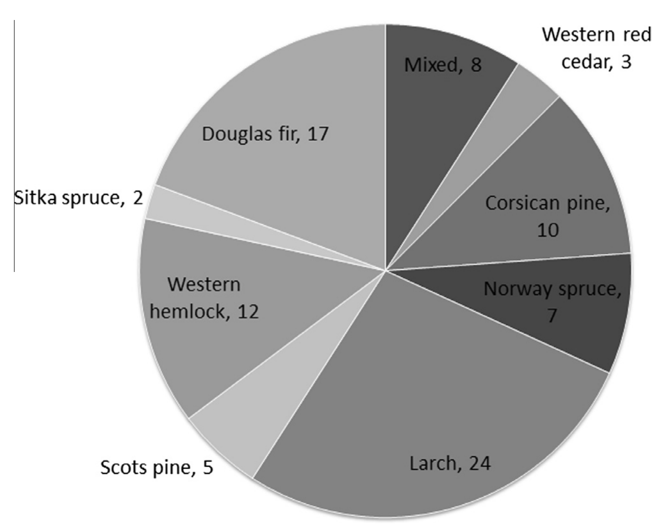

Fig. 1. Plantation crop species found in 88 PAWS stands surveyed in this study.

2001, and nineteen before 2001. A further twelve sites had been heavily thinned, six before and six after 2001. A more gradual, thinning approach had been taken on fifty-one sites, twenty-nine before the first survey in 2001, and twenty-two between the two surveys.

Sites were surveyed in spring/early summer on both occasions. Work began in the southwest of the country (Cornwall) and progressed northwards in order to ensure that as many species as possible were in flower at the time of the survey. A range of ecological and site variables were recorded, and these are detailed below.

The purpose of the original survey in 2001 was to establish whether or not 'ancient woodland features' (including flora, dead wood, old trees, epiphyte communities, and archaeological features) remained extant in PAWS, and so the methods used were designed to gather information rapidly across a large number of sites and locations. Each PAW stand was carefully searched and the identities and abundance of all plant species recorded. Abundance was judged using the systematic DAFOR scale (classing species as Dominant, Abundant, Frequent, Occasional, Rare; see (Kent and Coker, 1992). Forest mensuration and silvicultural data were also collected, including basal area measurements, crop species, and management status.

The repeat survey in 2009 used the same methods but with a number of systematic additions. We were aware of the need to ensure consistency of approach, particularly in the scoring of vegetation abundance. The principal field researcher (Curtis) who undertook the 2001 survey trained the 2009 field researcher (Adams) and assisted in the resurvey of the first six stands. A more detailed inspection was carried out of four 2 m $\times$ 2 m quadrats randomly located in each stand. This increased the chance that we would find cryptic species that might otherwise have been hidden beneath taller vegetation and allowed more objective quantification of abundance. It gave us greater confidence in concluding that species present in 2001 had disappeared or had substantially declined in abundance. It will also provide a more robust sampling framework for assessing future changes. Voucher specimens of hard-to-identify species were collected and brought back to the Oxford University Herbarium for expert identification and to serve as a reference collection during the field work. A full list of species is given in Appendix 2 which also gives details of their ecology.

The canopy cover in each stand was estimated from an average of four measurements per stand, one in the centre of each flora quadrat, made using a canopy-scope (Brown et al., 2000). Canopy cover was measured at head-height and therefore reflects the cover of residual plantation crop trees, veteran trees and any regeneration which had grown taller than 2.0 m. Estimates of basal area were also made from the same four points per stand using a simple (basal area factor 5) angle gauge.

We used the Met Office UKCP09 5 km^2 gridded annual data sets in order to compute average rainfall, maximum number of consecutive dry days and the number of growing degree days for each site for the period 2001–2006. There is likely to be significant topography-related variation in rainfall within these 5 km^2 areas which may mean that these figures do not accurately represent the climate in our plots. We downloaded 5 km^2 gridded data on total Nitrogen deposition from the Centre for Ecology and Hydrology Pollutant Deposition website (http://www.uk-pollutantdeposition.ceh.ac.uk accessed November 2009) in order to calculate average values for each site for the period 2004–2006.

2.2. Analysis

Two methodological challenges were presented by the nature of the research question and the data available. These were (a) dealing with differences in the way that initial and repeat surveys were carried out, and (b) selecting plant species that are largely restricted to woodland habitat. These challenges, and the solutions applied in our analysis, are explained below.

2.2.1. Dealing with differences in survey execution

The resurvey was carried out eight years after the initial survey and by a different field researcher. It was therefore necessary to make provision for practitioner and seasonal differences affecting the recording of the abundance of plant species. As far as reasonably possible we carried out surveys around the same date in 2009 as they were done in 2001. We deliberately over-compensated in our field surveys in 2009, by adding in detailed quadrat samples, and then focused in our analysis on either losses or significant declines in the abundance of species in 2009 compared to 2001. We are confident that our more meticulous survey in 2009 is unlikely to have overlooked species that were frequent in 2001. We have not examined species gains or small changes in abundance because we cannot be wholly confident that plants were not overlooked in the 2001 survey. This sets a deliberately high bar for any signal of a change or differential change in species composition.

2.2.2. Selecting "woodland" plant species

The purpose of our research is to explore the outcomes of different restoration treatments on the survival of a characteristic woodland flora. We therefore need to distinguish woodland species from species that are not specifically associated with ancient woods. We took the following approach (see also the species lists in Appendix 2).

One hundred and eighty of the 224 species of vascular plant identified during this survey were classified as 'generalists' because they are recorded as occurring (with a frequency > 20%) in both woodland and other community types in the National Vegetation Classification (Rodwell, 1991). This group included coarse weeds such as *Urtica dioica* and *Chamerion angustifolium*, invasive species such as *Impatiens glandulifera*, and species characteristic of open habitats such as *Festuca ovina* and *Silene vulgaris*.

The remaining 44 species were classified as "woodland specialists". These were species recorded in the NVC as occurring (with a frequency > 20%) in woodland communities alone.

In addition, we noted whether our species had been identified as "ancient woodland indicators species" (AWIs) in Kirby et al. (2006). This study compiled data from twelve lists of ancient woodland vascular plants suggested for different parts of Britain, totalling 158 ground flora species, excluding trees and shrubs.

2.3. Data analysis

In our analysis we have sought first, to discover whether there is a relationship between the flora of PAWS sites and their environment following restoration, and then to identify those management or environmental factors that are associated with significant loss of woodland species in our study sites over an eight year period.

For the first analysis we have used the detailed floral inventory and environmental measures made in 2009 to carry out a canonical correspondence analysis (CCA, ter Braak and Verdonschot, 1995) a multivariate ordination method, which extracts environmental gradients from the data and uses them to examine the relative similarity of species and species assemblages. We judged CCA to be a more appropriate method of ordination than indirect ordination methods because our objective was to describe how species respond to particular sets of observed environmental variables rather than to explore community structure. Initially, all environmental variables were included in the analysis. We included the eight most common of the ten plantation tree species we recorded, as separate binary dummy environmental variables. Two, Japanese

Larch (*Larix kaempferi* (Lamb.) Carrière) and Western Red Cedar (*Thuja plicata* Donn ex D.Don.) were excluded to avoid the environmental variables becoming linear combinations of each other. Nevertheless, there was still a significant problem of multicollinearity among the environmental variables. We used variance inflation factors to assist in selecting variables to remove from the analysis and redundancy analysis to identify those environmental variables that contributed most to the variability of the plant species assemblages and hence should be included in the analysis. The final analysis included four environmental variables, basal area, canopy scope, crop species and mean annual rainfall.

In order to identify those management or environmental factors associated with substantial loss of woodland species, we used both the number of woodland specialist species and the number of AWI species that had declined in abundance by more than two abundance categories (scored on the DAFOR scale) between 2001 and 2009 per site as the response variables in separate general linear models. Twelve explanatory variables were tested (Table 1). The original number of woodland specialist or AWI species present in 2001, was included in all models in order to allow the effect of initial differences in species richness to be statistically eliminated. The number of ruderal (*R*) or competitive species *sensu* (Grime, 1974) that had increased by more than two abundance categories between 2001 and 2009 was used as a variable in order to find out whether competition from these species contributed to woodland specialist species decline.

We used only those stands treated between the 2001 and 2009 surveys (post-2001) for this analysis as we have no record of how many or which species had been lost from plots treated prior to our first survey.

We used a general linear model to examine the relationship between loss of AWIs and woodland specialists and ecological and environmental variables. Thirty-two different models were tested using up to five parameters. The modified form of Akaike's Information Criterion (AICc) for small sample sizes and least-squares models was used to select the most parsimonious model from amongst them. It is based on the least-squares model fit with a penalty term that measures the degree to which the complexity of the model leads to over-fitting (and thus an inflated R^2 value).

$$AIC_c = n.\ln(\hat{\sigma}^2) + 2K\frac{2K(K+1)}{n-(K-1)}$$

where n is the sample size, K is the number of parameters in the model and $\hat{\sigma}^2$ is (residual sum of squares/n).

3. Results

Fig. 2 shows the breakdown of vascular plant species identified in our study by habitat association. It is worthy of note that of the

Table 1
Environmental variables.

Description	Name
Site	Site
Stand (within a site)	Stand
Number of woodland specialist species present in 2001	W2001
Annual mean rainfall (mm), 2005–9	PPN
Annual mean growing degree days, 2005–9	GrowDD
Altitude (m)	Alt
Canopy scope score	Canopy
Basal area (m^2/ha)	BA
Management (control, thinned, clear-fell)	Management
Nitrogen deposition (kg N ha^{-1} y^{-1})	Nitrogen
PAWS crop tree species	Species
Plantation crop age (years)	Crop Age

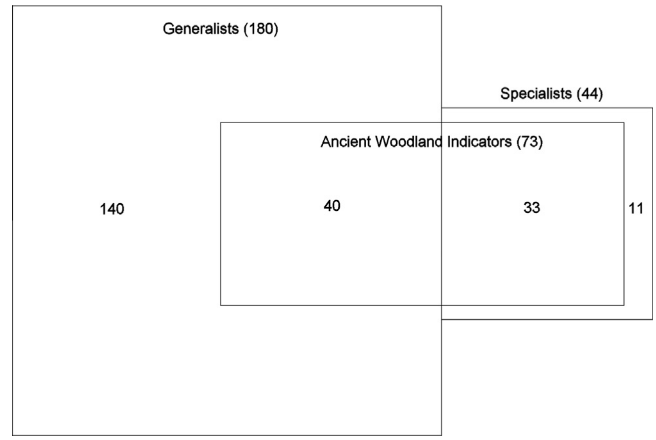

Fig. 2. Distribution of plant species identified in our study by habitat association. Woodland specialist species (Specialists) occur (with a frequency > 20%) in woodland communities alone in the National Vegetation Classification (Rodwell, 1991). Generalist species occur in woodland and other types of habitat. The ancient woodland indicator species (AWI) category includes both generalists and specialists and is defined according to Kirby et al. (2006).

73 species of ancient woodland indicator species found, only 33 were classified as woodland specialists. This reinforces the conclusion that many AWIs are, in reality, indicators of long habitat persistence (or ecological continuity *sensu* Nordén and Appelqvist (2001)). Trait analysis of British AWIs reveals that poor dispersal resulting in low colonising ability may be responsible for their absence from secondary woodlands and presence in long undisturbed non-woodland habitat (Kimberley et al., 2013). Fig. 3 shows the distribution across Ellenberg light values (Ellenberg et al., 1991) of plant species in our three ecological categories (as determined for the British flora by Hill et al., 1999). It is clear that the woodland specialist group contains species which are more shade tolerant than AWI and generalist plants.

In more than half of the PAW stands that we surveyed in this study we found only two or fewer species of woodland specialist plant. However, half of the stands had six or more AWI species and one stand had twenty AWI species and ten woodland specialist species. Only four stands had no AWI or woodland specialist plants. It is possible that since all of our sites were found within Woodland Trust reserves they may have had greater richness of woodland species than PAWS stands in general in the UK. Nevertheless, our surveys confirm that there are a large number of woodland specialist and AWI plants to be found in PAWS stands and that their protection should be a conservation priority.

3.1. Canonical correspondence analysis

A multiple correlation species/environment score of 0.904 for this ordination indicates that a high proportion of the variation in species composition between our sites is explicable by the environmental variables. A Monte Carlo test (with 1000 replicates) shows that the amount of variability explained by the environmental variables is significant for the first three canonical axes ($p < 0.05$). The primary axis of this ordination was strongly correlated with basal area and canopy openness whilst Axis 2 is correlated with altitude and rainfall. The latter should be of no surprise since it is well-known that there is a strong NW-SE gradient in plant species composition in Britain (Hill, 1991) driven largely by climate and altitude. Forest light environment would seem to be a major determinant of plant community composition, once countrywide variation in rainfall and regional variation in soil acidity have been taken into account. The ordination diagram

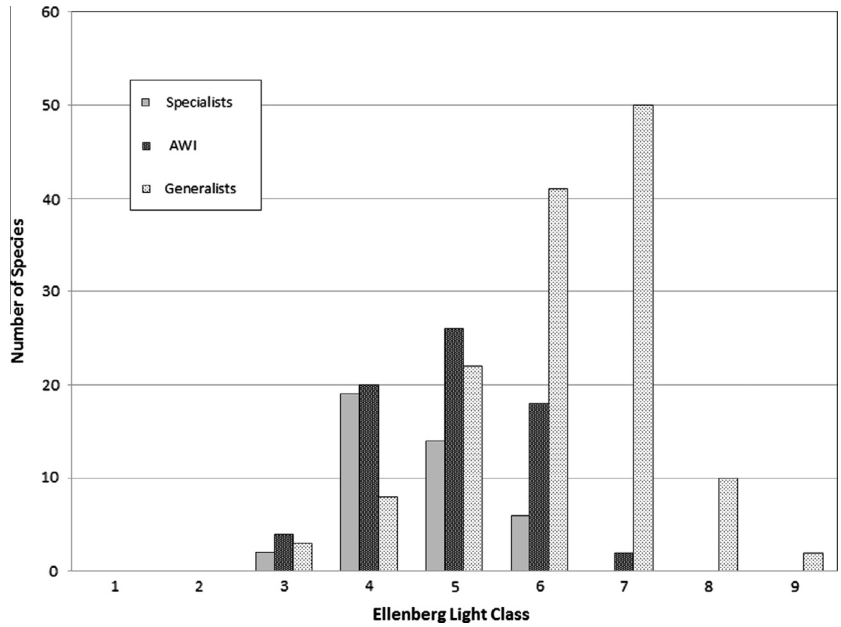

Fig. 3. Distribution of species across Ellenberg light classes (Ellenberg et al., 1991) in three ecological categories, woodland specialists, ancient woodland indicator species and generalists.

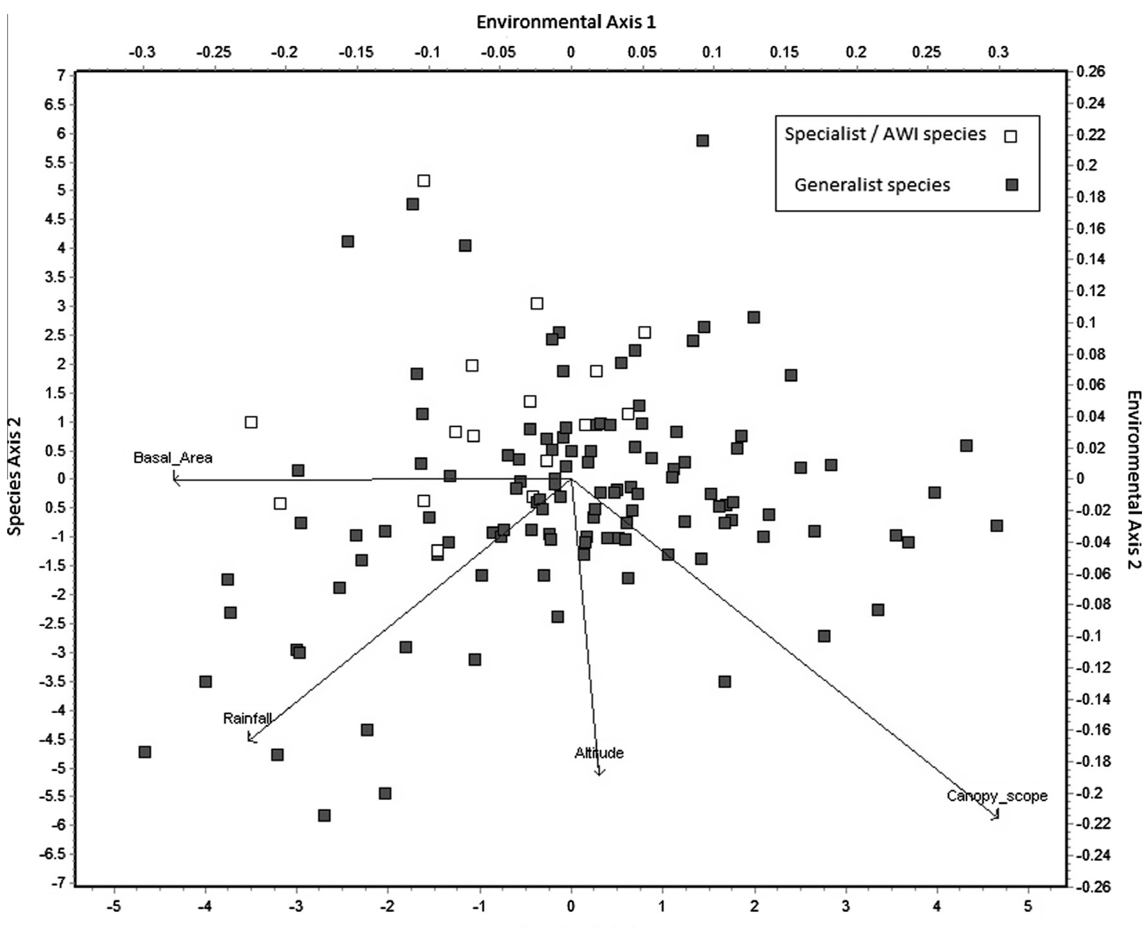

Fig. 4. Species ordination by canonical correspondence analysis using floristic and environmental data from the 2009 survey of PAWS stands.

(Fig. 4) shows that most woodland specialist species are associated with environments with a high basal area and low canopy openness. It is also noteworthy that relatively few woodland specialist and AWI species have low loadings on Axis 1 or high loadings on Axis 2, indicating that, in the main, our wetter, upland PAWS sites lacked these species.

3.2. Loss of species in treated plots

These data allow comparison of the flora of unrestored PAWS stands with that following the removal of some or all of their exotic tree crop. Almost all stands lost species regardless of the type of treatment. There were very few species gains, and those that we recorded comprised rare or occasional plants that we could not be confident had not been overlooked during the 2001 survey.

Two significant models were found explaining decline in woodland specialists and the most parsimonious model (adjusted $R^2 = 65\%$) was:

Woodland specialist loss = Woodland specialists 2001 + Canopy Scope 2009.

The coefficient for Canopy Scope 2009 was positive implying that the more open the site the greater the loss of woodland specialist species had been. None of the other ecological, environmental or treatment variables accounted for significant variation in woodland specialist species decline, once initial differences between stands in woodland specialist species richness had been taken into account.

Only one significant model was found explaining loss of AWI species:

$$\text{AWI loss} = \text{AWI 2001}$$

This model suggests that those sites with a greater initial richness of AWI species were likely to lose more after treatment. None of the other variables tested accounted for significant variation in AWI species loss.

Although, because of the nature of the initial survey of our PAWS, we are cautious about drawing conclusions about increases in species abundance, some species showed consistent and substantial increases in those plots that had been clear-felled. These included the tree species *Fraxinus excelsior* and *Crataegus monogyna*, shrubs including *Cytisus scoparius*, *Ulex europaeus* and *Erica cinerea*, and some generalist grasses, rushes and sedges.

4. Discussion

This study set out to explore forest restoration objectives by investigating whether the twin aims of conifer removal and the conservation of ancient woodland associated flora communities are complementary or in conflict.

Often a degraded habitat will have a number of potential values worthy of restoration and the approach taken will depend on those which are ranked most highly. For example, PAWS may offer potential biodiversity, aesthetic, habitat, heritage and recreational benefits. Not all of these will be present or of equal value in all PAWS. Woods vary hugely, and some are much more valuable and sensitive than others. Management guidelines which propose a one-size-fits-all approach to restoration risk compromising the different values of individual sites. A key component of any restoration plan should therefore be an initial condition assessment in which irreplaceable features and characteristics of high conservation value are identified (Section 8: Society for Ecological Restoration International Science & Policy Working Group, 2004).

Our first finding is that not all PAWS have many woodland specialist or AWI species. Fewer than three woodland specialist species were found in half of the stands surveyed. These stands may well have a number of other potential values worthy of restoration, for example the preservation of old trees and dead wood habitat, and development of a restoration plan for sites such as these might well give greater priority to the protection or enhancement of these values. Clear-felling might well be a sensible restoration strategy for stands with a low diversity of woodland specialist species provided that it can be done in a way which minimises site disruption.

We found that woodland specialist species were most commonly found in PAWS with a high basal area and low canopy openness and were less common in open, acidic and wetter sites. It is perhaps unsurprising that these highly shade-tolerant plants have survived best in an environment where they may avoid competition from faster-growing, light-dependent species.

Acidic, wetter sites were more common in the upland areas of Britain included in our survey. These may also be sites where wind-throw, access and landscaping issues may suggest that a clear-felling strategy may be desirable. However, in our experience other conservation values can be vulnerable to the impact of clear-felling in these locations. For example, remnant veteran trees, which have developed a tall narrow crown as a result of lateral competition from a plantation crop, can be very vulnerable to wind-throw (Read, 2000; Urata et al., 2012; Pretzsch, 2014).

Our second important finding is that the loss of woodland specialist species is associated with higher levels of canopy opening during restoration. This general finding is in accordance with expectations, given the functional characteristics of woodland specialists. Those plants which have survived for long periods in deep understory shade typically have a suite of traits that adapt them to maximise light interception and utilisation. These traits often make such plants vulnerable to light and heat stress effects if the canopy is suddenly removed. We found that the understorey community of woodland specialist species was not resilient to complete removal of the tree canopy. It is likely that some of these species could continue to survive for many years in PAWS without active intervention. Our results indicate that where restoration is desirable it should be done gradually in order not to lose these valuable shade-loving species. Nevertheless, we found no evidence that as a group, ancient woodland indicator species suffered higher than average mortality when the exotic tree canopy was completely removed.

Similar results have been found elsewhere. The effects of four different methods of removing an invasive conifer crop on subsequent vegetation succession were examined at conservation sites in South Island, New Zealand (Paul and Ledgard, 2009). The study found that although clear-felling created a flush of vigorous plant growth, this was not long-lasting, and the end result was reduced plant biodiversity. Better results were obtained when trees were killed with herbicide and left standing, leading to progressive changes in the light and moisture environment.

Our study considers only the impacts on plants. A large part of forest biodiversity is the invertebrate and microbial communities; there is little evidence of the impacts of different restoration strategies on these groups.

In some situations clear-felling may have advantages:

- In those sites where there is a high likelihood of a native canopy being established rapidly through natural regeneration open conditions can encourage strong seedling growth (Harmer et al., 2012; Spracklen et al., 2013).
- Clear-felling may be the only practical approach in areas prone to wind throw, where there are access issues or where a good return from timber sales is necessary in order to support management.

- Intrusive exotic plantations have detracted from the sense of place and cultural identity in some locations. Their complete removal is important for aesthetic reasons.

However, taken as a whole our results suggest that as woodland specialists and AWI plants are found in PAWS, and these are a conservation priority, at the very least an important part of the ancient woodland flora community would be better served by a restoration approach that is focused less on conifer removal and more on the moderation of light and shade levels. This is an important finding for PAWS management, because it supports the case for gradual restoration as a default approach for those stands that have remnant populations of woodland specialist species. Our work emphasises the importance of an initial condition assessment in which irreplaceable features and characteristics of high conservation value are identified and prioritised.

Our study is also instructive for other restoration situations, because it highlights the potential for conflicts between seemingly complementary restoration objectives. In this case it shows how an arguably 'purist' definition of restoration, which focuses on returning site conditions to an 'original' state, may in fact damage some of the most valuable and characteristic components of the system in question. We share the view of Paul and Ledgard (2009) that when assessing the restoration of an ecosystem dominated by an alien species, the impact of the control operations on the affected ecosystem, particularly the associated vegetation successions, needs to be carefully considered.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2015.03.030.

References

Aubin, I., Messier, C., Bouchard, A., 2008. Can plantations develop understory biological and physical attributes of naturally regenerated forests? Biol. Conserv. 141, 2461–2476, <http://dx.doi.org/10.1016/j.biocon.2008.07.007>.

Ball, D.F., Stevens, P.A., 1981. The role of 'ancient' woodlands in conserving 'undisturbed' soils in Britain. Biol. Conserv. 19, 163–176, <https://dx.doi.org/10.1016/0006-3207(81)90032-X>.

Boucher, Y., Arseneault, D., Sirois, L., 2009. Logging history (1820–2000) of a heavily exploited southern boreal forest landscape: insights from sunken logs and forestry maps. For. Ecol. Manage. 258, 1359–1368, <http://dx.doi.org/10.1016/j.foreco.2009.06.037>.

Brown, N., Jennings, S., Wheeler, P., Nabe-Nielsen, J., 2000. An improved method for the rapid assessment of forest understorey light environments. J. Appl. Ecol. 37, 1044–1053, <https://dx.doi.org/10.1046/j.1365-2664.2000.00573.x>.

Buckley, Y.M., Brockerhoff, E., Langer, L., Ledgard, N., North, H., Rees, M., 2005. Slowing down a pine invasion despite uncertainty in demography and dispersal. J. Appl. Ecol. 42, 1020–1030. http://dx.doi.org/10.1111/j.1365-2664.2005.01100.x.

Cruickshank, M.G., Morrison, D.J., Lalumière, A., 2009. The interaction between competition in interior Douglas-fir plantations and disease caused by *Armillaria ostoyae* in British Columbia. For. Ecol. Manage. 257, 443–452, <http://dx.doi.org/10.1016/j.foreco.2008.09.013>.

Degrave, F., Malchair, S., De Schrijver, A., Geudens, G., Gielis, L., Staelens, J., Carnol, M., Lust, N., Verheyen, K., Van De Steene, K., Van Herzele, A., Vandaele, L., Hens, L., Schram, A., Verbeke, T., Bouma, J.J., 2006. Feasibility of forest conversion: ecological, social and economic aspects (FEFOCON): Final Report of the PODOII program. Scientific Support Plan for a Sustainable Development Policy (SPSD II). Belgian Science Policy, p. 93 pages.

Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W., 1991. Zeigerwerte von Pflanzen in Mitteleuropa. Scripta Geobotanica 18, 1–248.

Felton, A., Lindbladh, M., Brunet, J., Fritz, Ö., 2010. Replacing coniferous monocultures with mixed-species production stands: an assessment of the potential benefits for forest biodiversity in northern Europe. For. Ecol. Manage. 260, 939–947, <http://dx.doi.org/10.1016/j.foreco.2010.06.011>.

Forestry Commission, 2011. The UK Forestry Standard. Forestry Commission, Edinburgh.

Garfitt, J.E., 1953. The rehabilitation of devastated woodlands. Forestry 26, 28–32, <http://dx.doi.org/10.1093/forestry/26.1.28>.

Halme, P., Allen, K.A., Auniņš, A., Bradshaw, R.H.W., Brūmelis, G., Čada, V., Clear, J.L., Eriksson, A.-M., Hannon, G., Hyvärinen, E., Ikauniece, S., Iršėnaitė, R., Jonsson, B.G., Junninen, K., Kareksela, S., Komonen, A., Kotiaho, J.S., Kouki, J., Kuuluvainen, T., Mazziotta, A., Mönkkönen, M., Nyholm, K., Oldén, A., Shorohova, E., Strange, N., Toivanen, T., Vanha-Majamaa, I., Wallenius, T., Ylisirniö, A.-L., Zin, E., 2013. Challenges of ecological restoration: lessons from forests in northern Europe. Biol. Conserv. 167, 248–256, <http://dx.doi.org/10.1016/j.biocon.2013.08.029>.

Harmer, R., Morgan, G., Beauchamp, K., 2011. Restocking with broadleaved species during the conversion of *Tsuga heterophylla* plantations to native woodland using natural regeneration. Eur. J. Forest Res. 130, 161–171, <https://dx.doi.org/10.1007/s10342-010-0418-8>.

Harmer, R., Kiewitt, A., Morgan, G., 2012. Effects of overstorey retention on ash regeneration and bramble growth during conversion of a pine plantation to native broadleaved woodland. Eur. J. Forest Res. 131, 1833–1843, <https://dx.doi.org/10.1007/s10342-012-0636-3>.

Hickler, T., Vohland, K., Feehan, J., Miller, P.A., Smith, B., Costa, L., Giesecke, T., Fronzek, S., Carter, T.R., Cramer, W., Kühn, I., Sykes, M.T., 2012. Projecting the future distribution of European potential natural vegetation zones with a generalized, tree species-based dynamic vegetation model. Glob. Ecol. Biogeogr. 21, 50–63. http://dx.doi.org/10.1111/j.1466-8238.2010.00613.x.

Hill, M.O., 1991. Patterns of species distribution in Britain elucidated by canonical correspondence analysis. J. Biogeogr. 18, 247–255, <https://dx.doi.org/10.2307/2845395>.

Hill, M.O., Mountford, J.O., Roy, D.B., Bunce, R.G.H., 1999. ECOFACT 2a Technical Annex – Ellenberg's indicator values for British Plants. Institute of Terrestrial Ecology, Huntingdon, p. 46.

Hirata, A., Sakai, T., Takahashi, K., Sato, T., Tanouchi, H., Sugita, H., Tanaka, H., 2011. Effects of management, environment and landscape conditions on establishment of hardwood seedlings and saplings in central Japanese coniferous plantations. For. Ecol. Manage. 262, 1280–1288, <http://dx.doi.org/10.1016/j.foreco.2011.06.025>.

Hodge, S.J., Peterken, G.F., 1998. Deadwood in British forests: priorities and a strategy. Forestry 71, 99–112, <https://dx.doi.org/10.1093/forestry/71.2.99>.

JNCC, 2004. Common Standards Monitoring Guidance for Woodland. Joint Nature Conservation Committee.

Jonášová, M., van Hees, A., Prach, K., 2006. Rehabilitation of monotonous exotic coniferous plantations: a case study of spontaneous establishment of different tree species. Ecol. Eng. 28, 141–148, <http://dx.doi.org/10.1016/j.ecoleng.2006.05.008>.

Kenk, G., Guehne, S., 2001. Management of transformation in central Europe. For. Ecol. Manage. 151, 107–119, <http://dx.doi.org/10.1016/S0378-1127(00)00701-5>.

Kent, M., Coker, P., 1992. Vegetation Description and Analysis. John Wiley & Sons, Chichester, UK.

Kimberley, A., Blackburn, G.A., Whyatt, J.D., Kirby, K., Smart, S.M., Hermy, M., 2013. Identifying the trait syndromes of conservation indicator species: how distinct are British ancient woodland indicator plants from other woodland species. Appl. Veg. Sci. 16, 667–675, <https://dx.doi.org/10.1111/avsc.12047>.

Kirby, K.J., Pyatt, D.G., Rodwell, J., 2006. Characterization of the woodland flora and woodland communities in Britain using Ellenberg values and functional analysis. In: Working and Walking in the Footsteps of Ghosts. Wildtrack Publishing, Sheffield Hallam University, UK.

Laarmann, D., Korjus, H., Sims, A., Kangur, A., Stanturf, J.A., 2013. Initial effects of restoring natural forest structures in Estonia. For. Ecol. Manage. 304, 303–311, <http://dx.doi.org/10.1016/j.foreco.2013.05.022>.

Lindenmayer, D.B., Franklin, J.F., Lõhmus, A., Baker, S.C., Bauhus, J., Beese, W., Brodie, A., Kiehl, B., Kouki, J., Pastur, G.M., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., Volney, J., Wayne, A., Gustafsson, L., 2012. A major shift to the retention approach for forestry can help resolve some global forest sustainability issues. Conserv. Lett. 5, 421–431. http://dx.doi.org/10.1111/j.1755-263X.2012.00257.x.

Lust, N., Muys, B., Nachtergale, L., 1998. Increase of biodiversity in homogeneous Scots pine stands by an ecologically diversified management. Biodivers. Conserv. 7, 249–260, <https://dx.doi.org/10.1023/a:1008892620387>.

Madsen, P., Löf, M., 2005. Reforestation in southern Scandinavia using direct seeding of oak (*Quercus robur* L.). Forestry 78, 55–64. http://dx.doi.org/10.1093/forestry/cpi005.

Mason, W.L., Quine, C.P., 1995. Silvicultural possibilities for increasing structural diversity in British spruce forests: the case of Kielder Forest. For. Ecol. Manage. 79, 13–28, <http://dx.doi.org/10.1016/0378-1127(95)03618-0>.

Nordén, B., Appelqvist, T., 2001. Conceptual problems of ecological continuity and its bioindicators. Biodivers. Conserv. 10, 779–791, <https://dx.doi.org/10.1023/a:1016675103935>.

Onaindia, M., Ametzaga-Arregi, I., San Sebastián, M., Mitxelena, A., Rodríguez-Loinaz, G., Peña, L., Alday, J.G., 2013. Can understorey native woodland plant species regenerate under exotic pine plantations using natural succession? For. Ecol. Manage. 308, 136–144, <http://dx.doi.org/10.1016/j.foreco.2013.07.046>.

Paul, T.S.H., Ledgard, N.J., 2009. Vegetation succession associated with wilding conifer removal. New Zealand Plant Prot. 62, 374–379.

Peterken, G.F., 1974. A method for assessing woodland flora for conservation using indicator species. Biol. Conserv. 6, 239–245, <https://dx.doi.org/10.1016/0006-3207(74)90001-9>.

Peterken, G., 1996. Natural Woodland: Ecology and Conservation in Northern Temperate Regions. Cambridge University Press, Cambridge.

Pretzsch, H., 2014. Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures. For. Ecol. Manage. 327, 251–264, <http://dx.doi.org/10.1016/j.foreco.2014.04.027>.

Pryor, S., Smith, S., 2002. The Area and Composition of Plantations on Ancient Woodland Sites. The Woodland Trust, Grantham, UK, p. 51.

Pryor, S.N., Curtis, T.A., Peterkin, G.F., 2002. Restoring Plantations on Ancient Woodland Sites. The Woodland Trust, Grantham, UK.

Quine, C., Humphrey, J., 2010. Plantations of exotic tree species in Britain: irrelevant for biodiversity or novel habitat for native species? Biodivers. Conserv. 19, 1503–1512. http://dx.doi.org/10.1007/s10531-009-9771-7.

Rackham, O., 2003. Ancient Woodland. Castlepoint Press, Colvend.

Read, H.J., 2000. Veteran Trees: A Guide to Good Management (IN13). English Nature, Peterborough.

Rodwell, J. (Ed.), 1991. British Plant Communities Volume 1: Woodlands and Scrub. Cambridge University Press, Cambridge.

Seidl, R., Rammer, W., Lasch, P., Badeck, F.W., Lexer, M.J., 2008. Does conversion of even-aged, secondary coniferous forests affect carbon sequestration? A simulation study under changing environmental conditions. Silva Fennica 42, 369–386.

Smith, S., Gilbert, J., 2003. National Inventory of Woodland and Trees: Great Britain. Forestry Commission, Edinburgh.

Society for Ecological Restoration International Science & Policy Working Group, 2004. The SER International Primer on Ecological Restoration. Society for Ecological Restoration International, www.ser.org & Tucson.

Spiecker, H., Hansen, J., Klimo, E., Skovsgaard, J., Sterba, H., von Teuffel, K. (Eds.), 2004. Norway spruce conversion-options and consequences. Brill, Leiden.

Spracklen, B.D., Lane, J.V., Spracklen, D.V., Williams, N., Kunin, W.E., 2013. Regeneration of native broadleaved species on clearfelled conifer plantations in upland Britain. For. Ecol. Manage. 310, 204–212, <http://dx.doi.org/10.1016/j.foreco.2013.08.001>.

ter Braak, C.J.F., Verdonschot, P.F.M., 1995. Canonical correspondence analysis and related multivariate methods in aquatic ecology. Aquat. Sci. 57, 255–289.

The Woodland Trust, 2009. Ancient woods: a guide for woodland owners and managers (www.woodlandtrust.org/publications), Grantham, UK.

Thompson, R., Humphrey, J., Harmer, R., Ferris, R., 2003. Restoration of Native Woodland on Ancient Woodland Sites. Practice Guide. Forestry Commission, Edinburgh.

Truscott, A.M., Mitchell, R.J., Palmer, S.C.F., Welch, D., 2004. The expansion of native oakwoods into conifer cleared areas through planting. For. Ecol. Manage. 193, 335–343, <http://dx.doi.org/10.1016/j.foreco.2004.01.047>.

Turner, J., Gessel, S., Lambert, M., 1999. Sustainable management of native and exotic plantations in Australia. New Forest. 18, 17–32. http://dx.doi.org/10.1023/A:1006545722281.

UK BAP, 1994. Biodiversity: the UK Action Plan. HMSO, London.

Urata, T., Shibuya, M., Koizumi, A., Torita, H., Cha, J., 2012. Both stem and crown mass affect tree resistance to uprooting. J. For. Res. 17, 65–71. http://dx.doi.org/10.1007/s10310-011-0249-6.

Wang, J., Li, D., Ren, H., Yang, L., 2010. Seed supply and the regeneration potential for plantations and shrubland in southern China. For. Ecol. Manage. 259, 2390–2398, <http://dx.doi.org/10.1016/j.foreco.2010.03.015>.

Yamagawa, H., Ito, S., Nakao, T., 2010. Restoration of semi-natural forest after clearcutting of conifer plantations in Japan. Landscape Ecol. Eng. 6, 109–117, <https://dx.doi.org/10.1007/s11355-009-0088-1>.

Zerbe, S., 2002. Restoration of natural broad-leaved woodland in Central Europe on sites with coniferous forest plantations. For. Ecol. Manage. 167, 27–42, <https://dx.doi.org/10.1016/S0378-1127(01)00686-7>.