A comparison of clearfelling and gradual thinning of plantations for the restoration of insect herbivores and woodland plants

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Summary

1. Testing restoration methods is essential for the development of restoration ecology as a science. It is also important to monitor a range of taxa, not just plants which have been the traditional focus of restoration ecology. Here we compare the effects on ground flora and leaf-miners, of two restoration practices used when restoring conifer plantations.

2. Two methods of restoration were investigated: clearfelling of plantations and the gradual thinning of conifers over time. Unrestored plantations and native broadleaved woodlands were also surveyed, these representing the starting point of restoration and the reference community respectively. The study sites consist of two forest types (acidic *Quercus* woodland and mesotrophic *Fraxinus* woodland) enabling us to compare the two restoration methods in different habitat types. We use a well-replicated, large-scale study system consisting of 32 woodland plots, each 2 ha in size.

3. There were 179 plant species identified in the plots. Clearfelled plots had greater overall ground flora species richness than other management regimes (thinned, unrestored plantation and native woodland), but the richness of woodland plant species did not differ between clearfelled, thinned, native woodland and unrestored plantation plots.

4. More than 10,000 leaf-miners comprising 122 species were collected. An increased plant species richness was associated with increased leaf-miner species richness under all management regimes except clearfelled plots.

5. Forest type did not affect the response to restoration method, i.e. there was no interaction between management regime and forest type for any of the variables measured.

6. ***Synthesis and applications.*** Both the clearfelling and gradual thinning approaches to plantation restoration maintained the woodland species in the ground flora of plantations. However, these restoration methods differed in their effects on the leaf-miner – plant species richness relationship. It is often assumed that during restoration increases in plant-species richness lead to increases invertebrate herbivore richness, but this was not the case on clearfelled sites. This study demonstrates the importance of testing and comparing restoration methods, and monitoring invertebrates as well as plants during restoration.

Keywords

Ancient woodland, ground flora, herbaceous layer, herbivore community, leaf-miners, PAWS, plant community, plantation management, species richness

Introduction

Ecological restoration is essential for creating resilient ecological networks, ensuring sustainable provision of ecosystem services, and conserving threatened species and habitats (Young 2000; Hobbs & Harris 2001; Lawton *et al*. 2010). The restoration of degraded forests is taking place across the globe, and although forests vary in structure and species composition, similar methods are used for forest restoration worldwide (Stanturf, Palik & Dumroese 2014). In Britain the restoration of native woodland from plantations on ancient woodland sites has received increasing attention (Pryor, Curtis & Peterken 2002; Thompson *et al.* 2003; Harmer & Thompson 2013). Ancient woodland sites have had no other land use since at least1600AD in England and Wales, or 1750AD in Scotland (Peterken 1977)). Native forests on ancient woodland sites are important habitats for many rare and threatened species (Peterken 1993), but between the 1930's and 1990's 40% of the remaining such woodlands in Britain were converted to plantations, mostly of non-native conifers (Spencer & Kirby 1992; Pryor & Smith 2002). Due to the increased recognition of the value of native woodland it is now policy to restore these plantations (Harmer, Kerr & Thompson 2010). Despite being greatly changed from native woodland, they often retain features such as veteran trees, coppice stools and remnant ground flora (Pryor, Curtis & Peterken 2002), making them good candidates for the successful restoration of native forest.

Degraded forests can be restored through clearfelling of the existing canopy, or by removing trees over an extended period of time (Stanturf, Palik & Dumroese 2014). Whilst the effects of different conifer removal regimes on tree regeneration have been investigated on plantations on ancient woodland sites (Harmer & Kiewitt 2006;

Harmer, Kiewitt and Morgan 2012), there has been little investigation into effects on other taxa. As different restoration approaches cause disturbances of different intensities and patterns they are likely to have a different impact on the ground flora (Roberts & Gillliam 2014).

This study compares two restoration methods – clearfelling planted conifers versus their gradual removal – and compares these to native woodland (as a reference community) and to conifer plantations on ancient woodland sites not undergoing restoration (the starting point of restoration). We focus on the effects on the ground flora and insect herbivore communities. Although the effects of tree-removal practises on the ground flora community have begun to be explored, they are still not well understood (Gilliam 2014). The plant diversity of forests is largely determined by the ground flora (Gilliam 2007), and it is important to conserve woodland ground flora species during restoration as many are slow to re-colonise once lost (Brunet & von Oheimb 1998; Hermy et al. 1999).

Restoration studies are often botanical in focus (Young 2000; Ruiz-Jaen & Aide 2005), and it is often assumed that successful restoration of the plant community leads to the restoration of higher trophic levels. The diversity of herbivorous invertebrates is indeed often correlated with the diversity of the plant community (Brown & Hyman 1986; Crisp, Dickinson & Gibbs 1998; Siemann, Haarstad & Tilman 1999; Rowe & Holland 2013), and there is evidence to suggest that restoring the diversity and structural complexity of vegetation will lead to the restoration of Hemipteran assemblages in *Eucalyptus marginata* (Donn ex Sm.) forests (Moir *et al.* 2005). However, other taxonomic groups and habitats need to be studied in order to determine if this is a general effect or specific to certain taxa or habitats. Here we investigate leaf-mining insects. These have not been widely used in restoration ecology but, as a species rich guild of specialist herbivores including species from four insect orders (Coleoptera, Diptera, Hymenoptera and Lepidoptera (Connor & Taverner 1997)), they are a useful group for monitoring restoration. They are also easy to collect and, as they live inside their food plant, host-plant relationships can be accurately determined.

This study has three objectives: 1) To determine whether the two restoration methods differ in their impact on the plant species richness of the ground flora and woodland specialist plants; 2) To assess whether plant species richness is correlated with leaf-miner species richness; 3) To test whether the efficacy of the two restoration approaches is affected by the type of woodland community being restored.

Materials and methods

Field sites

The study was carried out in the Forest of Dean, UK; a temperate forest spanning 106 km^2 in the West of England (51.789 N, -2.546 W). The forest was previously exploited for minerals and stone as well as timber, and contained areas managed as coppice and wood pasture (Herbert 1996). The forest currently consists of a mix of native broad-leaved and non-native conifer species.

Thirty-two plots were chosen, each 2 ha in size: eight plots managed as native broadleaved woodland (herein native plots), eight within conifer plantations not undergoing restoration (herein plantations), eight within conifer plantations undergoing gradual removal of planted trees for restoration (herein thinned plots), and eight within clearfelled conifer plantations (herein clearfelled plots). All plots were on ancient woodland sites. All plots were at least 15 m from the forest or clearfell edge. Plots were spread across eight locations (blocks), with each block containing one plot under each management regime.

The eight blocks consisted of two different forest types. Four of the blocks were on acidic *Quercus* woodland (National Vegetation class W10 (*Quercus robur - Pteridium aquilinum - Rubus fruticosus*) (Rodwell, 1991)) and four were on mesotrophic *Fraxinus* woodland (National Vegetation class W8 (*Fraxinus excelsior - Acer campestre - Mercurialis perennis*) (Rodwell, 1991)). Both these woodlands are widespread in lowland Britain. For plantations, thinned plots, and clearfelled plots the forest type refers to woodland that existed before conifer planting occurred. There was evidence of deer presence, an important factor in determining the plant species composition of forests (Waller 2014), in all plots.

On thinned plots, conifers are thinned every 5 years with thinning concentrated around native broadleaves. Plantations are also thinned every 5 years, with the pattern of thinning determined to maximise conifer growth. In the clearfelled plots all conifers were felled, and on all but one of these plots native broadleaves were planted. Native plots are thinned at most every 10 years depending on the degree of crown competition. Restoration commenced on thinned plots between 7 and 4 years prior to this study. Clearfelled plots were felled between 4 and 10 years prior to this study. Where possible plantations, thinned plots, and clearfelled plots in the same block had been planted with the same tree species. Plantations, thinned plots, and clearfelled plots were planted between 1958 and 1976, and in the same block were planted at most eight years apart (see Table S1 in Supporting Information for further plot information).

Plant sampling and classification

Plots were sampled for plants every four weeks between late April 2011 and July 2011, with each of the 32 plots being sampled three times. Plots within the same block were sampled on the same or consecutive days. During each sampling round a 100 m x 2 m transect, or on plots narrower than 100 m (due to the forest shape) multiple transects with a combined area of 200 m^2, were randomly placed in each plot. A gap of 1 m was left between transects shorter than 100 m to prevent plants being counted twice. All transects within a plot were parallel, and transects used for different sampling rounds were at least 5 m apart.

Along each transect all vascular plants excluding Lycopodiopsida were identified. Plants with a diameter at breast height less than 5 cm, and shorter than 2 m, excluding the native trees planted on clearfelled plots, were counted as ground flora and each species was assigned a species cover score (Fehmi 2010) using the Domin scale; 1 = <4 % species cover - very scarce, 2 = <4 % - scarce, 3 = <4 % - scattered, 4 = 4–10%, 5 = 11–25%, 6 = 26–33%, 7 = 34–50%, 8 = 51–75%, 9 = 76–90%, 10 = 91–100% (Mueller-Dombois & Ellenberg 1974). Domin scores were back-transformed to continuous percentage cover values using the Domin 2.6 transformation (Currall 1987). Following transformation the mean abundance of each species from the three sampling rounds was calculated. These mean values were used in the statistical analyses. Species in the ground flora were classed as woodland species if "broad leaved, mixed and yew woodland" was identified by Hill, Preston and Roy (2004) as one of their broad habitats in the British Isles.

Leaf-miner sampling

Plots were sampled for leaf-miners between late April 2011 and August 2011. Each of the 32 plots was sampled four times. Plots within the same block were sampled on the same or consecutive days. The same transects were used as for plant surveys, with an additional round of sampling, following the same transect methodology, in August 2011. Along each transect all leaves up to 2 m above the ground were inspected for leaf-mines and all leaves with mines collected.

Leaf-miners were reared in the laboratory. The combination of leaf-mine morphology, host plant species and adult miner morphology was used to identify leaf-miners using the British Leafminers website (n.d.) and Pitkin *et al.* (n.d.).

Statistical analyses

Objective 1: Do the two restoration methods differ in their impact on the ground flora? The effect of restoration method on the total ground flora and woodland species ground flora were analysed using generalized linear mixed effects models. Management regime (native, plantation, thinned or clearfelled), forest type (acidic *Quercus* or mesotrophic *Fraxinus*), and their interaction were modelled as fixed factors to analyse their effects on total ground flora species richness and woodland species ground flora richness of plots. Block was added as a random effect to all models to account for the blocked design of this study.

To evaluate the similarity in species composition of ground flora and woodland species ground flora between management regimes the Bray-Curtis dissimilarity was used. Non-metric multidimensional scaling (NMDS) was used for visual inspection of the similarities between plots. The effects of management regime, and the interaction between management regime and forest type on the community composition of ground flora and woodland species ground flora were analysed using permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001) with 9999 permutations. Data were permuted within blocks to account for the nesting of plots within blocks. Significant differences may be due to different within-group variation or different mean values (Warton, Wright & Wang 2012). Therefore, prior to all

PERMANOVA analyses a test for homogeneity of multivariate dispersion was performed using 9999 permutations (Anderson 2006). For all such tests no difference in multivariate dispersion was found between plots of different types, and we are confident that significant results from PERMANOVA reflect differences in mean values.

Due to the split-plot design of this study, with management regime assigned to plots within blocks and forest type assigned to whole blocks, the main effect of forest type could not be analysed. It uses a different error term from the main effect of management regime and the forest type - management regime interaction (Snedecor & Cochran 1989), and the software used to perform PERMANOVA did not allow the use of two different error terms.

Objective 2: Is plant species richness correlated with leaf-miner species richness?

Rarefied leaf-miner species richness was calculated for each plot to adjust for differences in abundance (Gotelli & Colwell 2001). This estimated the expected species richness if 10 leaf-mines were sampled in each plot; the smallest number of mines found in a plot with the exception of one plot where no mines were found. Estimates made using a rarefied sample size of 50 individuals were comparable, but led to plots being excluded due to having <50 mines. A rarefied sample size of 10 was therefore preferred to maximise the plot sample size.

Rarefied richness was analysed using a general linear mixed effects model. The plant species richness of plots, as well as management regime, forest type, and all two-way interactions between these were modelled as fixed factors. Block was added as a random effect to all models to account for the blocked design of this study.

Objective 3: Is the efficacy of the two restoration approaches affected by forest type?

Forest type was included in the models described above. Although the effect of forest type on ground flora species composition could not be statistically assessed using our statistical models, PERMANOVA was able to determine if forest type interacted with management regime to affect species composition. The main effect of forest type on ground flora composition was determined graphically using NMDS.

Model simplification and statistical software

Maximum models were simplified using likelihood ratio tests (Bolker 2008). Explanatory variables were retained in models, and considered significant, if their removal resulted in a significant change in model deviance. The validity of final models was checked using visual examination of residuals (Bolker *et al.* 2009). *Post hoc* Tukey tests were performed for all pair-wise comparisons of fixed factors, and interactions between fixed factors, retained in optimal models, with *P* values adjusted using the false discovery rate method (Benjamini & Hochberg 1995; Verhoeven, Simonsen & McIntyre 2005; Pike 2011). If plant species richness, or an interaction between plant species richness and another variable, was retained in the optimal model of leaf-miner richness this was analysed graphically using effect displays (Fox, 2003). These show the predicted relationship between main effects and their interactions on the response variable, as modelled using linear models such as those performed here. Generalized linear mixed effect models used the Poisson distribution and log link function (Bolker *et al.* 2009), and all linear models were fitted by maximum likelihood estimates.

All analyses were conducted in R (R Core Team 2012). Package 'lme4' (Bates, Maechler & Bolker 2012) was used to fit mixed models. Tukey tests were carried out in the 'multcomp' package (Hothorn, Bretz & Westfall 2008). Effect displays were produced using the 'effects' package (Fox 2003). Package 'vegan' (Oksanen *et al.* 2012) was used for NMDS plots, tests for homogeneity of multivariate dispersion, PERMANOVA, and rarefaction.

Results

Objective 1: Do the two restoration methods differ in their impact on the ground flora? One hundred and seventy-nine ground flora species were identified in the 32 plots, 167 to species level and 12 to genus, comprising 110 genera in 53 families (see Table S2). Of these 86 were woodland species, comprising 69 genera in 47 families. Management regime had a significant effect on species richness (Likelihood ratio test: χ^2 = 65.35, d.f.= 3, P<0.001) and clearfelled plots had significantly more ground flora species overall than other plots (Fig. 1a). However, all plots contained woodland species and there was no significant effect of management regime on woodland species richness (Likelihood ratio test; χ^2 = 1.83, d.f.= 3 , P = 0.607, Fig. 1b).

The overall ground flora community composition differed significantly between management regimes (Pseudo F = 4.05, d.f. = 3, P<0.001). Plantations and thinned plots had a similar community composition intermediate between that of native and clearfelled plots (Fig. 2a). The woodland species subset of the ground flora community showed a different pattern from that of the ground flora in general. Woodland species composition differed between management regimes (Pseudo F = 4.08, d.f.=3, P <0.001) but thinned, plantations and clearfelled plots overlapped in their composition whilst native plots had a different woodland species composition (Fig. 2b).

Objective 2: Is plant species richness correlated with leaf-miner species richness? In total 10,025 mines were collected. Of these 9771 could be identified to at least order level and comprised 122 species (see Table S3): 68 Lepidoptera species and four Lepidoptera taxa identified to genus level, 38 Diptera species and two Diptera taxa identified to genus level, 11 Hymenoptera species and one Hymenoptera taxon identified to order level, and two Coleoptera species.

The relationship between plant and rarefied herbivore species richness was not consistent between the different management regimes. Thus, there was a significant interaction between plant species richness and management regime (Likelihood ratio test: χ^2 = 15.20, d.f.= 3, P = 0.002). On plantations, thinned and native plots, there was a positive relationship between leaf-miner species richness and plant species richness (Figs. 3a, 3b, 3c). However, on clearfelled plots there was a negative relationship between leaf-miner species richness and plant species richness (Fig. 3d).

Objective 3: Is the efficacy of the two restoration approaches affected by forest type?

There was a significant effect of forest type on both total ground flora species richness (Likelihood ratio test: χ^2 = 5.61, d.f.= 1, P = 0.018) and woodland species richness (Likelihood ratio test; χ^2 = 7.69, d.f.= 1 , P = 0.006) with mesotrophic *Fraxinus* plots having a greater mean species richness than acidic *Quercus* plots in both cases (Total ground flora species; 49.36 ± 8.5 vs. 32.19 ± 5.85; Woodland species; 23.56 ± 1.83 vs.13.75 ± 2.79). Plots on the two different forest types also differed in total ground flora species composition (Fig. 2a) and woodland species composition (Fig. 2b).

However, there was no interaction between management regime and forest type affecting either total ground flora community composition (Pseudo F = 1.33, d.f. = 3, P = 0.110), total ground flora species richness (Likelihood ratio test: χ^2 = 4.46, d.f.=

3, P = 0.216), woodland species composition (Pseudo F = 1.28, d.f. = 3, P = 0.173), or woodland species richness (Likelihood ratio test; χ^2 = 1.83, d.f.= 3, P = 0.605). Neither was there an effect of forest type on leaf-miner species richness (Likelihood ratio test: χ^2 = 0.69, d.f.= 1, P = 0.407). Thus the two restoration approaches have the same impact on each type of woodland.

Discussion

During restoration it is important not only to re-establish, but to also maintain any species native to the target habitat already present. Both of the restoration methods studied here maintained woodland ground flora species. However, the restoration methods differed in their effects in other ways. Clearfelled plots had greater ground flora species richness than thinned plots, and leaf-miner species richness increased with plant species richness on thinned plots but not on clearfelled plots. Forest type did not interact with the restoration method, demonstrating that the two approaches have a consistent effect on different plant communities.

There are two caveats to consider when interpreting these results. Firstly, plant community data from plots prior to clearfelling or the onset of thinning were not available. Therefore, any differences seen between plots cannot be conclusively attributed to their management. However, there is no reason to suspect that the plant communities under the different management regimes differed systematically prior to restoration. Secondly, logistical constraints meant that leaf-miners were only sampled from vegetation up to 2 m tall, i.e. the tree canopy was not sampled. However, clearfelled plots had few trees taller than 2m, and the canopy of plantations and thinned plots mainly consisted of conifers. Although conifers do host leaf-miners no mines were found on conifer leaves during this study. We are therefore confident that the samples from plantations, clearfelled and thinned plots reflect their leaf-miner community. The native plots, however, had an extensive canopy cover of broadleaved trees and their species richness of leaf-miners may be higher than reported here.

The effect of restoration method on ground flora

The potential of plantations on ancient woodland sites to be restored to native woodland was confirmed by the presence of many woodland species, such as *Arum maculatum* (L.), *Mercurialis perennis* (L.), and *Anemone nemorosa* (L.) in their ground flora. Indeed plantations had the same number of woodland species in their ground flora as native plots. Furthermore, neither approach to removing conifers resulted in a decline in woodland ground flora species as restoration plots had the same number, and a similar composition, of woodland ground flora species as unrstored plantations. Due to the slow migration of many woodland plants (Brunet & von Oheimb 1998; Hermy *et al.* 1999) maintaining their populations is an important requirement of plantation restoration, and both approaches to restoration achieved this.

The thinning regime studied here differs little from the management regime on plantations not undergoing restoration, and both regimes result in a similar level of disturbance. This explains the similarity in woodland species composition and richness on these plots. Clearfelling of forests often results in the decline and loss of woodland species (Hannerz & Hånell 1997; Roberts & Zhu 2002; Godefroid, Rucquoij & Koedam 2005), here though clearfelled plots had the same number of woodland species as the other management regimes. There are four mechanisms whereby ground flora species may reappear on sites following disturbance such as that caused by clearfelling; survival *in situ*, vegetative regeneration, regeneration from the seed bank, and regeneration from dispersed propagules (Roberts and Gilliam 2014). Due to the absence of pre-restoration species lists we cannot be certain if these woodland species were present in the community before felling, or if they have subsequently colonised or regenerated from the seed bank of the clearfelled plots. However, they are unlikely to have all germinated from the seed bank, as, with the exception of *Rubus fruticosus* (L. agg.), woodland species do not produce long-lived seed banks (Thompson, Bakker & Bekker 1997). Furthermore, many woodland species have poor dispersal capabilities (Brunet & von Oheimb 1998; Hermy *et al.* 1999; Verheyen *et al*. 2003). However, *Deschampsia* cespitosa (L.) P. Beauv., and A. *nemorosa*, both dispersal limited woodland species (Verheyen & Hermy 2001), were found on plantations as well as clearfelled plots. It is therefore most likely that survival *in situ* and vegetative regeneration from surviving vegetation are the mechanisms responsible for the appearance of woodland species in the ground flora of clearfelled plots, suggesting that remnant woodland species populations can survive clearfelling at least for the four to 10 year post-felling window during which this study was conducted. Many woodland species take advantage of canopy gaps and soil disturbance (Brunet, Falkengren-Grerup & Tyler 1996; Brunet, Falkengren-Grerup & Tyler 1997), and removal of the canopy can increase flowering, seed production, or the vegetative spread of some woodland species (Hughes & Fahey 1991; Mayer, Abs & Fischer 2004), aiding their survival following clearfelling. Furthermore, the abundant *Pteridium aquilinum* (L.) Kuhn cover on the clearfelled plots may have allowed shade tolerant woodland plants to survive (Pakeman & Marrs 1992).

Clearfelled plots had the greatest overall ground flora species richness. Canopy opening of abandoned coppice also results in an increase in species richness (Vild *et al.* 2013), and the species richness of clearfelled plots may reflect the community present following historical coppicing or clearfelling for timber. Clearfelling results in soil disturbance, more light reaching the ground (Ash & Barkham 1976; Collins & Pickett 1988; Mitchell 1992) and an increased availability of colonisation sites, leading to an increase in species richness through the dispersal of propagules into clearfelled plots and/or regeneration from the seed bank (Roberts & Zhu 2002; Pykälä 2004). This is reflected in the species composition of clearfelled plots, which contained many ruderal and grassland species such as *Chamerion angustifolium* (L.), *Buddleja davidii* (Franch.) and *Ranunculus acris* (L.).

The woodland species composition of plantations, clearfelled or thinned plots did not resemble the native plots. This is likely due to the age of native plots; they have existed as native woodland for decades, or centuries, enabling the establishment of slow colonising woodland species. There is no list of ancient woodland indicator species for the Forest of Dean, but species such as *A. nemorosa*, *M. perennis*, and *Ilex aquifolium* (L.), have been identified as ancient woodland species in other regions (Hermy *et al.* 1999; Rose & O'Reilly 2006). While these species were present in plantations, thinned plots, and clearfelled plots, they were more abundant in the native plots. Continued monitoring is required to see if the woodland species composition of clearfelled and thinned plots moves towards that of native plots.

The relationship between plant species richness and leaf-miner species richness

The diversity of phytophagous invertebrates often follows that of the plant community (Brown & Hyman 1986; Crisp, Dickinson & Gibbs 1998; Siemann, Haarstad & Tilman 1999; Rowe & Holland 2013), and leaf-miner species richness did increase with plant species richness on plantations, thinned and native plots. Most leaf-miners are specialists on a small number of related host-plants (Memmott, Godfray & Gauld 1994). Therefore, as plant species richness increases more niches are available for leaf-miner species, and more leaf-miner species are able to establish in the community. However, greater plant species richness did not necessarily lead to greater species richness of leaf-miners. On clearfelled plots leaf-miner species richness did not increase as plant species richness increased, demonstrating that the relationship between plant species richness and invertebrate herbivore species richness can differ under different management regimes.

Although not measured here, clearfelled plots had greater, denser, vegetation cover than the other plots. The vegetation cover on clearfelled plots may make it difficult for leaf-miners to locate host plants in species rich communities using visual or chemical cues (McNair, Gries & Gries 2000; Jactel *et al.* 2011; Dulaurent *et al.* 2012), preventing them from establishing. This could occur through reduced resource concentration, whereby herbivores are less able to find host plants when they do not form dense stands (Root 1973), and/or reduced focal plant apparency, whereby herbivores are less able to find host plants when they are concealed by taller non-host plants (Floater & Zalucki 2000; Hughes 2012; Castagneyrol et al. 2013). When plant species richness is lower, but the vegetation cover is high, these mechanisms will not occur, and leaf-miners may be even more likely to establish due to the ease of locating host plants when they form dense stands. Further investigation is needed to determine if these mechanisms explain our results.

The effect of forest type on restoration outcome

Forest type had no effect on leaf-miner species richness, but did affect the species richness of the ground flora and richness of woodland species in the ground flora, with mesotrophic *Fraxinus* plots having a greater species richness of both these groups. However, there were no significant interactions between forest type and management regime. Differences between the forest types are differences in the number of species present and not in the patterns of species richness between management regimes. This is important as it means that, for these two forest types at least, the results from a study of the ground flora community on one forest type can be applied to the other, saving time and money.

Conclusions

Both restoration methods conserved the woodland plant species richness of sites during restoration. This has important management implications. Which restoration method to use depends on many factors, but the results here suggest that both can be considered. However, clearfelling may be the only option possible on sites that cannot easily be visited multiple times for thinning, and these results suggest that this will not be at the expense of the woodland ground flora. Clearfelling also requires less time and money. We found that the method of restoration influenced the relationship between plant and herbivore species richness. Therefore, species higher up the food chain, such as herbivores, should also be monitored during restoration.

Restoration aims to restore the integrity of degraded systems, and this necessarily involves observing more than just plant species.

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Figures

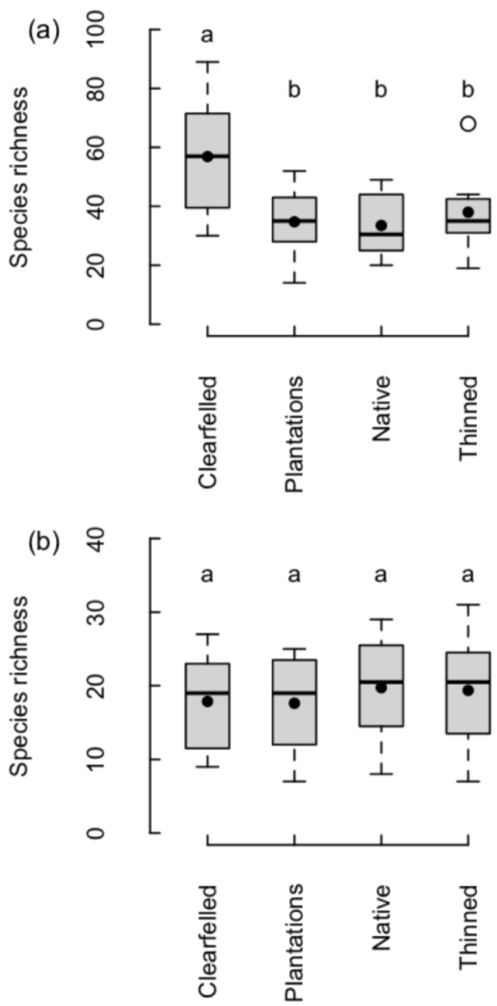

Figure 1. Plant species richness in the four types of plot: a) The total ground flora species richness of plots under different management regimes; b) The woodland ground flora species richness. Different letters within each panel indicate significant differences ($P < 0.0001$).

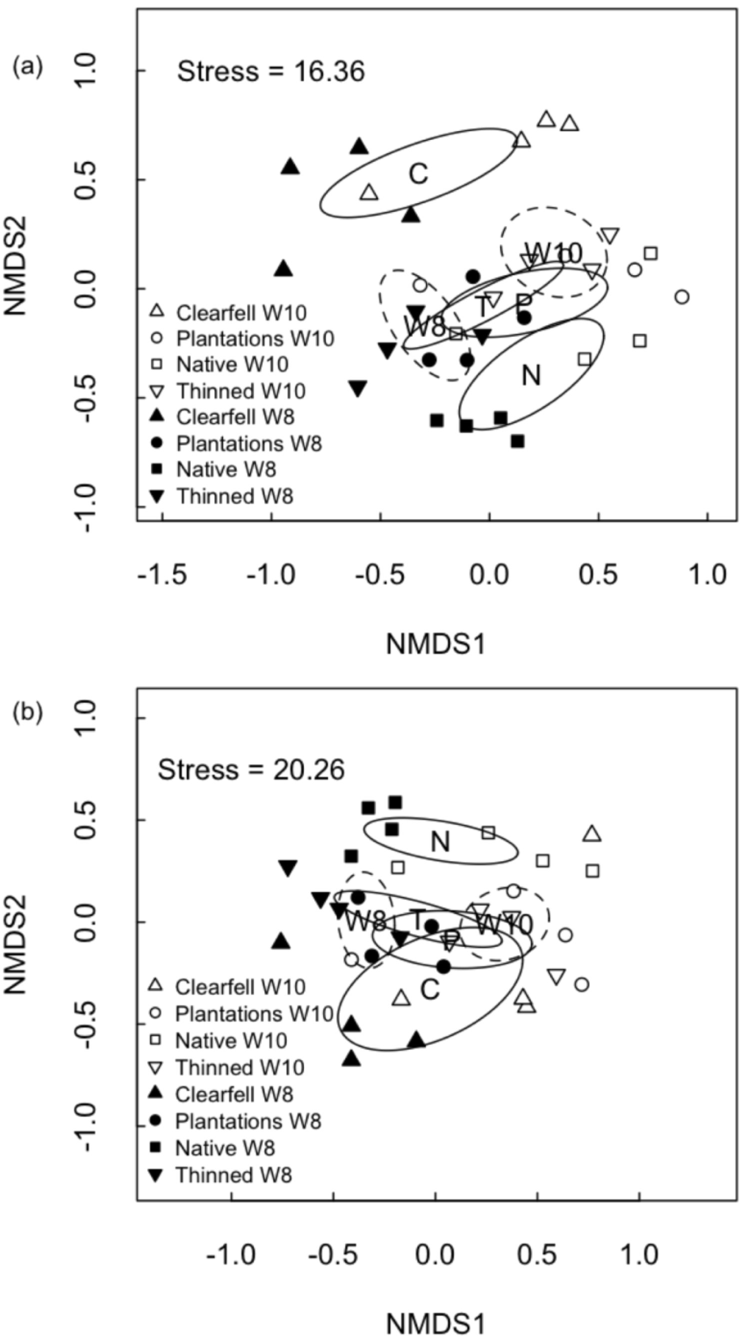

Figure 2. Nonmetric multidimensional scaling plot of the composition of the ground flora (a), and the woodland species in the ground flora (b). Each point represents a plot. Ellipses represent 95% confidence intervals of the mean score of management regimes (solid lines) and mean score of forest types (dashed lines).

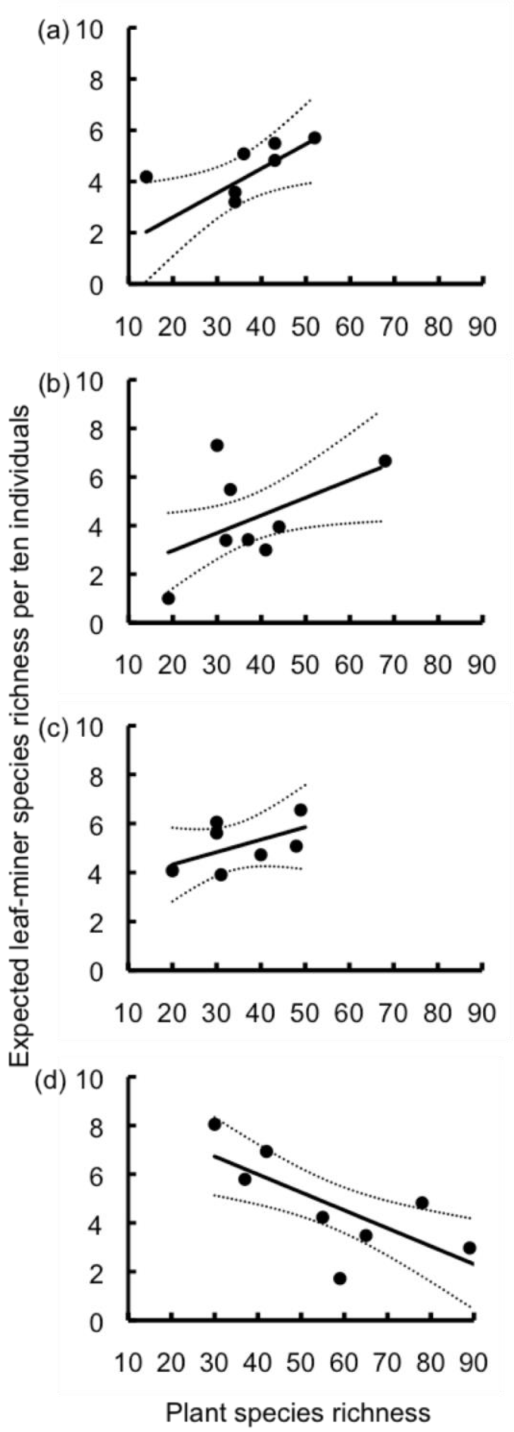

Figure 3. The relationship between plant species richness and rarefied leaf-miner species richness for (a) plantations, (b) thinned plots, (c) native plots, and (d) clearfelled plots. Dashed lines indicate 95% confidence intervals. The underlying model is a general linear mixed model with site as a random effect.

Supporting Information

Additional supporting information may be found in the online version of this article:

Table S1. Details of the study plots used in this study.

Table S2. Plant species found in the ground flora of study plots.

Table S3. Leaf-miner species found in the ground flora of study plots.