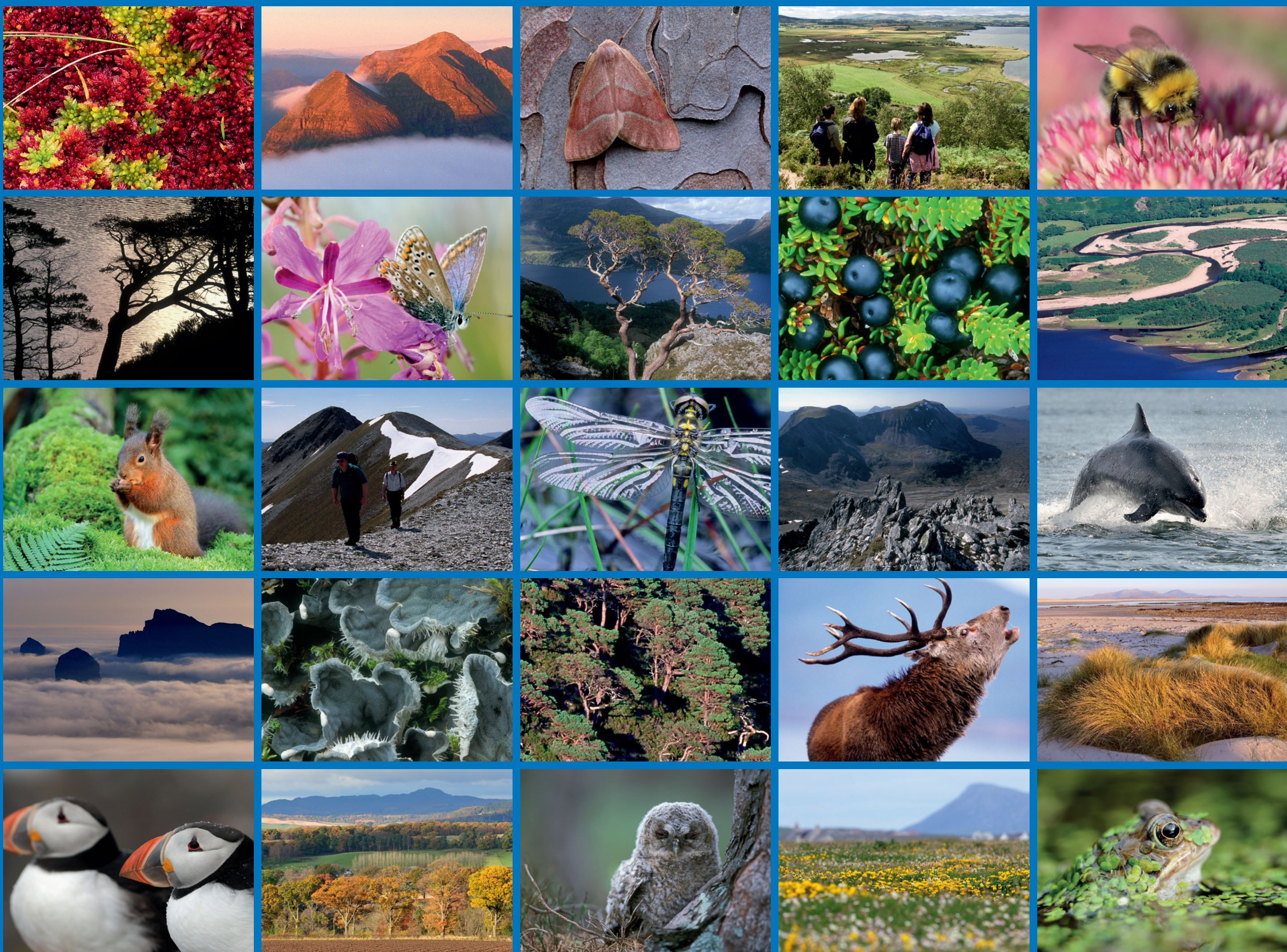
Scottish Natural Heritage
Research Report No. 1157

The effect of clearing invasive *Rhododendron ponticum* on the native plant community of Atlantic oak woodland



Scottish Natural Heritage
Dualchas Nàdair na h-Alba
nature.scot

RESEARCH REPORT

Research Report No. 1157

The effect of clearing invasive *Rhododendron ponticum* on the native plant community of Atlantic oak woodland

For further information on this report please contact:

Dr David Genney or Jeanette Hall
Scottish Natural Heritage
Great Glen House
INVERNESS
IV3 8NW
Telephone: 01463 725000
E-mail: david.genney@nature.scot
jeanette.hall@nature.scot

This report should be quoted as:

Maclean, J.E., Genney, D., Hall, J., Mitchell, R.J., Burslem, F.R.P. & Pakeman, R.J. 2019. The effect of clearing invasive *Rhododendron ponticum* on the native plant community of Atlantic oak woodland. *Scottish Natural Heritage Research Report No.* 1157.

RESEARCH REPORT

Summary

The effect of clearing invasive *Rhododendron ponticum* on the native plant community of Atlantic oak woodland

Research Report No. 1157
Project No: 014299
Lead Author: Janet Maclean
Year of publication: 2019

Keywords

Atlantic oak; bryophyte; epiphyte; invasive species; legacy effects; restoration; *Rhododendron ponticum*; seed bank.

Background

Rhododendron ponticum is widely recognised as one of the most problematic non-native invasive species currently threatening Scottish biodiversity. By forming extensive, single-species stands it effectively excludes native plant communities from their natural habitats and has been identified as posing a particular threat to Atlantic oak woodlands, which are of high conservation value due to their rich bryophyte and lichen communities. Increased awareness of its detrimental impacts, coupled with the discovery that it can act as a host for the plant pathogen *Phythopthera ramorum*, has recently lead to a large increase in *R. ponticum* removal all across Scotland. Little is know, however, about how sites recover following the removal of *R. ponticum*, and whether native communities are adequately restored.

This report summarises the main findings from a PhD project investigating site recovery following the removal of invasive *R. ponticum* from Atlantic oak woodland sites across the West coast of Scotland. Recovery of the understorey plant community and the epiphytic bryophyte community were both considered in detail, in addition to elucidating changes in soil chemistry and in the soil seed bank to identify any major barriers to site recovery. Supplementary restoration techniques, such as seed addition, microsite creation, and chemically treating the soil were also field-trialled to investigate the efficacy of incorporating these techniques into *R. ponticum* removal programmes.

Main findings

- Dense *R. ponticum* stands were confirmed to be highly detrimental to native plants, showing dramatically reduced levels of cover and species richness in both the understorey and the epiphytic communities compared to uninvaded sites.

- Cleared sites did not regain the understorey community composition found in uninvaded sites even up to 30 years after the successful removal of invasive *R. ponticum* stands.

- Common understorey bryophyte species recovered well following *R. ponticum* clearance and came to dominate the vegetation at the expense of forbs and grasses, which did not recover.

- Epiphytic bryophytes also recovered well following *R. ponticum* removal, returning to levels of cover, species richness and community composition found in uninvaded plots by 10 – 20 years after clearance. This evidence relates only to common species found in general surveys, however, as targeted surveys of rare species were not carried out due to logistical constraints.

- Both the number and species richness of viable seeds in the soil seed bank was greatly reduced under dense *R. ponticum* stands compared to uninvaded sites.

- Cleared sites also displayed a low species richness of viable seeds in the soil seed bank, but were indistinguishable from uninvaded sites in terms of the total number of viable seeds, due to a preponderance of birch seeds. Very few viable *R. ponticum* seeds were detected at cleared sites, suggesting that widespread re-invasions are unlikely to arise from the seed bank. The presence of some *R. ponticum* seeds at half the cleared sites, however, emphasises that periodic monitoring should be carried out at all sites to prevent these isolated seeds growing into adult bushes from which a new invasive population could form.

- Re-seeding with native species was shown to be a successful way of restoring native vascular plants following *R. ponticum* clearance, particularly when coupled with the creation of suitable microsites for germination (by clearing the existing bryophyte layer). Further uptake of this restoration technique will require careful site-by-site consideration, taking local conservation objectives into account.

- No evidence of a chemical legacy of *R. ponticum* in the soil was discovered, suggesting that chemical impacts do not pose a significant barrier to site recovery and further treatment of the soil following clearance is unnecessary.

For further information on this project contact:
Dr David Genney or Jeanette Hall, Scottish Natural Heritage, Great Glen House,
Leachkin Road, Inverness, IV3 8NW.
Tel: 01463 725000 or david.genney@nature.scot or jeanette.hall@nature.scot
For further information on the SNH Research & Technical Support Programme contact:
Research Coordinator, Scottish Natural Heritage, Great Glen House, Leachkin Road, Inverness, IV3 8NW.
Tel: 01463 725000 or research@nature.scot

Table of Contents **Page**

Acknowledgements

This research was funded by SNH, the University of Aberdeen and the James Hutton Institute. The authors wish to thank all the people who very generously gave their time to help with site selection for this project, including; Stan Philips, Liz Prior, Hazel White, Claire Masson, Stan Whitaker and Elaine Jamieson at SNH; Ian McKee, David Anderson, Kenneth Knott and Colin Edwards at Forestry Commission Scotland; Kate Sampson and Lindsay Mackinlay at The National Trust for Scotland; Mary Elliott, Ilene Duncan, Duncan Broadfoot, Damon and Annie Kinneil, Peter Slan, Jennifer MacVicar, Robin Dixon and Sons, Andrew Nicol of Bute Estates and Michael James of Scottish Woodlands.

1. INTRODUCTION

1.1 History of *Rhoodendron ponticum* invasion in the U.K.

Rhododendron ponticum was first introduced to the U.K. as an ornamental plant in 1763 (Cross 1975). It was planted widely in gardens and parks for its appearance and grown over extensive areas as game cover on private estates (Dehnen-Schmutz *et al.* 2004). There are reports from 1849 onwards of *R. ponticum* spreading across the landscape from the original source populations and it is now naturalised across large areas, particularly affecting woodland and open hillside (Cross 1975; Dehnen-Schmutz *et al.* 2004). Mature stands form dense thickets from which native plants are almost entirely excluded. This dramatic impact on the native plant community, coupled with the extensive area affected, has lead to *R. ponticum* being recognised as one of the most important non-native invasive species currently threatening British wildlife (Edwards 2006; Long & Williams 2007; Parrott & MacKenzie 2013).

The native range of *R. ponticum* is principally located in a thin band to the South and East of the Black Sea (largely in Turkey) and a series of small, disjointed populations in Spain and Portugal (Cross 1975; Milne & Abbott 2000). Genetic analysis shows that the invasive British population is derived from the Spanish lineage, with a small amount of genetic material from the Portuguese populations also being present (Milne & Abbott 2000; Erfmeier & Bruelheide 2011). This is rather surprising given that the Spanish population is doing very poorly in its native range, where it is of conservation concern (Mejías *et al.* 2007). It seems, however, that due to changing climate conditions, these plants are now better adapted to the moist British environment than to the lengthy dry season present in their native habitat (Mejías *et al.* 2007). It also appears that the British population shows a degree of introgression with the congeneric *R. catawbiense,* likely the result of being allowed to hybridise freely in botanic gardens. Since *R. catawbiense* experiences colder conditions in its native North American range, it is likely that this introgression has allowed *R. ponticum* to better adapt to the cooler U.K. conditions, especially in northern Scotland (Milne & Abbott 2000).

1.2 Impacts of *R. ponticum* invasion

Established *R. ponticum* stands have been demonstrated to reduce biodiversity (Colak *et al*. 1998, Rotherham 1983; Long & Williams 2007), extirpate native species (Mitchell *et al*. 1997; SNH 2007) and prevent forest regeneration (Cross 1981; Rotherham 1983; Yildiz *et al.* 2009). There is some debate, however, as to how they achieve such complete dominance over native species, and indirect competition mediated through the secretion of allellopathic chemicals into the soil (for example polyphenols, which can inhibit the growth of other plants) has been suggested to play an important role, in addition to more direct mechanisms of competition for available resources such as reducing the ambient light reaching the understorey (Cross 1975; Rotherham 1983; Sutton & Wilkinson 2007). Whilst references to the toxic effect of *R. ponticum* are common in the conservation literature, it has recently been pointed out that the scientific basis for these claims is unclear (Merryweather 2012), and is likely based on laboratory studies which have detected polyphenols in *R. ponticum* tissues (Rotherham 1983, Rotherham & Read 1988), rather than being grounded in comprehensive field-based investigations. If *R. ponticum* bushes do release toxic compounds into the soil, this could greatly impact restoration following the clearance of invasive stands since such chemicals may persist in the soil, continuing to inhibit native plant growth long after the *R. ponticum* bushes have been removed (Wardle *et al.* 1998). If these lasting effects on soil toxicity do occur, then it is likely that more extensive restoration measures, such as soil chemical treatment or soil replacement, may be required in order to achieve conservation goals (Wardle *et al.* 1998).

In addition to its directly detrimental impact on the native plant community, *R. ponticum* has recently been identified as posing an additional threat to woody species by serving as a host for the important plant pathogen *Phytophthora ramorum*. Whilst *P. ramorum* principally affects larch trees in the U.K., is has also been found to affect beech, horse chestnut, Sitka spruce and several species of oak (www.forestresearch.gov.uk/tools-and-resources/pest-and-disease-resources/ramorum-disease-phytophthora-ramorum/). This threat of disease transmission has lead to a dramatic increase in *R. ponticum* clearance programmes, and extensive areas have now been cleared with the hope that native plant communities will subsequently regenerate. With most projects understandably prioritising the allocation of limited funds towards further *R. ponticum* control rather than subsequent site monitoring, little is consequently known about how sites recover following clearance. The typical assumption that the native community will gradually recover in the years following *R. ponticum* clearance is rarely tested and very few sites employ additional restoration measures to facilitate native community recovery.

1.3 Atlantic Oak woodlands and *R. ponticum*

One of the habitat types most at risk from invasive *R. ponticum* is the Atlantic Oak Woodland of Western Scotland (Long & Williams 2007; Edwards & Taylor 2008). This habitat is represented in Annex I of the EU Habitats Directive as *"Old sessile oakwoods with Ilex and Blechnum in the British Isles"* and is of high conservation importance due to its globally exceptional bryophyte and lichen communities (Long & Williams 2007; SNH 2007). Dubbed the 'Celtic rainforest' (Gilbert 2004; Long & Williams 2007), this habitat hosts many rare species, whose distributions are limited to the extreme western seaboard of Europe (Ratcliffe 1968; Porley & Hodgets 2005), though several intriguing species exhibit disjointed populations with similar habitats elsewhere in the world including British Columbia, the Himalayas, Yunnan province in China, and the Hawaiian islands (Ratcliffe 1968; Porley & Hodgets 2005). A single Atlantic oak woodland featuring a ravine and a variety of tree species can host over 200 bryophyte species in a spectacular display of diversity, comparable to that found in tropical rainforests (Porley & Hodgets 2005).

As with elsewhere in its invasive range, *R. ponticum* threatens the native bryophytes and other species of Atlantic oak woodlands by competitively excluding them from the area and limiting their distributions to small pockets where they can escape its negative impacts (Rodwell *et al.* 1991; Porley & Hodgets 2005; Long & Williams 2007). As the invasion progresses, these pockets become increasingly sparse and if the invasion is not controlled many species will be extirpated from the area (Long & Williams 2007). Substantial control efforts have now been undertaken in these areas of Atlantic oak woodland, but no formal monitoring has been undertaken to assess post-clearance recovery of native species (Edwards 2006; Edwards & Taylor 2008).

1.4 Project aims

This project aimed to elucidate what happens to the native plant community at Atlantic Oak woodland sites following the removal of invasive *R. ponticum*. It focussed on both the understorey plant community, since this is the most abundant and noticeable community and plays an important role for public appreciation of the woodlands, and the epiphytic bryophyte community, which is the community of most conservation concern. The specific questions were:

- **1a) How does the native understorey plant community change as *R. ponticum* increases in density during invasion?**
- **1b) How does the native understorey plant community change following *R. ponticum* clearance?**

Understanding how the understorey plant community changes during invasion and after clearance will reveal the extent to which changes that occur during invasion are reversed after clearance. This project included sites with up to 30 years of recovery following *R. ponticum* clearance to give a clear picture of community changes over ecologically relevant timescales.

2) How does the epiphytic bryophyte community change following *R. ponticum* clearance?

Focussing on changes to the epiphytic bryophyte community will reveal the extent to which this fragile and important community is threatened by *R. ponticum* invasion, and recovers following its clearance.

3) Is the native seed bank depleted during *R. ponticum* invasion and does it recover following clearance?

Understanding differences in the seed bank between uninvaded, invaded and cleared sites will reveal whether native seed availability presents a significant barrier to restoration following *R. ponticum* clearance.

4) Does *R. ponticum* exert a toxic legacy on the soil that could hinder site recovery following its removal?

Revealing whether suggested impacts of *R. ponticum* on soil chemistry inhibit native plants long after its removal will indicate whether more extensive restoration measures will be needed to overcome these impacts following clearance programmes.

5) What additional restoration techniques would be successful at facilitating site recovery following *R. ponticum* clearance?

Trialling different restoration techniques such as seed addition, creating better microsite conditions for seed germination, and soil treatments such as the addition of activated carbon and fertiliser to overcome toxic legacies in the soil, will reveal whether these represent beneficial additions to the restoration toolbox.

2. METHODS AND RESULTS

Full methodological details are available in Maclean (2016). Only a brief summary of the methods used is presented here as the focus of this report is in highlighting the implications for practical restoration purposes.

2.1 How does the native understorey plant community change a) as *R. ponticum* increases in density and b) after it is cleared?

This study utilised a series of 56 sites falling along a gradient of increasing *R. ponticum* density from uninvaded controls through to dense thickets; and a separate series of 37 sites falling along a gradient of increasing time since *R. ponticum* clearance up to a maximum of 30 years since initial clearance. This 'space-for-time' chronosequence approach uses several similar sites falling along a gradient to emulate the changes occurring at a single site through time, and is used in ecology to address questions that would otherwise require decades to monitor at a single site. Sites were selected based on the recommendations of regional SNH and Forestry Commission personnel and following discussions with local landowners. All cleared sites were subject to periodic follow-up treatments to ensure they remained free from *R. ponticum.* All sites were located in Atlantic oak woodlands on the west coast of Scotland in Argyll and Lochaber (Fig. 1). Oak (*Quercus Petraea* [Mattuschka] and *Q. robur* [Mattuschka]) and birch (*Betula pendula* [Roth] and *B. pubescens* Ehrh.) were the principle canopy species at all sites, with rowan (*Sorbus acuparia* L.), hazel (*Corylus avellana* L.) and ash (*Fraxinus excelsior* L.) also occurring with moderate frequency.

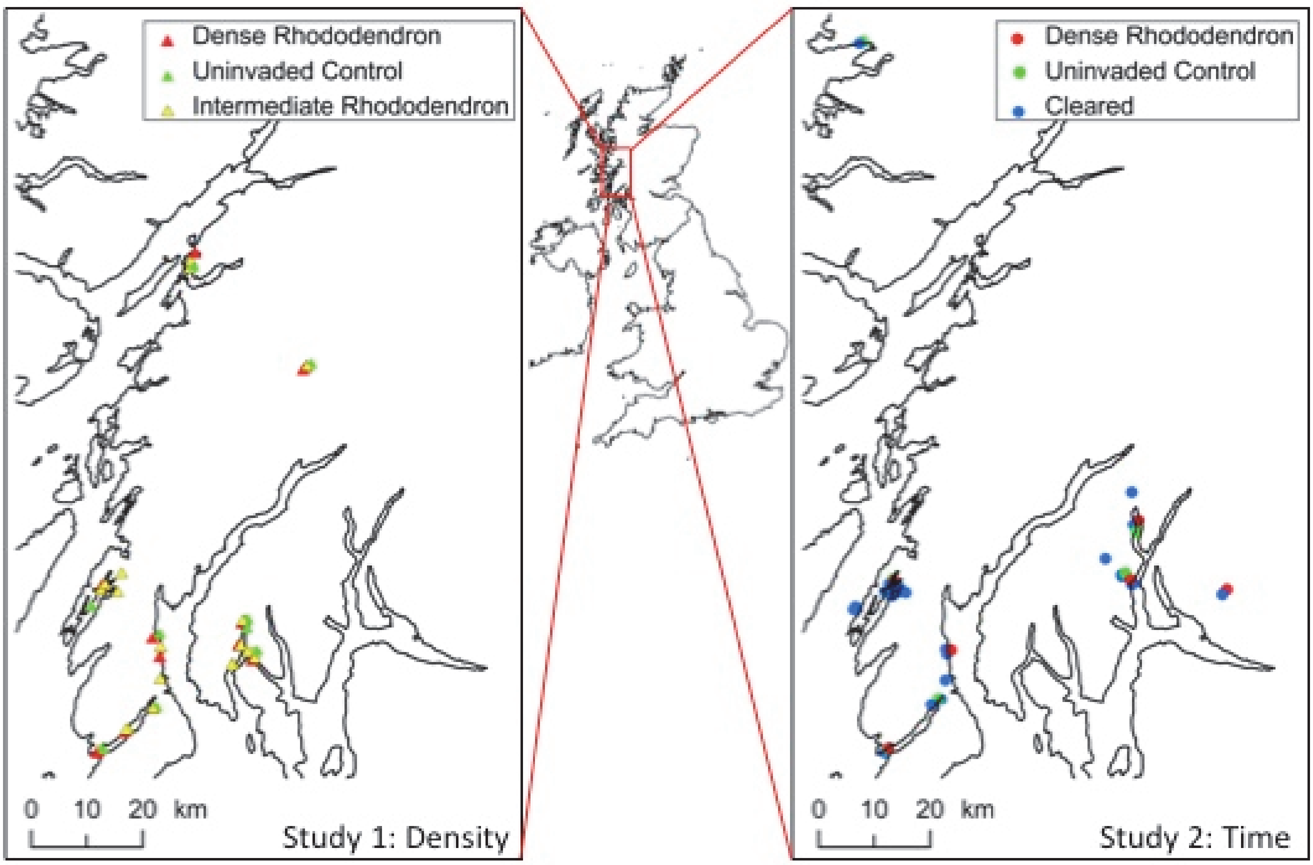


Figure 1. Map of study site locations for a) R. ponticum density – left; and b) time since R. ponticum clearance – right.

At each site a plant survey was carried out, recording the percent cover of all vascular plants, bryophytes and ferns found in nine 1 m^2 quadrats placed in a 20 m x 20 m grid. The total number of species (i.e. species richness) encountered across the nine quadrats at each site was also recorded. A series of mixed effect models were then used to determine the effect of a) increasing *R. ponticum* density and b) increasing time since *R. ponticum* clearance; on the percent cover, proportional abundance and species richness of the different taxonomic groups (forbs, grasses, bryophytes, ferns and woody species). Multivariate analyses (Redundancy Analysis) were then used to reveal overall changes in community composition as site recovery progressed with increasing time since *R. ponticum* clearance.

2.1.1 Results – Increasing R. ponticum density

In accordance with previous studies, both species richness and the total percent cover of the understorey plant community declined rapidly with increasing *R. ponticum* density (Fig. 2), although the pattern varied between species groups. Whilst percent cover of forbs, grasses and bryophytes decreased, cover of bryophytes declined less severely than that of forbs and grasses with increasing *R. ponticum* density, resulting in their forming a greater proportion of the overall community in sites with dense *R. ponticum* (Fig. 3). A broadly similar pattern was revealed for species richness, with forbs and grasses showing declining species richness as *R. ponticum* increased in density, although no significant changes were found for bryophyte species richness (Fig. 3). Ferns showed a significant slight decrease in percent cover as *R. ponticum* density increased, but no significant differences were found for their proportional abundance or their species richness. No significant effects of increasing *R. ponticum* density were found for woody species (Fig. 3). This lack of a major impact for ferns and woody species was likely due to the low overall abundance of both these groups, but may also suggest an ability of woody species to withstand invasion.

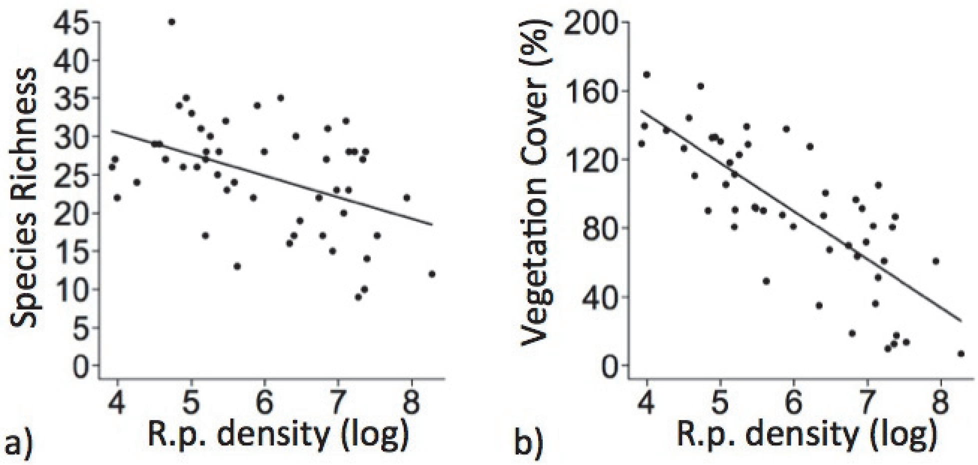


Figure 2. The effect of increasing R. ponticum density on (a) understorey plant species richness and (b) vegetation cover (percent cover). Plots range from a minimum of 50 bushes ha^{-1} (a low density covering of isolated bushes) to a maximum of 3,906 bushes ha^{-1} (high density mature stands with continuous canopy cover). For comparison, uninvaded control plots had an average of 30 species per site and an average percent cover of 144 %, being very similar to the values found in low density sites.

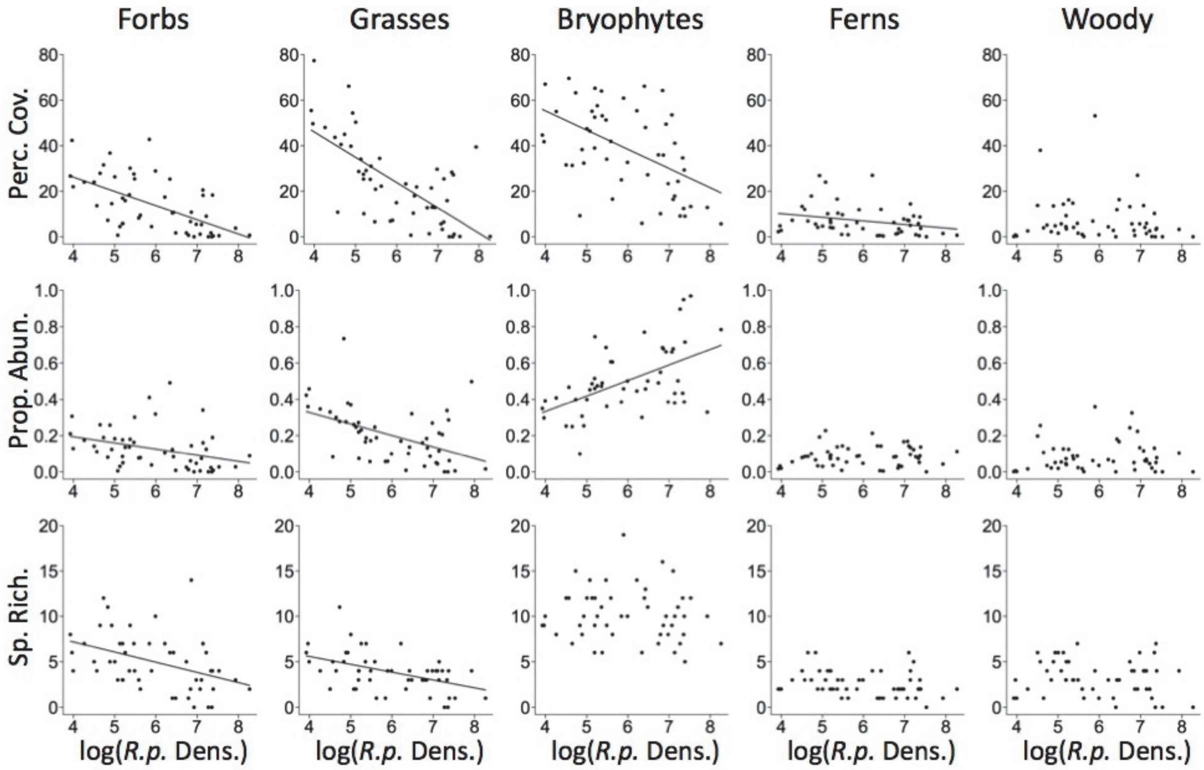


Figure 3. The effect of increasing R. ponticum density on the percent cover (row 1), proportional abundance (row 2) and species richness (row 3) of forbs, grasses, bryophytes, ferns and woody species. Species richness is the total over all nine quadrats in each plot, whereas percent cover and proportional abundance are averaged across the nine quadrats. A regression line is plotted for significant relationships only (P<0.05).

2.1.2 Results – Increasing time since R. ponticum clearance

Overall species richness increased as time since *R. ponticum* removal increased, and returned to levels indistinguishable from the uninvaded control sites by 10 to 20 years following clearance (Fig. 4). Percent cover, on the other hand, plateaued at around 100% cover, and never reached the greater than 100% cover seen in the uninvaded control sites, that is only possible when multiple layers of overlapping vegetation are present (Fig. 4). These contrasting results can be understood by looking at the effect on the different taxonomic groups separately (Fig. 5). It was revealed that bryophytes recovered well in the years following *R. ponticum* removal, regaining extensive cover. Forbs and grasses, however, did not recover in the years following *R. ponticum* removal, with their percent cover remaining significantly lower in cleared sites than in the uninvaded controls, and they never recovered sufficiently to provide a second layer of vegetation and therefore cover remained at less than 100%. In terms of proportional abundance of the different groups, cleared sites remained similar to densely invaded plots, having a higher proportion of bryophytes and a lower proportion of forbs and grasses than that found in uninvaded controls. Species richness emulated percent cover with bryophytes regaining a high species richness, and indeed exceeding the number of species found in uninvaded control sites, whereas forbs and grass species richness remained significantly lower in cleared sites than in uninvaded controls. As ferns and woody species were relatively unaffected by *R. ponticum* invasion, they did not show any dramatic responses to *R. ponticum* clearance, with any significant effects being of very low magnitude (Fig. 5).

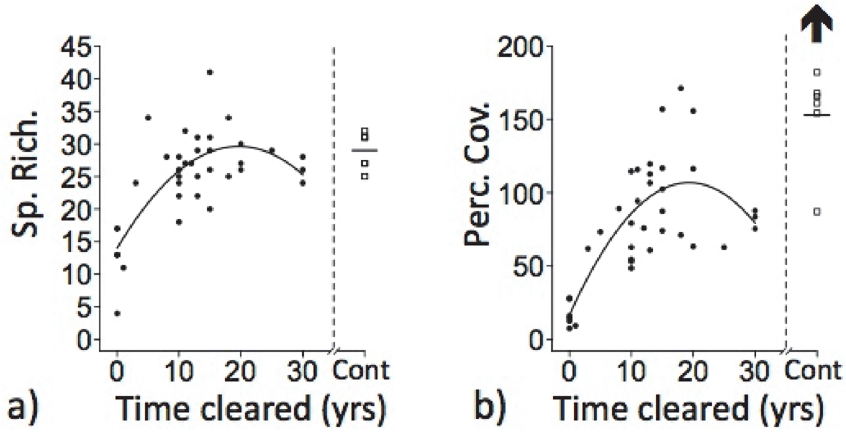


Figure 4. The effect of increasing time since R. ponticum removal on (a) understorey plant species richness and (b) vegetation cover (percent cover). Uninvaded control sites are also plotted for comparison, and the mean of these values is indicated with a horizontal bar. The arrow indicates that vegetation cover in these control sites was significantly higher than sites cleared 10-20 years ago, whereas there was no significant difference in species richness.

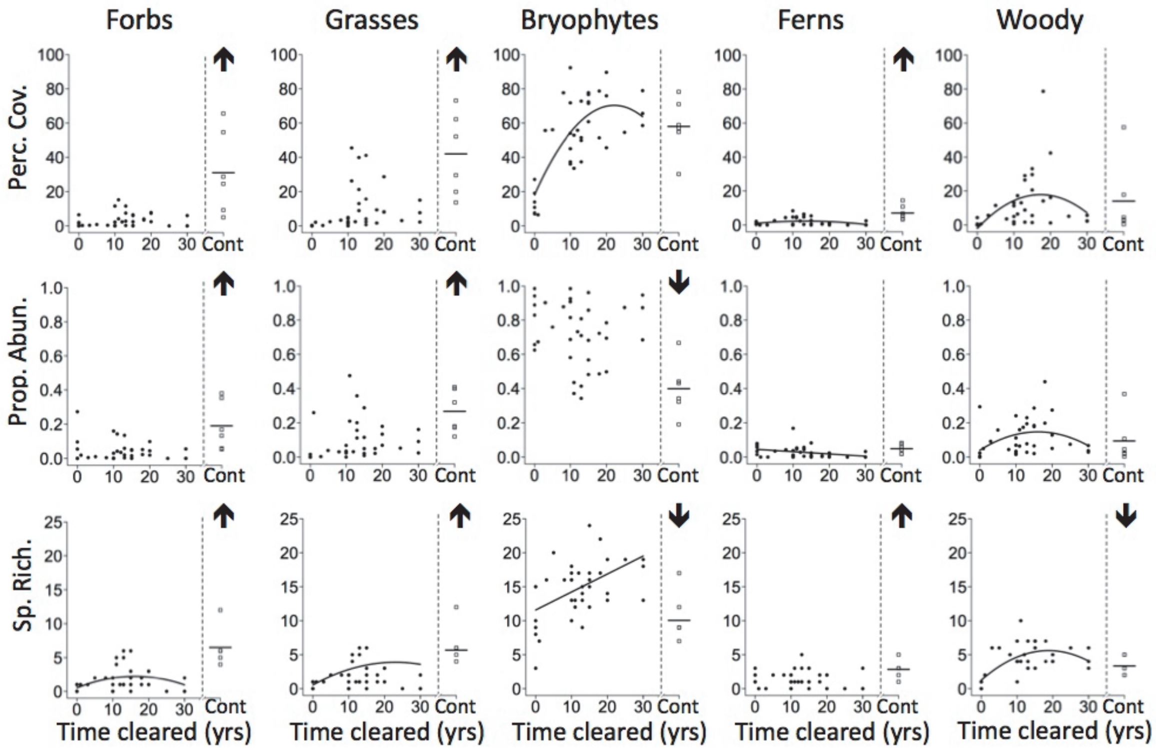


Figure 5. The effect of time since R. ponticum clearance on the percent cover (row 1), proportional abundance (row 2) and species richness (row 3) of forbs, grasses, bryophytes, ferns and woody species. The relationship is only plotted where significant at the P<0.05 level. Uninvaded control sites are plotted for comparison, with their mean value indicated by a horizontal bar. Arrows show the relationship between these control sites and the group of sites that were cleared 10-20 years ago; arrows pointing up denote that control sites have significantly higher values than the cleared sites; arrows pointing down denote that control sites have a significantly lower value than the cleared sites; and a lack of arrow denotes the lack of a significant difference.

Multivariate analyses looking at overall changes in community composition, as time since *R. ponticum* clearance increased, revealed that whilst the community did change in a predictable way following clearance (i.e. plots in a similar time period also had similar understorey communities), they were not gradually becoming similar to uninvaded control sites and instead formed unique novel communities, specific to cleared sites (Fig. 6). These communities differed from uninvaded control sites by being bryophyte dominated and lacking the typical compliment of forbs and grasses.

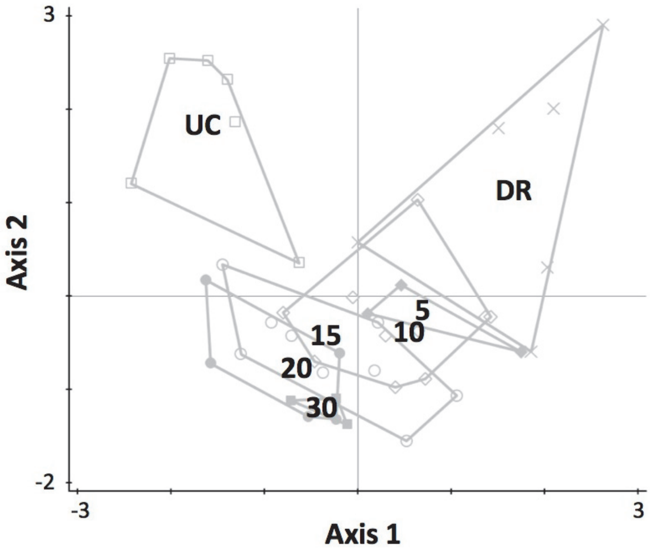


Figure 6. Classified plot diagram from a partial-RDA coding time since R. ponticum removal as levels of a factor and spatial block as a covariate. UC = uninvaded control sites; DR = dense R. ponticum sites (i.e. 'time 0'); 5-30 = number of years since R. ponticum removal. Sites follow a clear trajectory with increasing time from the top right of the diagram to the bottom left. This trajectory is not proceeding towards the community composition found in uninvaded control sites at the top left of the diagram.

2.1.3 Conclusions

Rhododendron ponticum invasion was highly detrimental to the native understorey community, with increasing density leading to a clear decline in the percent cover of forbs, grasses and bryophytes, and a decline in the species richness of forbs and grasses. Woody species, and to a lesser extent ferns, remained relatively unaffected by invasion, suggesting that tree recruitment may not be adversely affected. This may, however, be a product of the low number of tree seedlings encountered in the understorey community at all sites (including uninvaded controls) due to high levels of deer browsing.

The understorey community did not return to the community composition or overall percent cover found in uninvaded control sites even up to 30 years after successful clearance programmes. This was due to the failure of forbs and grasses to recover, and was partly offset by a strong bryophyte recovery with more species of bryophyte being found in cleared sites than in uninvaded controls. This included several species with an Atlantic distribution such as *Lepidozia cupressina* and *Dicranodontium denudatum*. This successful bryophyte recovery was likely aided by the lack of competition from the forbs and grasses. Further restoration measures are clearly needed to facilitate the recovery of native forbs and grasses following *R. ponticum* removal. However, these measures must take into account local conservation priorities, and aiding the recovery of forbs and grasses may actually be detrimental in areas where sensitive bryophytes species appear to be benefitting from the lack of competition. The successful recovery of bryophytes following clearance should in no way encourage complacency as to the importance of removing *R. ponticum* and ensuring that sites remain free from re-invasion. Dense stands were irrefutably demonstrated to be detrimental to all groups (apart from woody species) and the removal of this destructive invasive species remains a high conservation priority.

2.2 How does the epiphytic bryophyte community change following *R. ponticum* clearance?

This study utilised the same series of sites as the previous analysis looking at understorey community composition along a gradient of time since *R. ponticum* clearance. To assess the epiphytic bryophyte community at each site, nine oak trees and nine birch trees were selected at random within the 20 m x 20 m grid established to assess understorey community composition. In cases where insufficient trees of each species were available within the grid, the nearest suitable trees were utilised. A 30 cm tall by 10 cm wide mini-quadrat was placed on the North-facing side of each sample tree at the base of the tree and also at breast height to record the total percent cover of every plant species present in the quadrat (principally mosses and liverworts, but occasionally including ferns and vascular species). The total number of species encountered at each site (i.e. species richness) was also recorded. Survey data was therefore gathered for four separate 'quadrat-types': birch at the tree base ('birch lower'), birch at breast height ('birch upper'), oak at the tree base ('oak lower') and oak at breast height ('oak upper'). The total lichen cover in each quadrat was recorded (an average of 12% across the survey), but individuals were not identified to species-level and were therefore excluded from the statistical analyses.

A series of mixed effect models were then used to determine the effect of increasing time since *R. ponticum* clearance on the overall percent cover, proportional abundance and species richness. These analyses were also performed for mosses, liverworts, and Atlantic species separately. Multivariate analysis (Redundancy Analysis) was then used to reveal overall changes in community composition as site recovery progressed with increasing time since *R. ponticum* clearance. Bray-Curtis similarity indices were also calculated to monitor the difference in community composition between cleared sites and the nearest uninvaded control site.

2.2.1 Results

Results for overall percent cover of all epiphytic plant species were equivocal, with a significant increase as time since *R. ponticum* clearance increased for birch lower and oak upper quadrats, but no significant change detected for birch upper and oak lower quadrats Fig. 7). These equivocal results were due to different sub-communities responding to *R. ponticum* clearance in different ways, with liverworts showing a clear increase as time since *R. ponticum* clearance increased, but mosses showing no trend, or an actual decrease with time in the case of birch lower quadrats. Results for species richness revealed a similar trend (Fig. 8), with liverwort species richness increasing dramatically in the years following *R. ponticum* clearance, and mosses showing little change (Except in oak lower quadrats). In this case, the impact on liverworts produced an effect on overall species richness, which increased in the years following *R. ponticum* clearance.

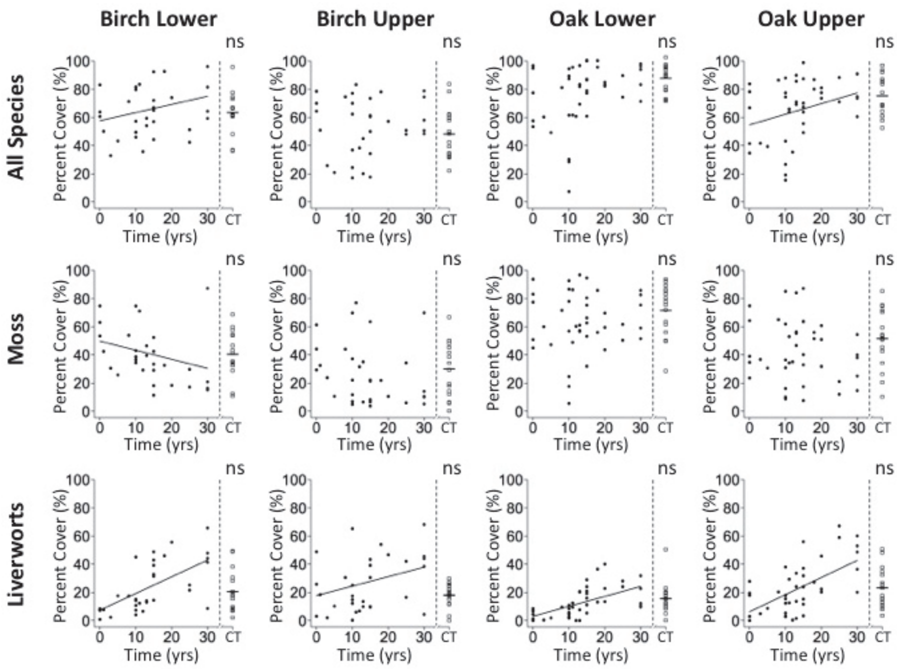


Figure 7. The difference in percent cover of all species (row 1), mosses (row 2), and liverworts (row 3) as time since R. ponticum clearance increased for all four quadrat types. Uninvaded control sites (CT) are plotted at the right of each graph for comparison with the mean value marked as a horizontal line. Regression lines are plotted where significant, and 'ns' denotes that there were no significant differences between sites cleared more than ten years ago and uninvaded control sites.

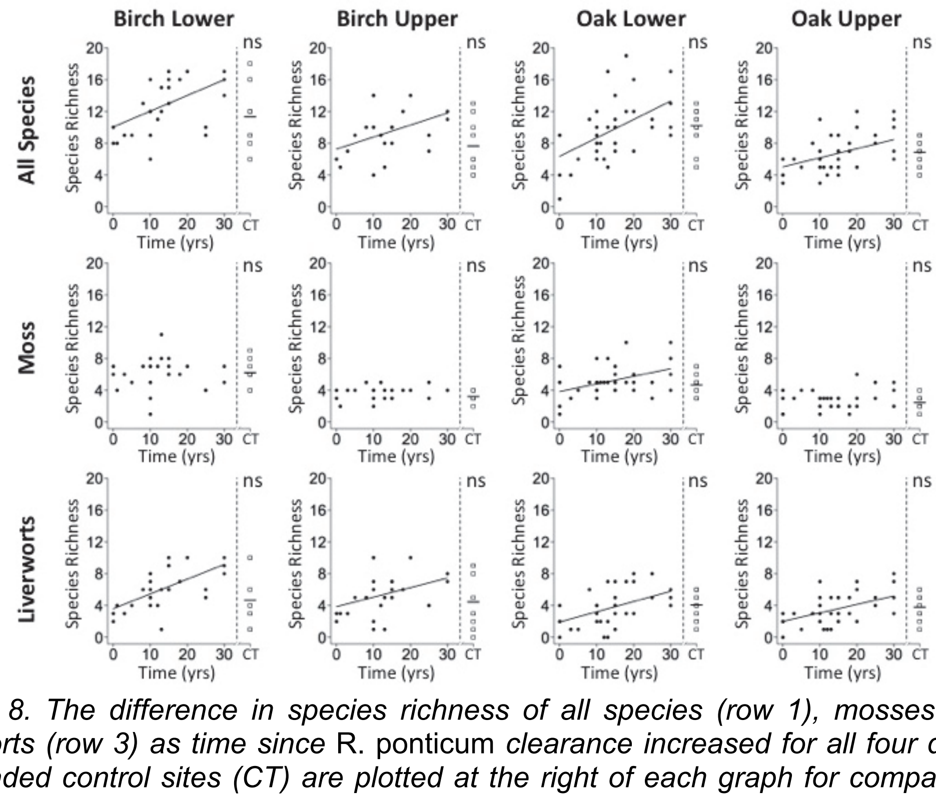


Figure 8. The difference in species richness of all species (row 1), mosses (row 2), and liverworts (row 3) as time since R. ponticum *clearance increased for all four quadrat types. Uninvaded control sites (CT) are plotted at the right of each graph for comparison with the mean value marked by a horizontal line. Regression lines are plotted where significant, and 'ns' denotes that there were no significant differences between sites cleared more than ten years ago and uninvaded control sites.*

In contrast to the understorey community, the multivariate analysis revealed little difference in overall community composition of the epiphytic plant community as time since *R. ponticum* clearance increased (Fig. 9). Indeed, there was even some degree of overlap between the community composition of uninvaded control sites and dense *R. ponticum* sites, suggesting that invasion does not affect the epiphytic plant community as much as the understorey community. Although the differences were not large, communities with 20 to 30 years of recovery following *R. ponticum* removal were more similar to uninvaded control sites than those with only 10 years of recovery, suggesting that the epiphytic plant community recovers well following clearance and will ultimately return to a similar composition to that found in uninvaded controls. Analysis of the Bray-Curtis similarity between cleared sites and the closest uninvaded control sites confirmed that there was little difference in community composition between sites falling into different time periods.

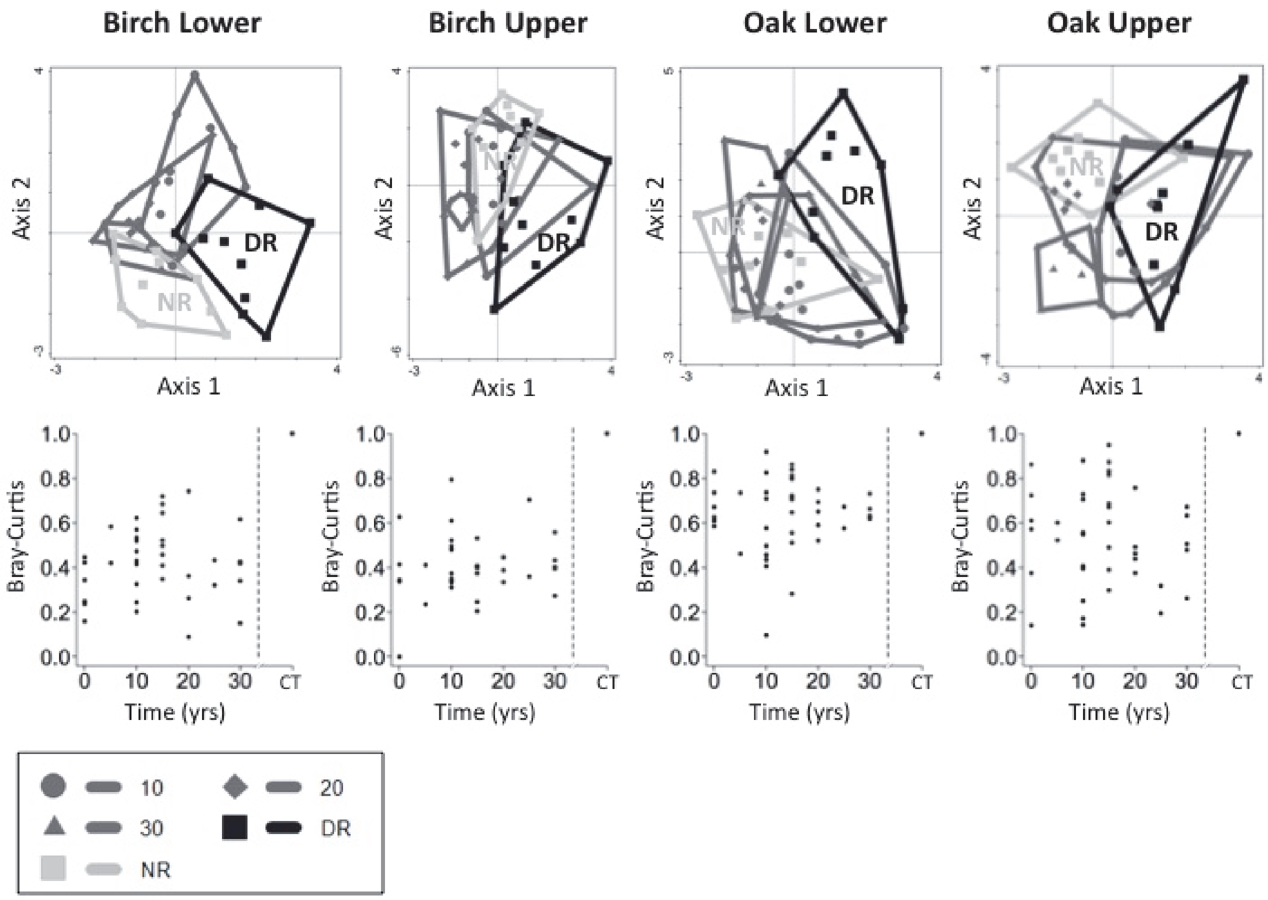


Figure 9. Change in community composition as time since R. ponticum clearance increased. Row 1 shows classified plot diagrams from the partial-RDA coding time since R. ponticum clearance as a categorical variable. The shapes delineate the extent of the sites belonging to the same time period. DR represents sites with dense R. ponticum ('Time 0') and NR represents sites with no R. ponticum (uninvaded controls). Row two presents the Bray-Curtis similarity index, comparing cleared sites to the relevant uninvaded control (CT) sites. Control sites have a value of 1, since they are necessarily identical to themselves. No significant increases in similarity were found as sites increased in time since R. ponticum clearance.

Focussing on the Atlantic species only revealed that they too recovered well, with both their overall percent cover and species richness increasing in the years following *R. ponticum* removal (Fig. 10). Comparing the communities found under dense *R. ponticum* stands with both cleared and uninvaded sites revealed that Atlantic species are associated with both cleared stands and uninvaded sites, but that dense *R. ponticum* is unequivocally bad for epiphytic Atlantic species (Fig. 11).

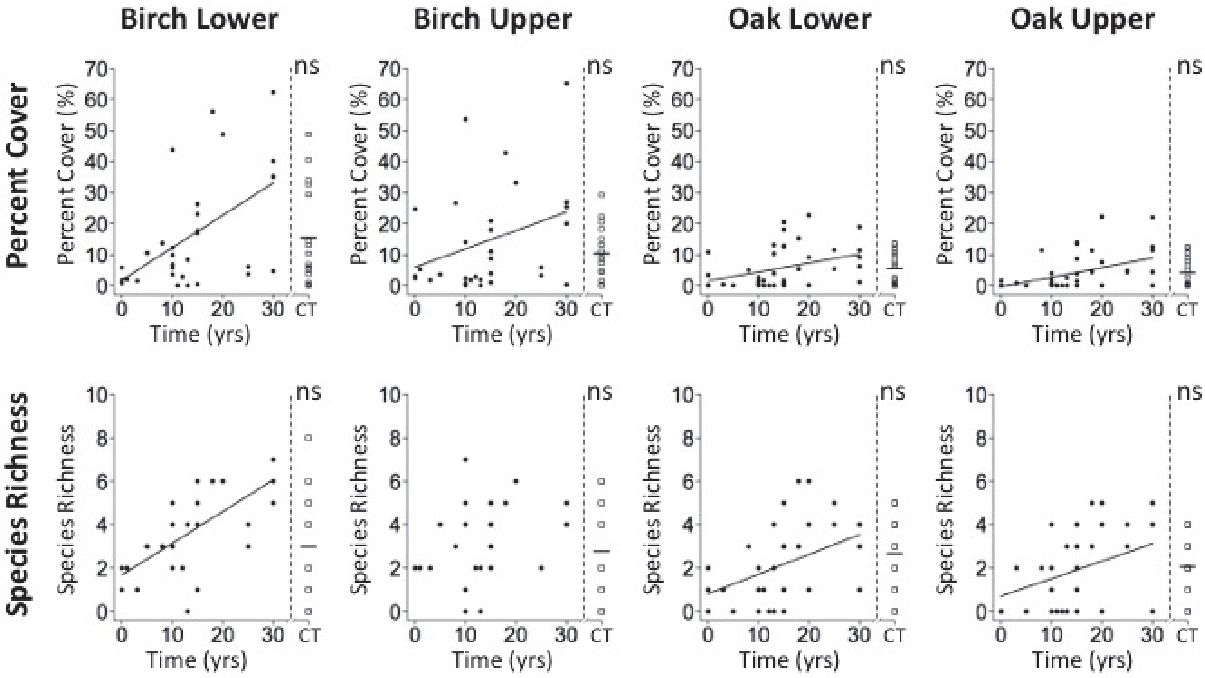


Figure 10. The difference in percent cover (row 1) and species richness (row 2) for Atlantic species as time since Rhododendron clearance increased. Uninvaded control sites (CT) are plotted at the right of each graph for comparison with the mean value marked as a horizontal line. Regression lines are plotted where significant, and 'ns' denotes that there were no significant differences between sites cleared more than ten years ago and uninvaded control sites.

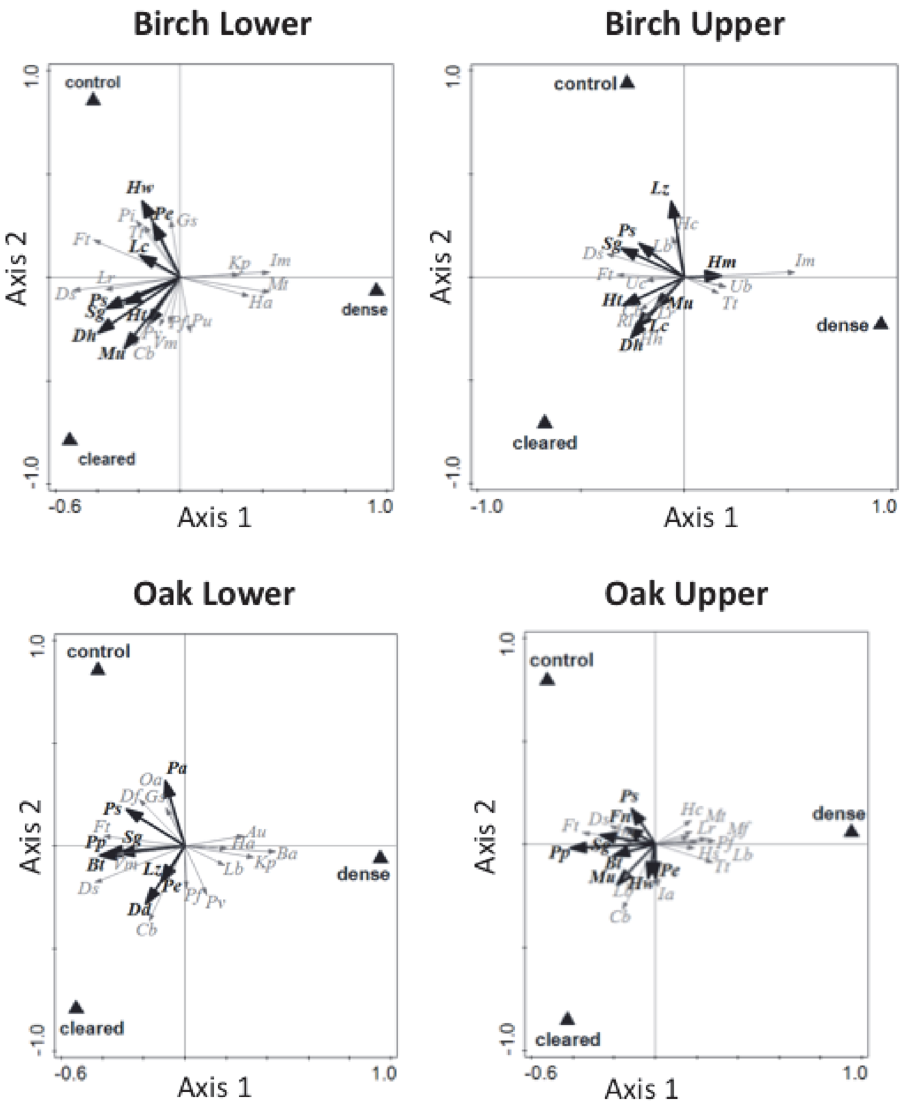


Figure 11. Response of Atlantic species to Rhododendron treatment. The graphs show the results of partial-RDAs revealing the affinity of different species for sites with dense Rhododendron, sites where Rhododendron had been cleared, and uninvaded control sites. Atlantic species (highlighted in bold) showed a clear preference for cleared and control sites. Species are: Au – Atrichum undulatum; Ba – Barbilophozia attenuata; Bt – Bazzania trilobata; Cb – Cephalozia bicuspidata; Dd – Dicranodontium denudatum; Df – Dicranum fuscescens; Dh – Drepanolejeunea hamatifolia; Ds – Dicranum scoparium; Fn – Frullania teneriffae Ft – Frullania tamarisci; Gs – Galium saxatile; Ha – Hypnum andoi; Hc – Hypnum cupressiforme; Hh – Hedera helix; Hm – Harpalejeunea molleri; Ht – Hymenophyllum tunbrigense; Hw – Hymenophyllum wilsonii; Im – Isothecium myosuroides; Kp – Kindbergia praelonga; Lb – Loeskeobryum brevirostre; Lc – Leptoscyphus cuneifolius; Lr – Lepidozia reptans; Lz – Lepidozia cupressina; Mt – Metzgeria temporata; Mu – Microlejeunea ulcina; Oa – Oxalis acetosella; Pa – Plagiochila atlantica; Pe – Plagiochila exigua; Pf – Polytrichum formosum; Pi – Pleurozium schreberi; Pp – Plagiochila punctata; Ps – Plagiochila spinulosa; Pu – Plagiothecium undulatum; Pv – Polypodium vulgare; Rl – Rhytidiadelphus loreus; Sg – Scapania gracilis; Tt – Thuidium tamariscinum; Ub – Ulota bruchii; Uc – Ulota crispa; Vm – Vaccinium myrtillus;

2.2.2 Conclusions

The epiphytic plant community, including Atlantic bryophyte species, was able to recover well in the years following *R. ponticum* clearance. Whilst invasion caused a marked decrease in overall abundance, the community still resembled that found in uninvaded sites and returned to a similar community composition by 20 to 30 years following clearance. This is an encouraging message that, whilst *R. ponticum* invasion is detrimental, the epiphytic plant community appears able to recover within a reasonable timescale once effective clearance has been achieved.

2.3 Is the native seed bank depleted during *R. ponticum* invasion and does it recover following clearance?

A greenhouse germination trial was conducted to compare the seed bank present at uninvaded control sites, densely invaded sites and sites that were cleared more than ten years previously. Ten sites were selected from each of these three categories out of the sites surveyed for the community composition study in section 2.1. At each site 40 soil cores of 5.5 cm diameter and 8 cm depth were collected and combined to give a single soil sample from each site. These samples were transported back to the greenhouse at the James Hutton Institute (Aberdeen) and spread out in trays at 1 cm depth to reveal what seedlings germinated from the seed bank present in the soil at each site. Greenhouse temperature was regulated at 20°C and natural daylight provided the sole source of light with daylength varying from a maximum of 17 h 55 min to a minimum of 9 h 30 min over the study period. Seed trays were monitored every week and emerging seedlings were identified, counted and then removed. The soil in each tray was thoroughly mixed after 10 weeks to bring new seeds to the surface. The study was allowed to run for 20 weeks from early June until late October by which time very few new seedlings were emerging from the trays. Control trays (containing sterile compost) revealed that greenhouse contamination (i.e. from Aberdeenshire seeds entering the greenhouse and germinating in the trays) was negligible.

The total number of seedlings emerging from the seed bank was divided by the total area of soil collected per site (0.095 m^2) to give the overall density of each species per 1 m^2 soil to 8cm depth for each site. One emerging seedling in the experiment is therefore equivalent to 10.5 seeds per m^2. Analysis of Variance (ANOVA) was used to test the effect of *R. ponticum* category (uninvaded, dense or cleared stands) on 1) the total number of seedlings to emerge from the seed bank, 2) native species richness of emerging seedlings, 3) the total number of grasses to emerge from the seed bank, 4) the total number of forbs to emerge from the seed bank, 5) the total number of *R. ponticum* seedlings to emerge from the seed bank and 6) the total number of birch *(Betula pendula)* seedlings to emerge from the seed bank. Redundancy analysis (RDA) was then used to compare the overall composition of the plant community emerging from the seed bank. Monte Carlo permutations (999 permutations) were used to assess if the three categories (uninvaded, dense or cleared stands) explained a significant amount of the variation in the species composition.

2.3.1 Results

Across the entire study, 6,572 individual seedlings emerged from the seed bank belonging to thirty-nine different species (although individuals of *Juncus* and *Carex* were identified to genus level only due to difficulties in accurately identifying these groups to the species level at the seedling stage). Table 1 presents the total counts for all species that were present in 5 or more sites across the experiment. *Betula pendula, Carex sp.* and *Juncus sp.* were commonly found in all three treatment types. A variety of additional species were commonly encountered in uninvaded control sites, whereas few other species were common in both dense and cleared sites apart from *R. ponticum* which was found germinating from the seed bank in all the dense sites and half of the cleared sites.

Table 1. List of principle species emerging from the seed bank. Table includes all species present in five or more sites across the whole experiment. The table lists the total number of seedlings that emerged across the whole experiment (total count) and the total number of sites where that species was present for each of the three R. ponticum categories. Species present in five or more sites per treatment are highlighted in bold.

Species	Total Count	No. Uninvaded Sites	No. Dense Sites	No. Cleared Sites
Agrostis canina	246	**10**	4	**5**
Agrostis capillaris	154	**9**	4	4
Anthoxanthum odoratum	356	**10**	2	3
Betula pendula	2872	**10**	**10**	**10**
Cardamine flexuosa	33	1	2	2
Carex sp.	141	**10**	**9**	**7**
Deschampsia flexuosa	19	**5**	1	4
Digitalis purpurea	211	**5**	**5**	3
Empetrum nigrum	12	2	2	4
Holcus lanatus	83	**9**	0	1
Holcus mollis	48	**7**	0	2
Hyacinthoides non scripta	262	**9**	3	0
Juncus sp.	669	**10**	**7**	**8**
Lysimachia nemorum	33	**5**	2	0
Melampyrum pratense	313	4	2	2
Oxalis acetosella	126	**9**	1	2
Potentilla erecta	168	**8**	2	2
Rhododendron ponticum	334	0	**10**	**5**
Rubus fruticosus	40	3	**7**	3
Sagina procumbens	136	**5**	**6**	2
Stellaria media	30	3	1	2
Stellaria holostea	14	4	1	0
Vaccinium myrtillus	14	2	1	2
Vaccinium vitus idaea	36	**6**	2	1
Veronica chamaedrys	10	2	4	1
Viola riviniana	35	**5**	0	0

No significant difference was detected in the total number of seedlings emerging from the different site types (uninvaded, dense or cleared; Fig. 12a). There was, however, a significant impact on the species richness of seedlings emerging at the different sites, with uninvaded sites having significantly more species emerging from the seed bank than dense or cleared sites (Fig. 12b). This discrepancy between the results for the total number of emerging seedlings and the species richness of those seedlings is explained by uninvaded sites featuring a wide variety of species with high numbers of forbs and grasses (Fig. 13), whereas dense and cleared plots featured very few grass seeds and only a moderate number of forb seeds. Instead, dense and cleared sites were strongly dominated by a single species; *R. ponticum* (Fig. 14) in the case of dense sites and *B. pendula* (Fig. 15) in the case of cleared sites. There was, however, a large variance in the number of *B. pendula* seedlings emerging from cleared sites, which resulted in no significant difference being found between the site types (Fig. 15). This can perhaps be explained by a high birch recruitment following *R. ponticum* clearance due to the dramatic increase in light intensity triggering germination in dormant seeds. In sites with low deer density these recruits would grow quickly to contribute additional birch seed to these sites by the time the soil samples were collected (at least ten years following *R. ponticum* clearance). In sites with high deer density, however, these recruits would never grow to produce seed of their own and so birch seedling emergence remained low at these sites.

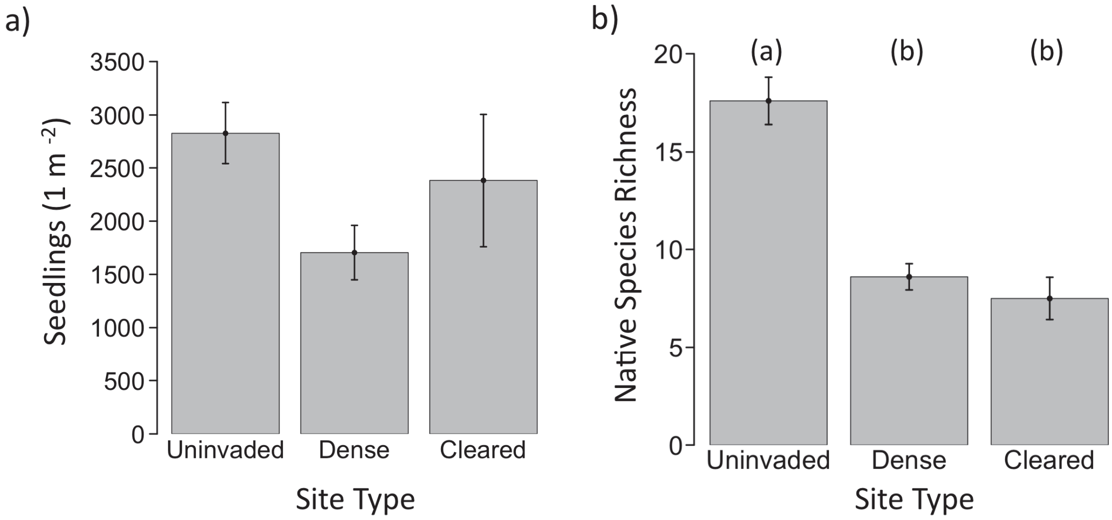


Figure 12. (a) Total number of seedlings that emerged from the seedbank (scaled to number per 1 m^2 of soil to a depth of 8cm) and (b) native species richness (total number of species encountered in each plot) in uninvaded, cleared and dense R. ponticum categories. Bars show averages for each R. ponticum category with standard errors.

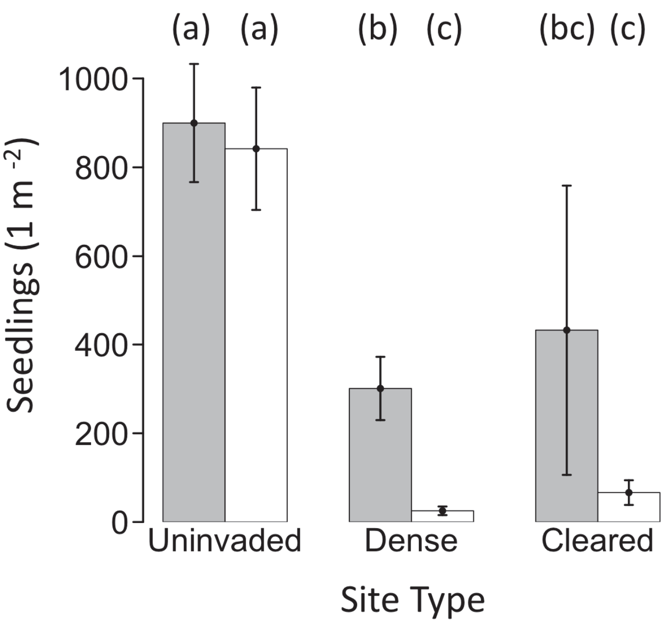


Figure 13. Total number of forb seedlings (gray bars) and grass seedlings (white bars) that emerged from sites in uninvaded, dense and cleared site types. Results are means ± 1SE.

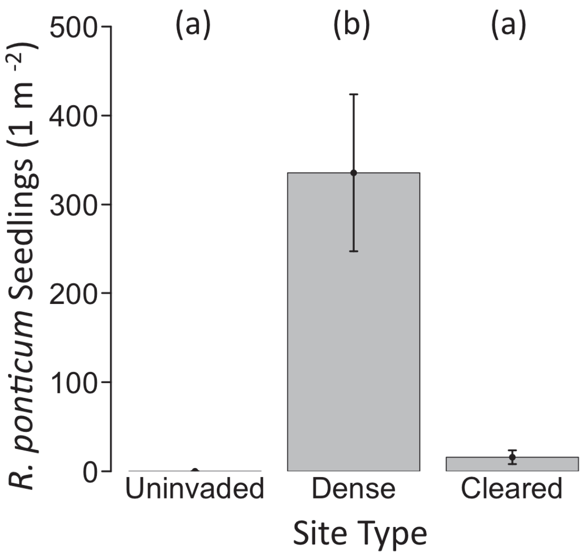


Figure 14. Number of R. ponticum seedlings that emerged from sites in uninvaded, cleared and dense R. ponticum categories (scaled to number per 1 m^2 of soil to a depth of 8cm). Bars show averages for sites in each category with standard errors.

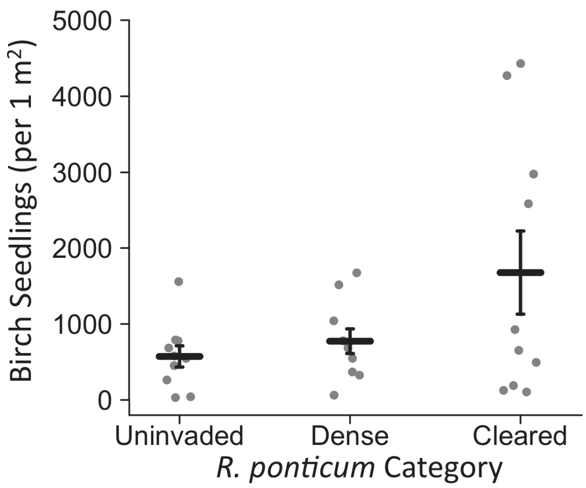


Figure 15. Total number of birch seedlings that emerged from sites in uninvaded, cleared and dense R. ponticum categories (scaled to number per 1 m^2 of soil to a depth of 8cm). Grey dots show the number of seedlings that emerged per 1 m^2 of soil in each site – the data is 'jittered' to reveal overlapping points. Bars show means for sites in each category with standard errors.

Redundancy Analysis (RDA) revealed that a significant amount of the variation in the emerging seedling communities was explained by *R. ponticum* category (Fig. 16a). Most species showed a clear affiliation with the uninvaded plots, apart from *R. ponticum, Rubus fruticosus* and *Veronica chamaedrys* which showed an affiliation with dense *R. ponticum* plots, and birch *(Betula pendula)* which showed an affiliation with cleared plots (Fig. 16b). This analysis clearly demonstrated that the seed bank present at uninvaded, dense and cleared sites was very different and showed that cleared sites lacked a sufficient diversity of native seeds to successfully recover in the absence of additional conservation measures.

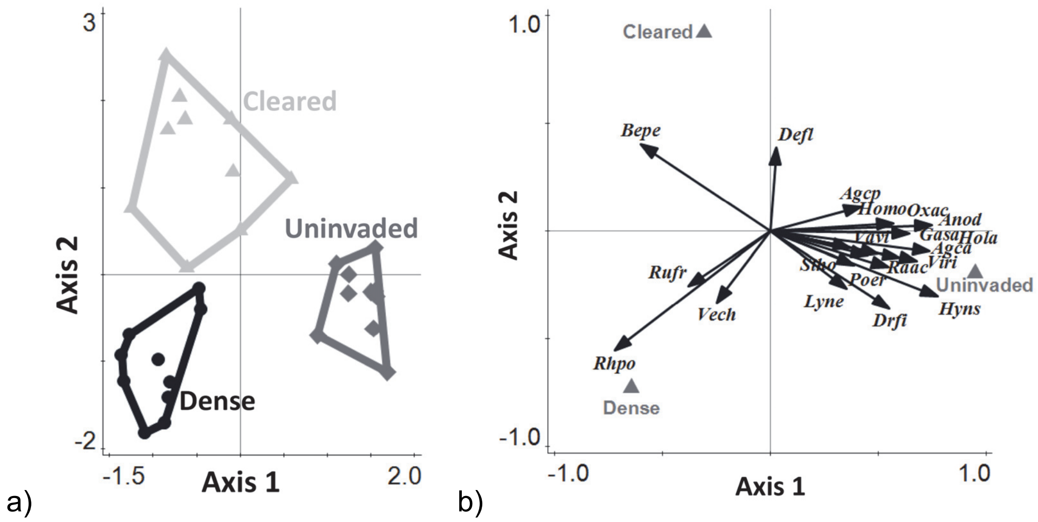


Figure 16. (a) Classified plot diagram and (b) species-environment biplot from an RDA of the community composition of seedlings emerging from the seedbank, using R. ponticum category (uninvaded, cleared or dense R. ponticum) as the only explanatory variable. Agca = Agrostis canina; Agcp = Agrostis capillaris; Anod = Anthoxanthum odoratum; Bepe = Betula pendula; Defl = Deschampsia flexuosa; Drfi = Dryopteris filix-mas; Gasa = Galium saxatile; Hola = Holcus lanatus; Homo = Holcus mollis; Hyns = Hyacinthoides non-scripta; Lyne = Lysimachia nemorum; Oxac = Oxalis acetosella; Poer = Potentilla erecta; Raac = Ranunculus acris; Rhpo = Rhododendron ponticum; Rufr = Rubus fruticosus; Stho = Stellaria holostea; Vech = Veronica chamaedrys; Viri = Viola riviniana.

2.3.2 Conclusions

Rhododendron ponticum invasion was demonstrated to be highly detrimental to the native seed bank, with densely invaded sites having half the number of species present in the seed bank as uninvaded control sites. The seed bank at cleared sites was similarly species poor, revealing that successful site recovery would not be possible relying only on the seed bank naturally present at cleared sites. The seed bank at cleared sites was, however, strongly dominated by birch, suggesting that tree recruitment may be facilitated by *R. ponticum* clearance in the absence of intensive deer browsing. This evidence suggests that whilst tree species may recover unaided, native grasses and forbs are likely to require additional management interventions, such as re-seeding, in order to recover successfully. Whilst reseeding is likely necessary to achieve the restoration of a full complement of native species, its implementation needs to be carefully considered taking local conservation priorities into account. Since commercially available seed stocks are unlikely to be of local provenance, the implications of introducing new genetic stock into an area, as well as considering the appropriate balance of species to introduce as seed, must be considered on a site-specific basis. Businesses that supply seeds from specified, regional stocks are useful in supplying appropriate seeds for many areas.

The low average number of *R. ponticum* seedlings emerging from the seed bank of cleared sites was highly encouraging, suggesting that re-invasion from the seed bank (or from novel seed arriving at the site) would be minimal, and confirming previous reports that *R. ponticum* does not form a permanent seed bank (Cross 1975). This contrasts somewhat with observations that sites are quickly recolonised following clearance efforts and strongly suggests that the rapid return of *R. ponticum* to these sites is due to small seedlings being missed and underground buds being insufficiently destroyed in the original clearance efforts. If initial clearance efforts are successful, the low levels of *R. ponticum* seed remaining in the soil should mean that complete eradication is feasible. The results presented in Table 1, however, revealed that half of cleared sites did have at least some *R. ponticum* seed present, suggesting that whilst *R. ponticum* seed density was very low at cleared sites, constant monitoring would be necessary to prevent these few seeds recruiting to form a seed producing adult population.

2.4 Does *R. ponticum* exert a toxic legacy on the soil that could hinder site recovery following its removal?

Soil samples were collected at each of the sites surveyed in section 2.1 to reveal changes to soil chemistry a) as *R. ponticum* density increased and b) in the years following *R. ponticum* clearance. These samples were analysed for C:N ratios and pH, and ion exchange soil probes were deployed at a subset of 20 sites along the *R. ponticum* density gradient to reveal changes in nutrient status (NO_3, NH_4, P, K, Ca and Mg).

2.4.1 Results

No significant changes in soil chemistry were discovered either as *R. ponticum* density increased (Fig. 17) or in the years following *R. ponticum* clearance (Fig. 18).

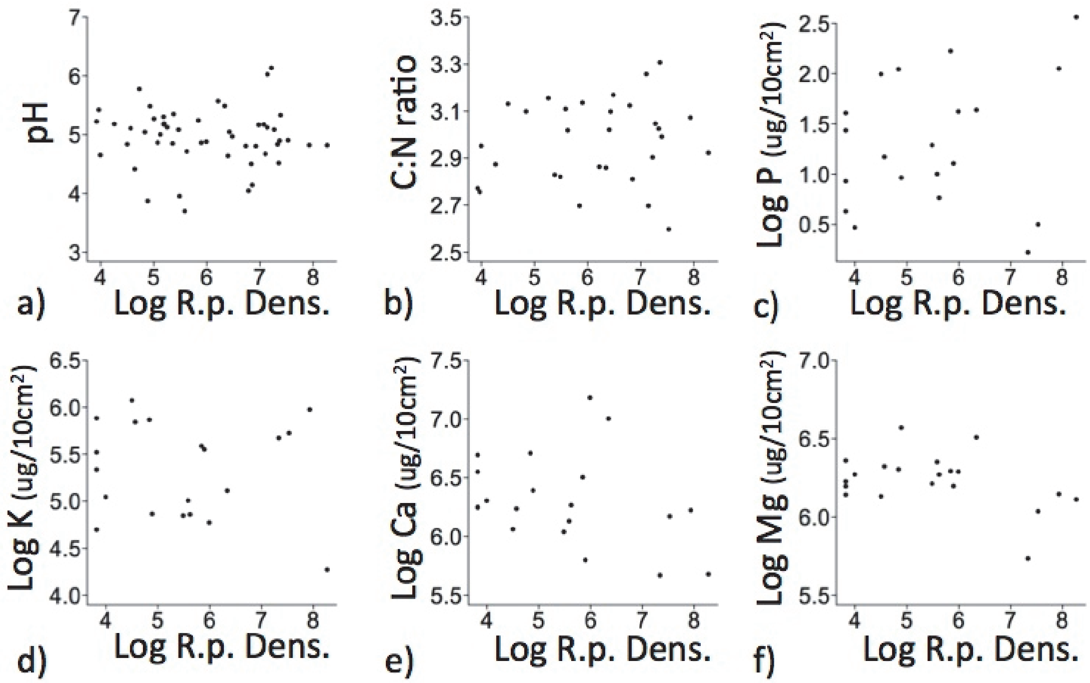


Figure 17. The effect of R. ponticum *density on (a) pH, (b) Carbon:Nitrogen ratio, (c) Phosphorus, (d) Potasium, (e) Calcium and (f) Magnesium. There were no significant changes in any measure of soil chemistry as R. ponticum density increased.*

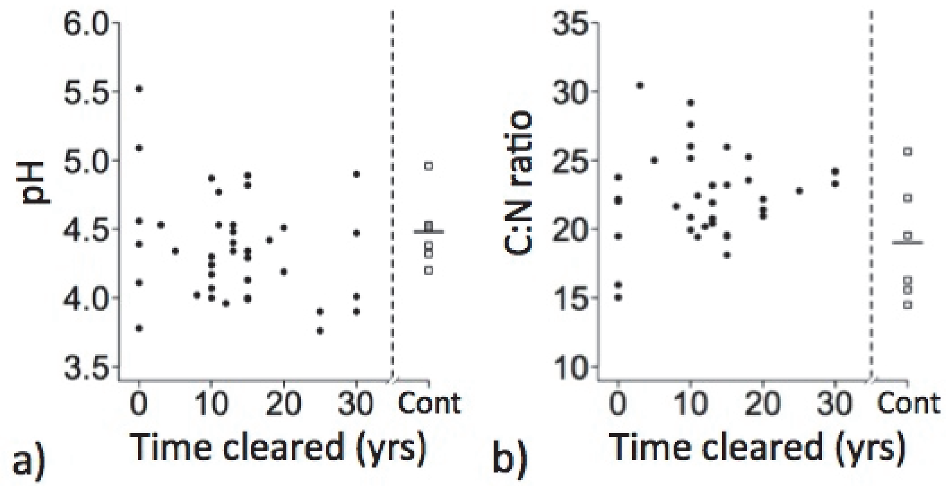


Figure 18. There was no effect of time since R. ponticum clearance on either (a) pH or (b) C:N ratio. Uninvaded control sites (Cont) are plotted for comparison and their mean value is denoted with a horizontal line.

2.4.2 Conclusions

Contrary to expectation, no evidence of *R. ponticum* exerting a 'toxic effect' on the soil was forthcoming, with no decrease in pH or nutrient availability being detected. Whilst it is possible that *R. ponticum* had an effect on a component of soil chemistry not measured in this analysis (such as polyphenol content or the mycorrhizhal community), seed addition experiments detailed below in section 2.5 suggest that native plants can grow in soil that has previously been subject to *R. ponticum* invasion. This suggests that there is no toxic legacy of *R. ponticum* invasion in the soil, but rather that seed limitation prevents the natural regeneration of native communities following the removal of invasive stands. The lack of a toxic legacy on soil chemistry is highly encouraging as it suggests that intensive management techniques such as large-scale soil treatments or soil replacement will not be necessary in order to achieve effective restoration following the clearance of invasive *R. ponticum*.

2.5 What additional restoration techniques would be successful at facilitating site recovery following *R. ponticum* clearance?

An experimental trial was carried out to understand the importance of a) seed limitation, b) microsite limitation and c) chemical legacy effects in the soil in hindering site recovery following the clearance of invasive *R. ponticum* stands. This experiment was carried out on National Trust for Scotland land in Merkland Wood on the Isle of Arran. This woodland had been subject to extensive *R. ponticum* invasion but had been successfully clear of invasive bushes since 1988. Similarly to other previously invaded sites, few native vascular plants had returned with the ground being largely covered with the common mosses *Thuidium tamariscinum* and *Kindbergia praelonga,* with a low cover of ferns and brambles. The addition of a seed mix (comprising 2 g *Agrostis capillaris* seeds, 2 g *Deschampsia flexuosa* seeds, 2 g *Anthoxanthum odoratum* seeds, 2 g *Hyacinthoides non-scripta* seeds and 1 g *Potentilla erecta* seeds, obtained from Scottish seed stock supplied by Scotia Seeds, Brechin) was used to test for seed limitation. The removal of the existing vegetation layer was used to test for microsite limitation, following the hypothesis that a dense bryophyte layer inhibits the germination and survival of any vascular plant seeds arriving at the site. The application of activated carbon (which mitigates any effect of *R. ponticum* toxins such as polyphenols) and fertiliser (which mitigates any nutrient depletion caused by *R. ponticum* invasion) was used to test for chemical legacy effects.

Experimental units of 1 m^2 were established using the following treatment combinations, with ten replicates per treatment: 1) seed only; 2) seed + activated carbon; 3) seed + fertiliser; 4) seed + vegetation removal; 5) seed + activated carbon + fertiliser; 6) seed + activated carbon + vegetation removal; 7) seed + fertiliser + vegetation removal; 8) seed + activated carbon + fertiliser + vegetation removal; 9) vegetation removal only; and 10) unmanipulated control. The activated carbon and fertiliser treatments were only applied in the presence of the seed mix to reduce the overall number of treatments to a reasonable number since theses treatments would have little application on their own.

The percent cover of every plant species present in each experimental unit was recorded after two years and used to calculate the total percent cover of all species, of the five species planted as seed, of all grasses, all forbs, all bryophytes, all woody species and all ferns. A full three-way anova was then constructed using ‘R’ statistical software to test the effect of vegetation removal, activated carbon and fertiliser on each of these measures.

2.5.1 Results

The vegetation removal treatment predictably caused there to be significantly less vegetation in the experimental units at the end of the experiment (Fig. 19). However, when this was coupled with seed addition the species added as seed effectively compensated for the removed vegetation and resulted in similar levels of vegetation cover as in unmanipulated controls (Fig. 19). However, the community present under the different treatments looked rather different, with seed addition causing a dramatic increase in grass cover and a small increase in forb cover, and vegetation removal principally causing a reduction in bryophyte cover (Fig. 20).

Adding seed without first removing the vegetation did not result in a significant increase in vegetation cover compared to the unmanipulated controls (Fig. 19). However, some of the species planted as seed did establish successfully where the vegetation was not removed (to give around 17% cover), albeit at a lower density than in the plots where the vegetation was also removed (which attained around 42% cover; Fig. 21). Contrary to expectation, adding activated carbon or fertiliser had no significant impact on the cover of species planted as seed (Fig. 21), confirming the results from section 2.4 above that site recovery following *R. ponticum* removal is not hampered by a toxic legacy in the soil.

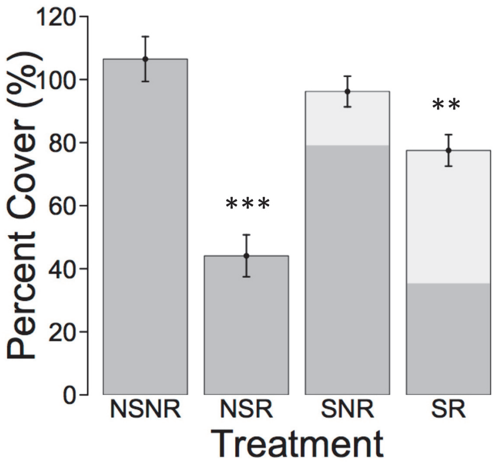


*Figure 19. Summed percent cover of all plant species present in the quadrats in 2015 with and without seed application and vegetation removal. NSRS = no seed, no vegetation removal (i.e. unmanipulated control); NSR = no seed, with vegetation removal; SNR = with seed, no vegetation removal; SR = with seed and with vegetation removal. The light grey areas show the cover of the five species that were planted as seed, whereas the dark grey areas show the cover of naturally occurring vegetation. *** Indicates a significant effect of the vegetation removal treatment at the P<0.001 level, ** indicates a significant interaction between the vegetation removal treatment and the seed addition treatment at the P<0.01 level.*

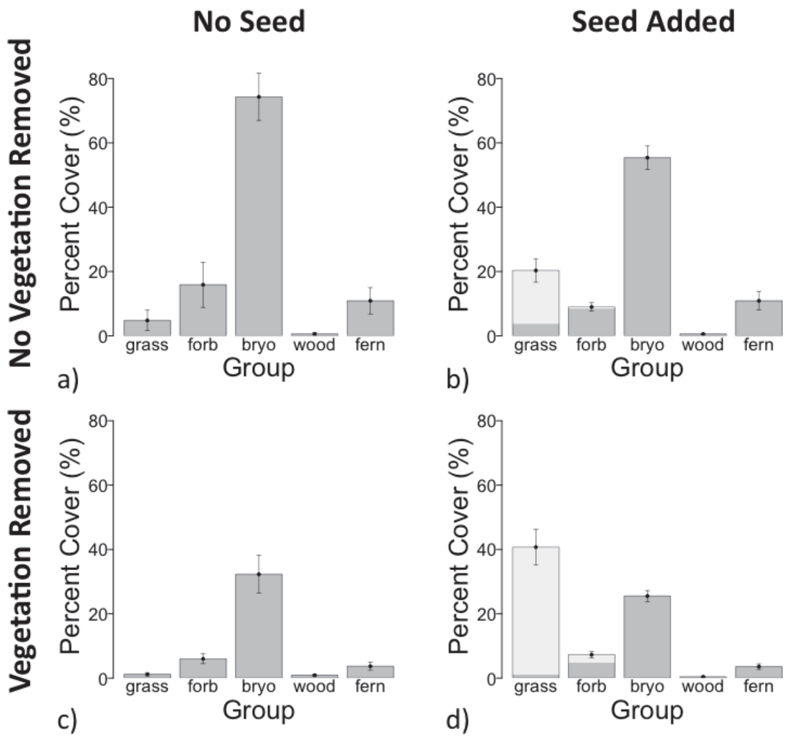


Figure 20. Effect of seed addition and vegetation removal on grasses, forbs, bryophytes (bryo), woody species (wood) and ferns. a) no seed, no vegetation removed; b) seed added, no vegetation removed; c) no seed, vegetation removed; d) seed added, vegetation removed. The light grey portion of the bars shows the percent cover of the five species planted as seed, whereas the dark grey portion of the bars shows the natural vegetation.

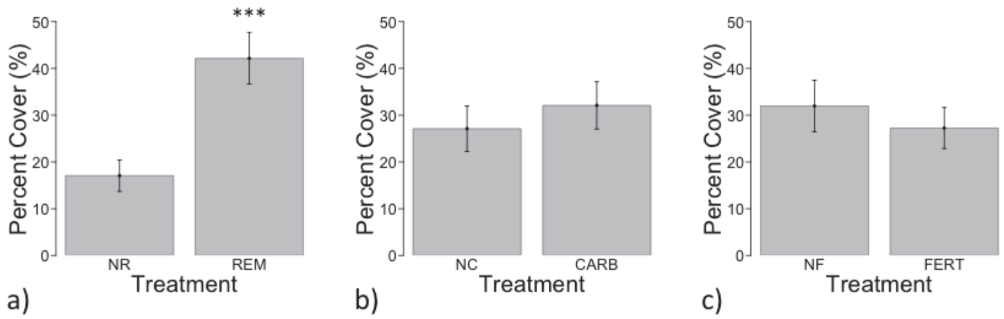


*Figure 21. Effect of a) vegetation removal, b) activated carbon, and c) fertiliser on the percent cover of species planted as seed. REM = vegetation removed, NR = no removal, CARB = activated carbon added, NC = no activated carbon added, FERT = fertiliser added, NF = no fertiliser added. Error bars show the standard errors in all graphs, *** indicates a significant result at the P<0.001 level.*

2.5.2 Conclusions

This experiment complemented the findings of section 2.4 above in confirming that chemical legacy effects in the soil are not a major factor in preventing the recovery of native vegetation following *R. ponticum* clearance. Instead it was revealed that the lack of native seed was the principle factor limiting site recovery, coupled with the presence of a dense bryophyte layer forming a significant barrier to establishment. This experimental trial demonstrated that seed addition can be an effective way of restoring elements of native vegetation that have been lost due to *R. ponticum* invasion. This technique does work in isolation, but is particularly effective when applied following the removal of the existing bryophyte layer. Bryophyte removal is likely to be important in encouraging seedling recruitment in similar sites that have been cleared for some time and have an established bryophyte layer. It may be that a seed application immediately following *R. ponticum* clearance, i.e. before the bryophyte layer forms, would be an optimal restoration strategy precluding the need for time consuming vegetation clearance.

These results are highly encouraging as they suggest that extensive soil treatments are unnecessary to combat any legacy of *R. ponticum* invasion and demonstrate that conditions following *R. ponticum* clearance are adequate for the successful growth of native species. Instead, it seems likely that the long history of invasion at most sites prevents the survival of native seed that was deposited in the soil seed bank before native plants became excluded by the dense *R. ponticum* stands. Native seed is therefore not present to establish following *R. ponticum* removal and the large areas subject to invasion mean that little seed arrives at the cleared sites since remaining native populations are typically a prohibitive distance away. This suggests that sites with only a moderate *R. ponticum* cover, where the native plant community persists interspersed with isolated *R. ponticum* bushes, should be able to recover well following clearance since effective source populations remain to drive recovery.

Whilst this study has demonstrated that seed addition is a successful strategy in increasing the establishment of native forbs and grasses following *R. ponticum* clearance, it must be emphasised that this is <u>not a blanket recommendation</u> to apply seed at all sites. The forb and grass community, particularly those species for which seed is available, is not necessarily of conservation concern but its restoration might be more important in relation to the visual impact – some people like to see a typical, diverse woodland community rather than a bryophyte mat when they visit. In some cases the wider bryophyte community features many species of conservation concern, and its protection is likely to be more important than the restoration of forbs and grasses at many sites. Indeed, the research presented in section 2.1 suggests that bryophytes likely benefit from the lack of competition with forbs and grasses. However, the majority of cover in the bryophyte may mat comprises common mosses such as *Thuidium tamariscinum* and *Kindbergia praelonga*, which are of little conservation interest. It will thus be important to consider the vegetation present at individual sites; where there is an existing bryophyte mat including a strong component of characteristic Atlantic species it might be appropriate to allow this to continue to develop. On newly cleared sites, on the other hand, seeding with a grass/ forb mix might enable more rapid recovery of the vegetation more generally.

3. OVERALL CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

Vascular plants and bryophytes responded very differently to *R. ponticum* clearance, with the vascular plant community failing to recover even 30 years after clearance, but the bryophyte community recovering well once the invasive stands had been removed. Recommendations are therefore presented separately for each community in the following sections.

Management decisions often involve trade-offs, not only based on allocating scant resources, but also on weighing the relative importance of different elements of the local community. This research has revealed a potential trade-off between the vascular plant and terrestrial bryophyte communities of Atlantic Oak woodland. Our research has suggested that restoring the vascular plant community may be detrimental to the terrestrial bryophyte community that forms following *R. ponticum* clearance. Whilst the latter generally comprises large common mosses, such as *Thuidium tamariscinum, Kindbergia praelonga*, and *Rhytidiadelphus loreus*, it may also include species of conservation concern on some sites. Land managers must therefore carefully consider their local conservation priorities before following any of the recommendations listed below.

The following caveats also apply to the recommendations presented here:

1) All research was carried out in Atlantic oak woodlands on the west coast of Scotland. Whilst the results might be a useful starting point for work on sites elsewhere caution is needed as different ecosystems, especially in different parts of the country, often respond in very different ways to the same treatment.

2) This study sought to capture the major patterns of community change as *R. ponticum* increased in density, and in the years following its clearance. Targeted surveys of particular species of conservation interest were therefore outwith the scope of this research. The recommendations presented here are consequently based on benefits to the overall vegetation and so those managing sites known to support species of particular conservation concern should monitor these species carefully if implementing the recommendations featured below.

3.1 Recommendations for the bryophyte community

- **The epiphytic bryophyte community recovers well following *R. ponticum* clearance in the absence of any further management interventions.**

The percent cover and species richness of epiphytic mosses was relatively unaffected by *R. ponticum* invasion and remained at similar levels in uninvaded, densely invaded and cleared sites. Anecdotal evidence suggests that populations under dense stands look unhealthy, being etiolated and producing few sporophytes, but are able to persist in surprising abundance and return to a healthier appearance following *R. ponticum* clearance (J. Maclean, pers obs).

The percent cover and species richness of epiphytic liverworts was greatly reduced under dense *R. ponticum* stands, but recovered well following clearance to reach levels indistinguishable from uninvaded control sites after around ten years of recovery. Site managers should therefore not be unduly concerned by low liverwort abundance immediately following *R. ponticum* removal, but should consider taking further action (e.g. carrying out translocations from neighbouring sites) if they still haven't returned after ten or more years.

This effective recovery included Atlantic bryophyte species such as *Bazzania trilobata; Dicranodontium denudatum; Dicranum scottianum*; *Drepanolejeunea hamatifolia; Frullania teneriffae; Harpalejeunea molleri; Lejeunea patens; Lepidozia cupressina; Leptoscyphus cuneifolius; Microlejeunea ulcina; Plagiochila atlantica; Plagiochila exigua; Plagiochila punctata; Plagiochila spinulosa* and *Scapania gracilis*, along with the filmy ferns *Hymenophyllum tunbrigense* and *Hymenophyllum wilsonii.*

- **The understorey bryophyte community recovers well following *R. ponticum* clearance in the absence of any further management interventions.**

Bryophytes in the understorey declined dramatically in abundance under dense *R. ponticum* stands, but retained levels of species richness similar to those found in uninvaded control sites. In the years following *R. ponticum* clearance, understorey bryophytes quickly increased in both percent cover and species richness, and actually reached a higher species richness in sites cleared 20 to 30 years ago than in uninvaded control sites. Many cleared sites featured lush, diverse bryophyte carpets including the Atlantic species *Dicranodontium denudatum* and *Lepidozia cupressina*. It appears likely that this unprecedented abundance of bryophytes in cleared sites benefitted from a lack of competition with the native forbs and grasses (which did not recover). Management decisions taken to benefit native forbs and grasses should therefore be undertaken with caution at sites featuring bryophytes of high conservation interest.

3.2 Recommendations for the vascular plant community

- **Native forbs and grasses require further management interventions to assist their recovery following *R. ponticum* clearance.**

- **Seed addition is an effective method of increasing native forb and grass cover, whereas treatments to the soil (such as applying activated carbon or fertiliser) are ineffective and unnecessary.**

Native forbs and grasses did not recover following *R. ponticum* clearance, remaining at low abundance and species richness even 30 years after removal of the invasive stands. An experimental trial at a single site, cleared 30 years previously, demonstrated that forbs and grasses planted as seed can grow at sites that were previously subject to *R. ponticum* invasion. This demonstrated that any toxic effects of *R. ponticum* on the soil do not present a significant barrier to site recovery and therefore soil treatments such as applying activated carbon (to mitigate the impact of polyphenols) or fertliser (to increase soil nutrient availability) are unnecessary. Seed addition was particularly effective when coupled with the removal of the existing bryophyte layer, which was demonstrated to inhibit the establishment of forbs and grasses introduced as seed. Seed addition has inherent concerns relating to the introduction of non-local genetic material and the selection of an appropriate mix of species to include, in addition to the previously discussed potentially detrimental impacts on the native bryophyte community. Any restoration project must therefore carefully weigh the pros and cons of introducing seed to a site following *R. ponticum* removal.

- **Native fern species may require further management interventions to assist their recovery following *R. ponticum* clearance.**

Ferns showed a significant decline in percent cover, though not species richness, as *R. ponticum* increased in density. They also showed significantly lower values of both these measures in sites where *R. ponticum* had been cleared than in uninvaded control plots. However, a very low cover of ferns in comparison to forbs, grasses and bryophytes across the survey meant that the magnitude of these differences was very small. Further study will be necessary to accurately assess the impact of *R. ponticum* invasion and clearance on the fern community and develop strategies to counter any negative effects.

- **Native woody species are largely unaffected by *R. ponticum* invasion and clearance; however, significant birch recruitment may occur following *R. ponticum* clearance at some sites.**

Native woody species did not show any significant changes with increasing *R. ponticum* density. In contrast, a 'humped' relationship was discovered over the 30 year range of times since *R. ponticum* clearance, revealing higher densities of woody species in the understorey at around 10 to 20 years since *R. ponticum* clearance. Since the survey only included understorey species, this pattern may suggest a period of tree recruitment following *R. ponticum* clearance, with these individuals growing past the understorey stage and becoming young trees by 20 years after clearance. Results from the seed bank study concurred with this interpretation, revealing that cleared sites exhibited a large increase in birch seedlings compared to densely invaded or uninvaded control sites. There was a large degree of variability, however, in both the understorey survey and the seed bank results, suggesting that extensive birch recruitment occurred at some sites but not others. A likely explanation is that *R. ponticum* clearance causes a big increase in light availability which triggers a period of birch recruitment. At sites with a low deer abundance, these seedlings grow to be adult trees, producing their own seed which adds to the local seed bank. At sites with a high deer abundance, however, germinating seedlings never make it past the sapling stage and so do not contribute to the adult population. Further research will be needed to confirm this hypothesis and build a more detailed picture of how *R. ponticum* invasion and clearance interacts with other factors to impact forest dynamics.

3.3 Recommendations for *R. ponticum* management

A large literature already exists giving practical recommendations on effective methods of *R. ponticum* clearance (for example Edwards 2006; Parrott & Mackenzie 2013; www.leverandmulch.co.uk), and this project did not directly investigate this topic. However, we wish to emphasise a couple of issues relating to *R. ponticum* clearance strategies that are relevant to the other results presented here.

- **Removing *R. ponticum* stands and conducting follow-up treatments to ensure that sites remain free from invasion continues to be a high conservation priority.**

The sites considered in this study had all been subject to effective *R. ponticum* removal, including follow-up treatments to remove any bushes escaping the initial clearance efforts. It has been well-documented that *R. ponticum* quickly re-invades in the absence of regular monitoring and follow-up treatment of sites (Edwards 2006). Our conclusion that elements of the native community can recover in the years following *R. ponticum* clearance is entirely dependant on that clearance being maintained. It can be assumed that if *R. ponticum* is allowed to recolonise then any benefit that clearance had to the native bryophyte community will be immediately reversed.

- **Clearing *R. ponticum* stands before they reach continuous canopy cover is likely to have a major benefit on the native plant community.**

The research presented here only investigated recovery at sites following the clearance of mature *R. ponticum* stands with complete canopy cover (i.e. the ‘worst affected’ sites). Whilst nobody has studied how recovery proceeds at sites that were cleared at intermediate *R. ponticum* densities, the gradual loss of species as *R. ponticum* density increased shown in Figs. 2 & 3 is suggestive that earlier intervention would preclude the loss of many species present at that site. If those species were never lost to increasingly dense *R. ponticum* then they would logically still be present following clearance, and their spread into the gaps created from removing isolated *R. ponticum* bushes would surely be expedited. Current management guidelines prioritise the clearance of the densest sites first, which is certainly a good strategy when focussing only on preventing the further spread of invasion, as the densest sites produce the most seeds (Edwards 2006). However, we suggest that prioritising clearance at some intermediate density sites, particularly those featuring the best examples of native Atlantic oakwood communities, may be good strategy when considering the impacts on native biodiversity.

4. REFERENCES

Colak, A.H., Cross, J.R. & Rotherham, I.D. 1998. *Rhododendron ponticum* in native and exotic environments, with particular reference to Turkey and the British Isles. *Journal of Practical Ecology and Conservation,* 2, 34-40.

Cross, J.R. 1975. *Rhododendron ponticum* L. *Journal of Ecology,* 63, 345-364.

Cross, J.R. 1982. The establishment of *Rhododendron ponticum* in the Killarney Oakwoods, S.W. Ireland. *Journal of Ecology*, 69, 807-824.

Dehnen-Schmutz, K., Perrings, C. & Williamson, M. 2004. Controlling *Rhododendron ponticum* in the British Isles: an economic analysis. *Journal of Environmental Management*, 70, 323-332.

Edwards, C. 2006. *Managing and controlling invasive rhododendron. Forestry Commission Practice Guide.* Forestry Commission, Edinburgh.

Edwards, C. & Taylor, S.L. 2008. *A survey and appraisal of Rhododendron invasion in Argyll and Bute.* Forest Research, Edinburgh.

Erfmeier, A. & Bruelheide, H. 2011. Maintenance of high genetic diversity during invasion of *Rhododendron ponticum*. *International Journal of Plant Sciences,* 172, 795-806.

Gilbert, O. 2004. *Lichens.* Scottish Natural Heritage, Perth.

Long, D. & Williams, J. 2007. *Rhododendron ponticum: Impact on lower plants and fungi communities on the west coast of Scotland.* Project no. 19412, Scottish Natural Heritage, Inverness.

Maclean, J.E. 2016. The effect of clearing invasive *Rhododendron ponticum* on the native plant community of Scottish Atlantic oak woodlands: Implication for restoration. Ph.D. dissertation, University of Aberdeen.

Mejías, J.A., Arroyo, J. & Marañon, T. 2007. Ecology and biogeography of plant communities associated with the post Plio-Pleistocene relict *Rhododendron ponticum* subsp. *Baeticum* in southern Spain. *Journal of Biogeography*, 34, 456-472.

Merryweather, J.W. 2012. Rhododendron poisons the soil, doesn't it? *Skye & Lochalsh Environment Forum.* http://www.slef.org.uk/userfiles/file/slef-pdfs/rhododendron_poisons_the_soil.pdf

Milne, R.I. & Abbott, R.J. 2000. Origin and evoluion of invasive naturalized material of *Rhododendron ponticum* L. in the British Isles. *Molecular Ecology*, 9, 541-556.

Mitchell, R.J., Marrs, R.H., Le Duc, M.G. & Auld. M.H.D. 1997. A study of succession on lowland heaths in Dorset, southern England: changes in vegetation and soil chemical properties. *Journal of Applied Ecology,* 34, 1426-1444.

Parrott, J. & Mackenzie, N. 2013. *A critical review of work undertaken to control invasive rhododendron in Scotland: A report commissioned by Forestry Commission Scotland and Scottish Natural Heritage.* Coille Alba, Inverness.

Porley, R. & Hodgets, N. 2005. *Mosses and Liverworts*. Collins, London.

Ratcliffe, D.A. 1968. An ecological account of Atlantic bryophytes in the British Isles. *New Phytologist*, 67, 365-439.

Rodwell, J.S. 1991. *British Plant Communities volume I: Woodlands and scrub. Nature Conservancy Council.* Cambridge University Press, Cambridge.

Rotherham, I.D. 1983. The ecology of *Rhododendron ponticum* L. with special reference to its competitive and invasive capabilities. University of Sheffield. PhD Thesis.

Rotherham, I.D. & Read, D.J. 1988. Aspects of the ecology of *Rhododendron ponticum* with reference to its competitive and invasive properties. *Aspects of Applied Biology*, 16, 327-335.

SNH, 2007. *A five year species action framework: Making a difference for Scotland's species.* Scottish Natural Heritage, Inverness.

Sutton, C.A. & Wilkinson, D.M. 2007. The effects of *Rhododendron* on testate amoebae communities in woodland soils in North West England. *Acta protozoologica,* 46, 333-338.

Wardle, D.A., Nilsson, M., Gallet, C. & Zackrisson, O. 1998. An ecosystem-level perspective of allelopathy. *Biological Reviews,* 73, 305-319.

Yildiz, O., Eşen, D. & Sarginci, M. 2009. Long-term site productivity effects of different *Rhododendron* control methods in eastern beech (*Fagus orientalis* Lipsky) ecosystems in the Western Black Sea region of Turkey. *Soil Use and Management,* 25, 28-33.

www.nature.scot

ISBN: 978-1-78391-802-7

Great Glen House, Leachkin Road, Inverness, IV3 8NW
T: 01463 725000

You can download a copy of this publication from the SNH website.

recycle

Scottish Natural Heritage
Dualchas Nàdair na h-Alba
nature.scot