POST-CLEARANCE EFFECTS OF RHODODENDRON ON THE FUNGAL COMMUNITIES OF THE EASTERN SIDELANDS OF LUNDY, BRISTOL CHANNEL

by

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ABSTRACT

Rhododendron ponticum is a constant problem on Lundy. We present the results of an experiment investigating the lasting legacy of *Rhododendron* following clearance and the time needed for natural regeneration of the plants and fungi in cleared areas. These results are discussed with particular reference to their implications for management and clearance on Lundy and in other areas in the future.

Key Words: *Rhododendron, fungi*, *acidification, regeneration, restoration, soils, time-series*

INTRODUCTION

The issue

Rhododendron ponticum L. is a rapidly spreading invasive shrub, introduced to the UK for its aesthetic beauty. The shrub has a tendency to spread outside of an introduction site and into adjacent ancient semi-natural woodland and grassland communities. As a result of many features of its biology, such as acidic leaf litter, dense canopy cover and allelopathic foliage, it has the capacity to dramatically alter the environmental conditions and the associated vegetation (Cronk *et al.*, 1995). In particularly sensitive areas in Britain, efforts are being made to manage the spread of the shrub and/or eradicate it (Dehnen-Schmutz *et al.*, 2004; Edwards, 2006). Lundy is one such area and efforts to eradicate the shrub are proving successful. Here we investigate the aftermath of *Rhododendron* colonisation on fungal communities and attempt to identify the timescale involved in recovery of the native flora and mycota.

Rhododendron as an invasive species

The high colonisation potential of *R. ponticum* is a result of the great number of seeds that it produces. Every flower head produces many thousands of seeds, which are efficiently dispersed by the wind. These swamp the seed bank for kilometres around the plant and cause it to out-compete the less abundant seeds and seedlings of native species (Stout, 2007).

In addition, the leaf litter of *R. ponticum* is highly acidic, similar to that of another ornamental shrub also belonging to the genus, the azalea (*Rhododendron* subgen *Tsutsuji* L.). As *R. ponticum* cover increases and its leaves begin to dominate the litter layer, the soil becomes altered in a way that makes it unsuitable for other species. *R. ponticum* is evergreen, so it sheds and regrows its leaves all year-round exerting a constant stress on the ground vegetation beneath the stand (Cronk *et al.*, 1995). This stress comes in two forms. Firstly, the presence of a thick evergreen shrub layer leads to reduced light levels, suppressing ground vegetation through light limitation. Secondly, the year-round supply of new leaves shed from the shrub leads to continuous addition of acidic leaf litter to the soil.

Rhododendron and Lundy

R. ponticum was first introduced to Lundy in the Millcombe valley in the early nineteenth century (Marren, 1973) from where it began to spread beyond the areas where it was originally planted (Chanter, 1877). In 1926 a wildfire cleared several large areas on the eastern side of the island providing a bare post-fire habitat, well suited for colonisation by *R. ponticum*. Once this fire had passed, the native vegetation was unable to regenerate as rapidly as *R. ponticum* which is adapted to fire-dominated landscapes such as those of its natural range in the Northern Mediterranean (Tabbush & Williamson, 1987; Compton, 1998).

The ideal conditions for *R. ponticum* colonisation, unfortunately, closely resemble those necessary for the healthy continuation of the Lundy Cabbage (*Coincya wrightii* O.E. Schulz), an endemic plant with its own associated fauna including the Lundy cabbage weevil (*Ceutorhynchus contractus pallipes* Crotch), the cabbage stem beetle (*Psyllioides chrysocephala* L.) and the Lundy cabbage flea beetle (*Psylliodes luridipennis* Kutschera, 1864).

The destructive potential of *R. ponticum* on the flora of Lundy was recognised in the 1940s when the then owner, Martin Coles Harman, approached the Lundy Field Society to request the implementation of *Rhododendron* control measures (Harman, 1950). Early attempts to control and reduce the spread of the shrub were unsuccessful due to regrowth from cut stumps, a result of the failure to apply herbicide to the cut surface.

In 1998 more concerted control and clearance efforts began with support from English Nature and a volunteer workforce. Eradication methods involved co-ordinated action of both staff and volunteers clearing the thickets and treating cut stumps with herbicide to kill the rootstocks (Compton, 1998). Twenty years on, these efforts have had a marked effect on the landscape, with the almost complete eradication of *Rhododendron* from the Eastern Sidelands.

Predicted impacts of *Rhododendron* colonisation

The acidic effect of *Rhododendron* informed the hypotheses of this study regarding fungal community responses following clearance of *R. ponticum,* as summarised in Figure 1.

We hypothesise that acidification of the soil will have a similar effect to the application of fungicide or herbicide, reducing the number of species capable of surviving in such an extreme environment, selecting for species able to cope with such hostile conditions.

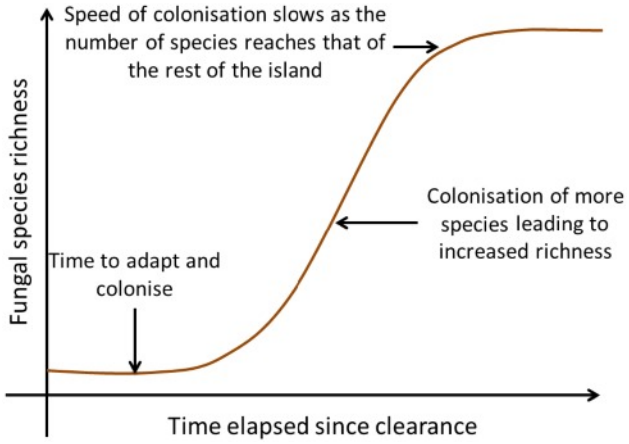

Figure 1: The predicted effects of time since clearance on fungal communities of cleared *Rhododendron* stands

Once the impact of acidic leaf fall is reduced or removed altogether (by removing the plant) the community would be expected to follow the pattern in Figure 1. Initially, there would be residual effects of the acidity on the soil. This means that existing saprotrophic fungi associated with the *Rhododendron* resource would take time to return soil pH to a level at which native fungi can colonise. When fungi begin to colonise, they have a stabilising effect upon the soil and bring the acidity closer to that of the non-colonised areas allowing more species of both fungi and plants to recolonise and grow in the area as fungal diversity is closely linked to plant diversity. This is shown in Figure 1 by the curve of increasing steepness over time. However this rate of increasing species richness (the number of species in a defined area) over time cannot be sustained. Eventually one of two things may happen. Firstly, there may be insufficient resources in the soil, such as nutrients, water or space, to support any additional fungi so the number of new species will tail off. Alternatively, the fungal community may reach the point whereby it has representative species from all of the fungal species present on the island due to the absence of inoculum of particular fungi in the vicinity. Such an effect is likely to be exacerbated in a small island habitat and may cause the plateau to be less pronounced as new spore migrations occur across the Bristol Channel from North Devon and South Wales.

Relevance of the study

Lundy is rich in fungi and is of particular importance for its high diversity of waxcaps (*Hygrocybe* spp.) (Hedger *et al.*, 2010). These fungi are highly sensitive to the fertilisation and ploughing of soils and thus are found only on unimproved grassland soils (Griffith *et al.*, 2002). As a result of agricultural intensification, waxcaps have become a conservation concern in the United Kingdom. Of all *Hygrocybe* species, 89% appear on IUCN red lists within Europe (Arnolds, 1993).

Understanding the soil processes and regeneration patterns on cleared land will enable the Eastern Sidelands to be managed for such rare species to encourage their persistence and reduce the risk of their loss through persisting effects of acidification on the island.

METHODS AND MATERIALS

Site Selection

A map of the history of *R. ponticum* clearance on Lundy over the past twelve years was obtained from Mr Steve Pratt (Lundy Ranger). One of the unique aspects of Lundy as a study site is the detailed records and maps available describing and recording eradication efforts undertaken since the 1990s, instigated by English Nature (now Natural England) in 1998 (Compton, 1998). This map was used to create a sampling strategy incorporating the year of clearance as a stratified variable and controlling for other environmental variables such as aspect, distance from village and slope (Figure 2).

Lundy provides ideal conditions for a controlled experiment. All the *R. ponticum* stands were located on the Eastern Sidelands and were sited on similar soils, and exposed to similar wind conditions, salt spray and temperature variation.

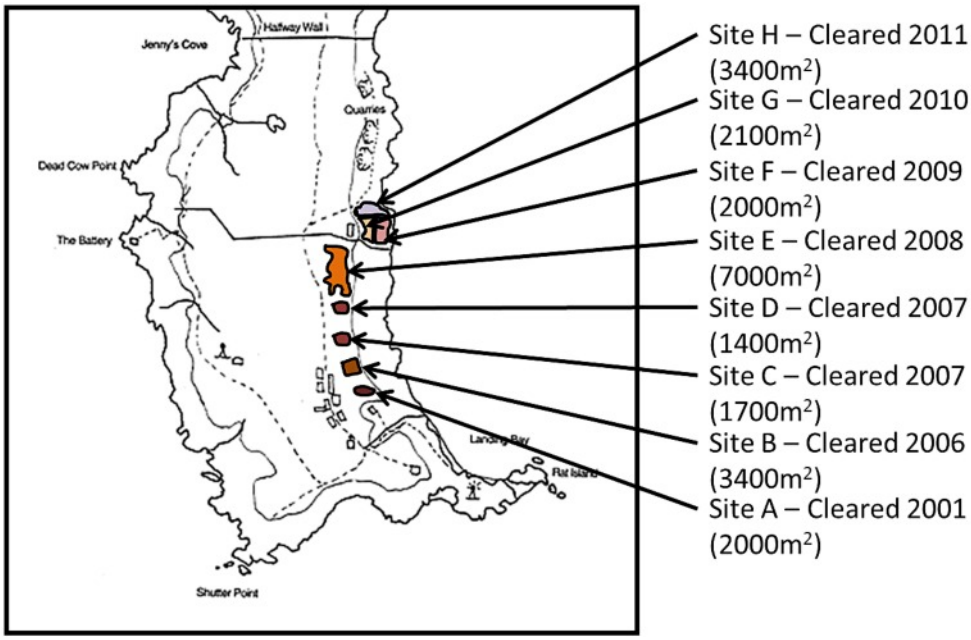

Figure 2: Location of fieldwork sites on the Eastern Sidelands of Lundy, Bristol Channel. Labels indicate the site identification, the year in which the site was cleared and the approximate area. Site locations were identified in collaboration with the Lundy Ranger, Steve Pratt

Field Measurements

Five quadrats were located within each of the eight sites (labelled A-H; see Figure 2). 1m² quadrats were placed at positions selected by means of a random walk using the most south-easterly point of the site as the origin. A random walk uses a list of random numbers to determine the steps taken along and up a grid from a pre-determined origin to cover the area in an unbiased manner. Within each quadrat the overall number of plant and fungal species, and their identities, were recorded. Plant identifications were carried out in the field whilst samples of each discrete fungal species were collected for DNA-barcode based identification at a later date.

Microclimate information was collected for each quadrat. Recorded variables were: aspect; slope; deadwood diameters; and soil pH. Soil pH was measured by dissolving 25g soil in 75ml tap water with added calcium chloride to remove impurities. This solution was then used as the basis for a pH test using the pH/EC/TDS Waterproof Family meter (Hanna Instruments) which had been calibrated using a range of standard pH solutions. Soil cores were taken to a depth of 10cm where possible or to the rocky substratum if this was shallower. The soil cores were homogenised prior to removal of the 25g sample.

Fungal identification

Fungal identifications were carried out using DNA extraction methods to overcome the issues of cryptic speciation and unreliable identifications (Dentinger *et al.,* 2010).

Samples for DNA extraction and analysis were collected in the field in two ways. Sporocarp samples were collected on FTA cards (Whatman PLC: Catalog#WB120411) and extracted using Whatman FTA protocol BD02 (www.whatman.com). Smaller sporocarps, bracket fungi and mycelia were collected in bags containing silica gel. Dried samples were extracted using the MoBio UltraClean Soil DNA Isolation Kit (MoBio Laboratories Inc., Solana Beach, California: Catalog#12800-100) using the included protocol (www.mobio.com).

The ITS region (ITS1, 5.8S and ITS2) of the DNA samples were amplified using PCR and the specific primers ITS1 and LR21. Amplified samples were then sequenced using the facility at the Natural History Museum, London, and edited in FinchTV version 1.4.0 (Geospiza Inc.). Species identities were obtained via reverse BLAST searches on GenBank (Benson *et al.*, 2007; Benson *et al.*, 2010) and added to the microclimate and plant identification data.

Data analysis

The parameter, fungal richness, was chosen for analysis as it circumvents many of the issues inherent in the use of biodiversity indices for fungal analysis. Fungal richness refers to the number of unique fungal species within a given unit area. In these analyses fungal richness is either by site (across all five quadrats), as in the Wilcoxon test, or an average value of all of the sites cleared in the same year, as in the community bar graph.

We tested for a relationship between fungal richness at each site and environmental variables using a generalized linear model (JMP version 10 SAS Institute Inc., Cary, NC). Soil pH was transformed from a logarithmic to a linear variable and therefore represents the concentration of hydrogen ions in the soil, a more direct measure of acidity. A higher concentration of hydrogen ions ([H+]) represents higher acidity and thus a lower pH, the therefore [H+] will be used throughout the results and discussion. A Wilcoxon test (JMP version 10 SAS Institute Inc., Cary, NC) was used to test for a relationship between soil acidity and time since clearance.

RESULTS

Regeneration of fungal species on cleared *R. ponticum* stands is variable. Some sites display high levels of fungal richness which seems independent of age. Fungal species mixes were different in more recently cleared sites, a consequence of the resources

available at a site. Grassland specific fungi were not observed in any sites, illustrating that the process of restoration and regeneration is incomplete. Plant communities had also yet to stabilise although this was not explicitly analysed in this investigation.

Factors associated with fungal richness

Visually the eight sample sites were very different both in terms of the vegetation present and the macrofungal occurrences (Plate 1). Sites which had been cleared longer had greater vegetation cover whilst patterns in the fungal morphotypes present were not clear cut. There was no significant effect of the site area and the fungal richness within the quadrats selected therein.

Plate 1: Photographs illustrating variations in plant communities in quadrats at different times since clearance. In each photograph a metre square quadrat is apparent for scale. Year of clearance is displayed in the top left of each photograph

A generalized linear model with a Poisson distribution assumption was run using all microclimatic variables, separated by site, and their effect upon fungal richness (the number of different fungal species in a quadrat). Table 1 shows the results of this model. P-values of less than 0.05 indicate a significant association between the factor and fungal richness in the study sites on Lundy. The overall model was not significant (p=0.0512, *d.f.*=5, 39) indicating that more variables and a greater intensity of sampling may be required in future field seasons; however, some individual variable effects were significant.

Factor	Degrees of Freedom	Chi-square	P-value
Year of Clearance	1	0.0025038	0.9601
[H+] Concentration	1	5.9683075	0.0146
Average Deadwood Diameter	1	2.3666393	0.124
Slope	1	1.0614588	0.3029
Aspect	1	0.518348	0.4715
Model (Difference)	5	11.0081	0.0512

Table 1: Results of a generalized linear model investigating the associations between multiple factors and fungal richness on Lundy, Bristol Channel. P-values of less than 0.05 indicate a significant association

Table 1 shows a significant association between fungal richness and acidity (p=0.0146, $d.f.$=1) although there is no support for an association between year of clearance and fungal richness (p=0.9601, $d.f.$=1). A scatterplot (Figure 3) visualising this effect shows that fungal richness decreases with increasing acidity. A Spearman's rank correlation testing this association was also significant (p=0.0020, Spearman's rho=-0.4478).

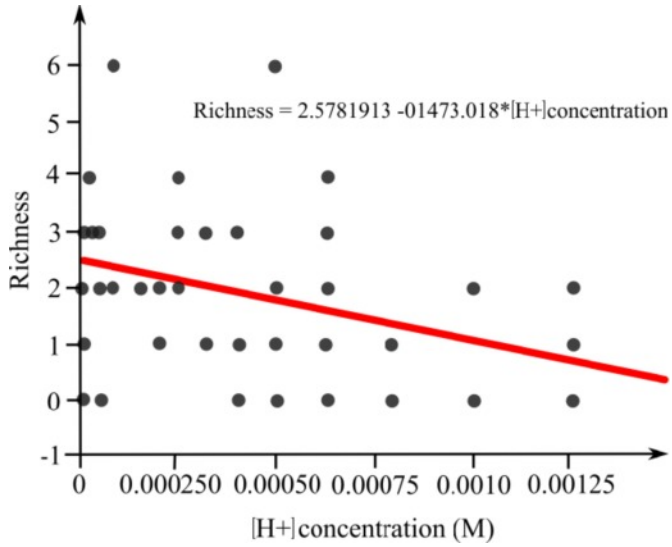

Figure 3: Scatterplot showing the association between acidity (concentration of hydrogen ions) and fungal richness. A line of best fit has been added (red line) and the correlation is significant (p=0.0020, Spearman's rho=-0.4478)

No significant interaction was found between [H+] concentration and the year of clearance so an interaction term was therefore not included in the final model. The analysis (Table 1), using the generalized linear model, demonstrated no significant associations between any of the other factors included in the model although further work with a greater sample size would be useful in determining whether deadwood diameter or volume was an important variable in determining the richness of fungi in a site as the p-value is around 0.1 (p=0.1240, $d.f.$=1) (Table 1) and so warrants further analysis and experimentation.

Links between soil pH and time since clearance

pH did not follow the trend we had anticipated. Acidity increased in the time following *R. ponticum* removal; sites which had been bare for longer displayed much lower pH soils than more newly cleared areas.

As discussed previously, soil acidity is significantly associated with fungal richness. It is assumed that time since clearance would have an impact upon soil pH as the breakdown of acidic leaf litter by colonising organisms leads to a reduction in acidity (an increase in pH). Across the sites, a pH range of 2.9-6.2 units was observed.

Again, the inverse logarithm of pH was used to ensure that the relationship between acidity (concentration of hydrogen ions ([H+])) and the year of clearance was tested. Since [H+] was not normally distributed and could not be transformed to fit a normal distribution, a Wilcoxon test was used to analyse the data. The model was highly significant (p=0.0305, *d.f.*=6). A Wilcoxon non-parametric comparison for each pair was carried out and the results are summarised in Figure 4. The pairwise comparisons do not wholly support the hypothesis; however, this is a consequence of the large range of values observed in the 2011 plots (Figure 5). This stark difference is potentially a consequence of the increased exposure of the 2011 site, which was on a cliff edge, to salt spray. When the 2011 plots were removed from the analysis, the trend of decreasing pH with age is consistent across years and the overall significance is increased (p=0.0086, *d.f.*=5). The significant differences observed between the values towards the centre of the range of years are indicative of soil processes working to alter the acidity.

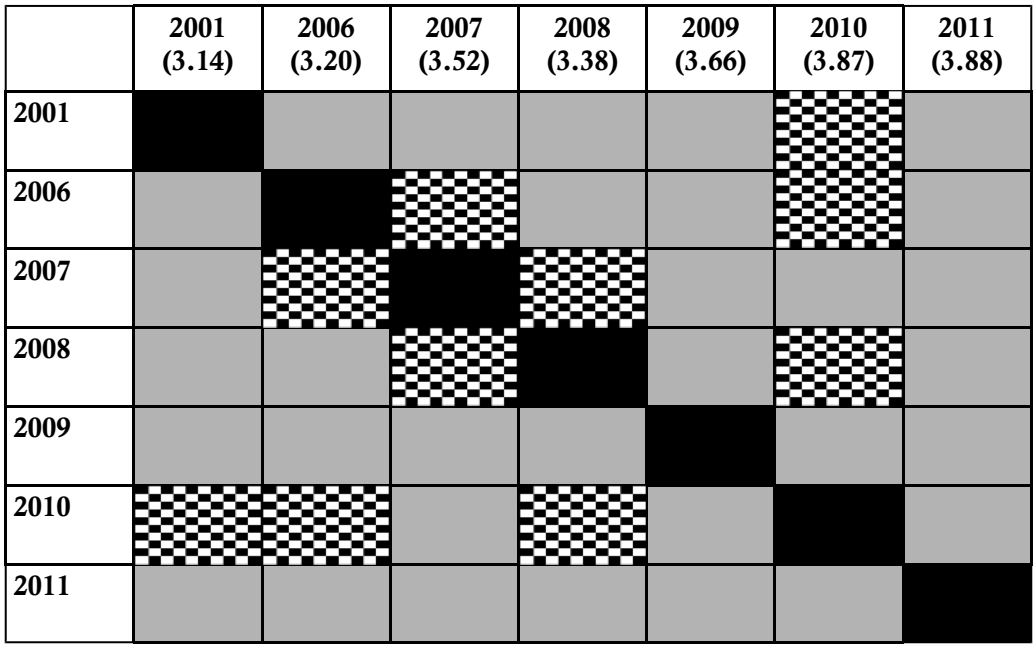

Figure 4: Matrix illustrating the pairwise Wilcoxon test results by year cleared. Black squares indicate a non-relevant test, pale grey squares indicate a non-significant result ($p>0.05$) and chequerboard hatched squares indicate a significant difference ($p<0.05$) between the acidities of soils in the two groups observed (row year and column year). Mean pH is indicated in brackets beneath the year of clearance

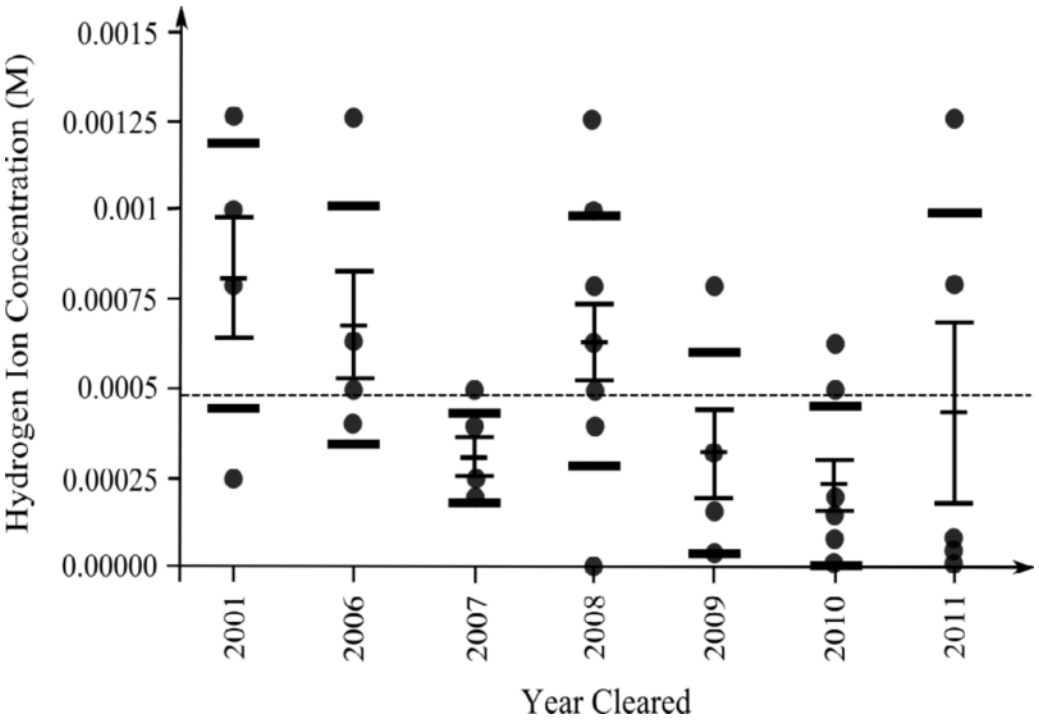

Figure 5: Plot of year cleared against soil acidity (hydrogen ion concentration). Filled circles indicate raw data, thin lines show the man value and error bar for each year. Thick lines show two standard deviations around the mean. The dashed line represents the grand mean of the dataset. Hydrogen ion concentration has been presented to reflect the results discussed in the text

A graphical representation of the trend shows that it functions in the opposite direction to that predicted (Figure 5). A Spearman's rank correlation test on the data was significant (p=0.0027, Spearman's rho=-0.4368). Control sites which had never been colonised by *Rhododendron* were not included in the analysis as a year of clearance could not be reliably entered, skewing the results, but demonstrated a natural pH of 5 ([H+] of 0.00001M). Therefore, even eleven years after clearance, soil pH had not begun to return to levels equivalent to those which had never experienced colonisation by *R. ponticum*.

Successional patterns in species occurrence

The study aimed to produce accurate fungal identifications from DNA samples, a relatively novel approach to ecological investigations of fungi. DNA identifications were cross referenced with morphological identifications carried out in the field to validate the method. Such activities enabled the investigation of successional patterns in species occurrence.

This study seems to have captured the very beginning of the succession from saprotrophic, wood-decaying species to the grassland species typical of the island. The fungal richness declines sharply two years after clearance (Figure 6). Longer-term studies and return surveying efforts in the future will capture the succession in progress providing quantitative information regarding regeneration on acidified land.

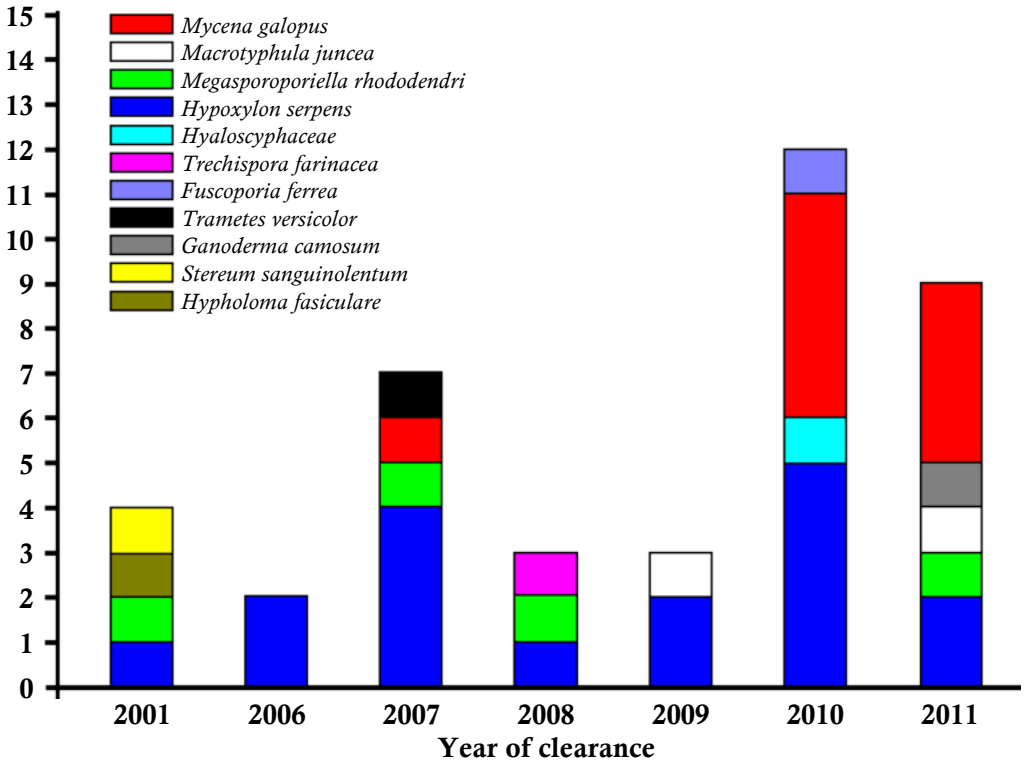

Figure 6: Bar chart illustrating the fungal species present in sites at different times elapsed since clearance. All fungal species named are associated with woodland sites and are found on leaf litter and woody debris. Species were identified from DNA specimens, of the ITS1-5.8S-ITS2 region, collected from fruit bodies and other fungal macrostructures in the field and amplified in the lab. Bacterial species were omitted from the results

The addition of a survey of soil fungal species and those without easily observable and collectable fungal structures will enhance this aspect of the study still further, adding greater breadth and depth to the survey. The decline two years after clearance could be a consequence of the increased prevalence of grassland species which tend to have more less-visible mycelia and are ephemeral fruiters.

DISCUSSION

The effect of time since *R. ponticum* clearance is more complicated than previously thought. Rather than following classical models of regeneration on bare ground, the fungal community suffers from lasting effects following the removal of *R. ponticum.* Such effects contradict our predictions and show that the fungal richness on cleared stands tends to decrease with time since clearance. However, it would appear that this effect is a consequence of soil pH changes as opposed to time since clearance alone. Such an effect underlines the importance of long-term monitoring in situations such as this. It is important to understand the continuing effects of *R. ponticum* colonisation on the soil system and its associated mycota.

The results of these studies are partially explained by the characteristics of the fungi identified in the plots (Figure 6). Where sporocarps and cords are present, they are of saprotrophic, wood-decaying fungi such as *Trametes versicolor* (L.) Lloyd and *Rhododendron* specialists such as *Megasporoporiella rhododendri* (Y.C. Dai & Y.L. Wei) B.K. Cui & Hai J. Li (Plate 2). Such fungi would not be expected to continue in a plot where the wood resource has been removed. Therefore, a reduction in saprotrophic species could be expected over time with a resultant shift from woodland to grassland species. The length of time covered by this experiment was insufficient to follow this transition and captures only the reduction in saprotrophic species over time. The grassland species are yet to recolonise in cleared areas. Future studies, revisiting the sites, should identify the time needed for this shift in habitat to occur, informing future management plans for areas similarly affected by *R. ponticum* invasion.

Plate 2: Dead rhododendron branch with white filamentous cords of *Megasporoporiella rhododendri* protruding from dead wood

The theory that acidic leaf litter leads to increased soil acidity on and around *R. ponticum* stands is contradicted by these data. Acidity follows a trend opposite to that expected, namely, acidity increases with time since clearance. This could be a residual effect of the remaining leaf litter, root stocks and brash, all of which may release acidic compounds as they break down. These results support previous work by Mitchell *et al.* which investigated heathland restoration after *Rhododendron* invasion. The study found that unless areas were litter stripped, the nutrient levels and pHs were unlikely to return to pre-invasion levels (Mitchell *et al.*, 1999). Mitchell *et al.* also suggest that deep root stocks and soil toxins may reduce the capacity for recovery at cleared *Rhododendron* sites.

Further work, investigating the mechanism behind this phenomenon, would be crucial to furthering our understanding of how plant and fungal communities would be expected to recolonise bare ground after *R. ponticum* clearance.

The plant communities in the area, although not presented explicitly in this paper, were also different from site to site and did not achieve the characteristics of the uncolonised land at any point within the observed eleven-year clearance window. The most mature cleared areas were dominated by sheep's sorrel *Rumex acetosella* L. and grasses, having passed through bare ground and fern-dominated communities prior to this state (Plate 1).

Vegetation, such as the Lundy cabbage, and several native grasses, such as *Holcus lanatus* L., are sensitive to the high pH of the land, even ten years after clearance. Therefore, it may be prudent to pilot a controlled liming experiment to test whether the soils can be restored to their pre-colonisation state, causing succession to become equivalent to that of the uncolonised sidelands. However, this method may prove detrimental to one of the groups of organisms the project is seeking to protect, the waxcaps. Waxcaps are very sensitive to anthropogenic changes in their habitats and have been shown to decline in areas where land has been limed (Griffith *et al.*, 2002). Therefore, although liming initially appears to be an ideal way of rescuing the landscape, its long-term effects could be far reaching.

A similar rescue and protection effect could be achieved by encouraging scrub growth by gorse (*Ulex* spp. L.) and bramble (*Rubus fruticosus* L. agg.) on cleared areas. Spiny shrubs protect young plants and fungi from grazing by Sika deer (*Cervus nippon* Temminck, 1838) and feral goats present on the island. It may be that bare ground highlights the presence of succulent young plants and fungi reducing their chance of establishment prior to grazing. By reducing grazing pressure species may become released from suppression and succession can proceed more rapidly.

A final restoration option would be simply to wait. Soils on the island have an average pH of 5. Many of the plants are acidophilic and may be able to tolerate soils of a wider range of pH than they are currently observed to be growing in. Only by waiting to observe the complete series of colonisations and losses can the baseline situation be understood. Without such a baseline other potential methods to increase the rate of restoration will not have anything against which to be judged, therefore reducing their potential use.

Therefore, we can be sure that there are changes in both plant and fungal communities on old *R. ponticum* stands in the years after clearance. As plants and fungi begin to recolonise they have a stabilising effect on these landscapes. This work is a critical first step in addressing the issue of the persistence of negative effects of *R. ponticum* leaf litter and associated activity on the soil, mycota and flora in an area. Future work, addressing the mechanisms of such longevity and extending this study into the future, will enable this question to be answered more completely.

There are, of course, implications resulting from the sampling method used in this study. As a consequence of our research emphasis on cord-forming fungi we sampled visible fungal structures and macro-fungi. Therefore, we were unable to detect non-fruiting fungal species with diffuse mycelia or many mycorrhizae. Therefore, our sampling methods may have had a bias towards the collections of woodland fungal species which are more likely to display these macro features. We are, however,

confident that our methods were appropriate for this study and provide a vital first step towards developing an understanding of the processes occurring post-rhododendron clearance. Future work, such as the inclusion of soil fungal screens of soil cores, will fill in the gaps in this study and enhance our knowledge further, creating a longitudinal study of the area with high scientific potential.

A better understanding of this process will enable protocols and policies to be developed and implemented to mitigate any detrimental effects and encourage the return of native flora in these areas without potentially damaging the rest of the system. The investigation reported here could be extended to other areas in which programmes of clearance are occurring to test how representative these processes and patterns are. Unfortunately, many other areas do not tend to have complete records, such as those for Lundy, which reduces the potential for a study to be as reliable and detailed. Lundy is therefore a critical site for *Rhododendron* research in Great Britain with particular relevance for acidic grasslands such as those in other granite areas such as Dartmoor and the Scottish Highlands.

CONCLUSIONS

This study hints at some practical management practices for mitigating the effects of *R. ponticum* colonisation post clearance. In an area such as Lundy, the scars on the landscape caused by clearance can detract from its aesthetic beauty. Therefore, restoring the native vegetation and fungal communities cover is a priority.

Fungal and plant communities are slow to recolonise an area post-clearance and do not return to pre-colonisation communities within the twelve year timescale studied.

The low significance of many of the effects on the fungal communities can be explained by the measurement used, fungal richness, which removes species identity and functional trait identity from the analysis. Plotting the change in fungal species over time illustrates the community turnover occurring in the plots (Figure 6). Plant communities remain suppressed post-clearance and begin to demonstrate shrub encroachment eleven years after clearance.

Lundy provides an opportunity for a long-term monitoring experiment were this experiment to be repeated into the future and include a litter stripping component. The island and the location of *R. ponticum* with reference to aspect, wind and sea spray conditions makes it an excellent natural laboratory, controlling for many variables which would otherwise be hard to account for. It would be comforting to think that the uncontrolled expansion of an ornamental shrub out onto the Eastern Sidelands could be of benefit to our understanding of post-invasion restoration enabling something positive to result from this ecological misadventure.

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