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The epiphytic bryophyte community of Atlantic oak woodlands shows clear signs of recovery following the removal of invasive *Rhododendron ponticum*

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ABSTRACT

Increased awareness of the negative impacts of invasive non-native species has led to a rapid increase in clearance programs around the world. One of the main goals of clearance is the restoration of native communities that were present pre-invasion. Little monitoring is typically carried out, however, to verify that native communities return without further management intervention in the years following invasive species removal. We investigated whether the epiphytic plant community of Atlantic oak woodlands, which principally consists of bryophyte species, returned after up to thirty years of recovery following the removal of the invasive non-native shrub *Rhododendron ponticum*. This community is of international conservation value and is particularly threatened by invasive *Rhododendron*. We revealed that the epiphytic plant community was able to recover effectively in sites that had been clear from *Rhododendron* for over fifteen years. This recovery included several species of particular conservation interest with highly restricted European distributions (i.e. 'Atlantic species' such as *Plagiochila heterophylla*). Total cover and species richness both returned to similar or even higher levels to those found in uninvaded control plots by fifteen or more years following clearance, despite being highly reduced within dense *Rhododendron* thickets. Overall community composition also recovered to resemble uninvaded control plots in the years following *Rhododendron* removal. These findings present an encouraging message that at least some native communities can return naturally in the years following invasive species removal and may not require further management interventions to speed their return.

1. Introduction

Invasive alien species are widely recognised as one of the major threats to worldwide native biodiversity (Genovesi, 2005; Mooney, 2005). Whilst an abundance of studies have investigated their impacts on aquatic communities, small mammals, insects and vascular plants, their impact on bryophyte communities has received little attention (Rothero, 2003; Genovesi, 2005; Mooney, 2005). Indeed, bryophytes remain a relatively overlooked element in conservation strategies and their response to restoration measures is rarely considered (Rothero, 2003; Long and Williams, 2007). Understanding how bryophyte communities respond to invasive non-native species and revealing whether they recover following control efforts will be vital to ensuring the future of this diverse group (Rothero, 2003; Long and Williams, 2007).

The bryophyte community of Scottish Atlantic oak woodlands is particularly rich and is recognised as being of internationally significant conservation value (Rothero, 2005; Long and Williams, 2007; Porley and Hodgets, 2005, pp.164), as well as being listed in the EC Habitats Directive Annex 1 as "old sessile oakwoods with *Ilex* and *Blechnum* in the British Isles" (JNCC, 2014). Invasion by non-native *Rhododendron ponticum* (hereafter *Rhododendron*) has been identified as one of the main threats to this habitat, since the characteristic humid climate and lack of temperature extremes which favour bryophyte diversity are also ideal for *Rhododendron* growth (Porley and Hodgets, 2005, pp.165; Rothero, 2005). Whilst there is clear evidence that *Rhododendron* invasion negatively impacts the understorey community (Cross, 1975; Rotherham, 1983; Maclean et al., 2017), there is little quantitative evidence for how it impacts the epiphytic community, including the diverse epiphytic bryophyte assemblage (Long and Williams, 2007). Equally little is known about how this community responds to removal of the invasive stands, a practice which has increased dramatically in recent years following the discovery that *Rhododendron* serves as a host for *Phytophthera ramorum*, the fungus responsible for sudden oak death in trees, which also presents a significant economic threat to larch trees

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in Scotland (Edwards and Taylor, 2008; Parrott and MacKenzie, 2013). Addressing this key knowledge gap and elucidating how the epiphytic bryophyte community responds to *Rhododendron* invasion and subsequent control is therefore of vital importance to assessing the efficacy of Atlantic woodland conservation strategies (Long and Williams, 2007; Parrott and MacKenzie, 2013).

Invasion by *Rhododendron* leads to a well-documented decline in native understorey plant communities, which appears to be principally mediated through reduced light intensity under the dense stands (Cross, 1975, Maclean, 2016). Since many epiphytic bryophytes are pre-adapted to low light conditions, this may facilitate their persistence during invasion (Porley and Hodgets, 2005, pp.148; Kiraly et al., 2013). Additionally, it may be that epiphytic species can persist higher up the tree trunk, above the most severe impacts of the invading *Rhododendron*, leaving small source populations to recolonise down tree trunks once the *Rhododendron* has been removed (Zartman, 2003; Pharo and Zartman, 2003). The dense shading effect of *Rhododendron* is likely to be reduced higher up the tree where light has less far to travel and can penetrate more easily (Cross, 1975). However, conditions higher up the trunk may be unsuitable because of decreased humidity and increased exposure to temperature extremes which may limit the ability of many epiphytic species to survive invasion by retreating up the trunk in this manner (Porley and Hodgets, 2005). Indeed, since mature *Rhododendron* bushes can attain heights of up to 8 m in wooded areas, it is very possible that even epiphytes will be unable to tolerate their influence and will become locally extinct in invaded areas (Edwards, 2006). Many bryophytes are reported to have limited dispersal capabilities, so it seems very likely that once they have been lost in an area, recolonisation will take many decades (Miles and Longton, 1992; Snäll et al., 2003; Söderström and During, 2005).

This study assessed the extent to which the epiphytic bryophyte community of Atlantic oak woodland recovered following the effective removal of invasive *Rhododendron* stands. To investigate this issue we utilised a series of sites where dense *Rhododendron* stands had been removed between one and thirty years ago. Using sites with up to thirty years of recovery following *Rhododendron* removal to allow us to investigate the long-term consequences of invasive species removal over ecologically relevant timescales. We used this series of sites to address the questions: in the years following *Rhododendron* clearance 1) does the total cover and species richness of the epiphytic plant community return to levels similar to those found in uninvaded control sites?; 2) does community composition return to a similar structure to that found in uninvaded control sites?; and 3) do Atlantic species (which have highly restricted European distributions and are of particular conservation importance) also recover?

2. Methods

2.1. Data collection

We identified and surveyed a series of 32 sites that were previously invaded by high density *Rhododendron* stands, but which had been cleared at different points in time between 1984 and 2013. We also surveyed 16 high *Rhododendron* density sites that have never been cleared and 16 uninvaded control sites for comparison with the cleared sites. Potential sites were identified following discussions with personnel at the regional Scottish Natural Heritage and Forestry Commission Scotland offices and meetings with local landowners with a substantial *R. ponticum* presence on their properties. Sites were chosen based on availability and also to ensure the even distribution of site types throughout the study area. Particular care was taken to ensure that dense *Rhododendron* and uninvaded control sites were fully interspersed with the cleared sites. This study design therefore conformed to the 'natural experiment' paradigm described by Diamond (1983), whereby site locations for experimental treatments (in this case uninvaded, dense or cleared *Rhododendron*) are determined by availability rather than following a strict experimental design with perfectly interspersed plots. This type of study is implemented due to constraints on conducting a strict experimental trial to answer the question under consideration (in this case the time constraint on the many decades necessary to grow and clear *Rhododendron* in an ideally designed field trial).

Sites were chosen to be as similar as possible to reduce variability not associated with their history of *Rhododendron* invasion. All survey sites were located on the west coast of Scotland in Atlantic oak woodlands around Argyll, Kintyre and Lochaber, between 55°76′ N and 56°90′. Atlantic oak woodlands are of high biodiversity value and are listed in Annex I of the EU Habitats Directive (old sessile oak woods with *Ilex* and *Blechnum* in the British Isles). Oak (*Quercus petraea* [Mattuschka] and *Q. robur* [Mattuschka]), and birch (*Betula pendula* [Roth] and *B. pubescens* Ehrh.) made up the majority of the tree community at all sites, with rowan (*Sorbus acuparia* L.), hazel (*Corylus avellana* L.), ash (*Fraxinus excelsior* L.), and holly (*Ilex aquifolium* L.) also occurring in moderate abundances. All sites consisted of ancient semi-natural woodland and were located > 100 m from any ravines or plantation forestry and none were subject to active management of the tree community (i.e. no harvesting, coppicing or removal of dead wood). *Rhododendron* was removed from all the cleared sites by cutting the *Rhododendron* bushes at the base and applying herbicide (usually triclopyr or glyphosate; Edwards, 2006), which represents the most common method of control currently used in Scotland (Edwards, 2006). *Rhododendron* clearance was periodically maintained at all sites to prevent its return; however, no additional management interventions were applied at the sites.

At each site we established a 20 m by 20 m plot to sample the epiphyte community. It was decided to sample from this defined, limited area, rather than using randomly selected trees dispersed throughout the entire woodland site in order to keep the survey area the same between different sites and to ensure that the entire survey plot had been subject to dense *Rhododendron* cover prior to clearance. Dense *Rhododendron* cover was defined as being a mature stand featuring closed canopy cover across the survey plot. For cleared sites, specific plot locations within the greater woodland site were located following discussions with the local land manager who could identify areas that had been subject to suitably dense *Rhododendron* cover prior to clearance.

To sample the epiphyte community, we randomly selected nine oak and nine birch trees within each plot to serve as sample trees. At a limited number of sites we were unable to identify nine trees of each species within the survey plot, in which case we extended the survey area to a 30 m by 30 m range. On the North-facing side of each sample tree we placed a 30 cm tall by 10 cm wide mini-quadrat at the base of the tree and also at breast height and recorded the total percent cover of every plant species present in the quadrat (principally mosses and liverworts, but occasionally including ferns and vascular species, especially at the tree base). Only the North-facing side of the trees was surveyed in order to maintain consistency between different trees, since the North side typically has a higher bryophyte abundance than the South side (Porley and Hodgets, 2005). We therefore gathered survey data 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).

Sites were split across ten spatial blocks with each block containing cleared, dense and uninvaded control sites. All surveys were conducted during summer 2014, apart from 13 uninvaded control site surveys and 11 dense *Rhododendron* surveys, which were conducted in summer 2013. These surveys were carried out in an identical manner and were used to supplement the 2014 dataset to maximise the uninvaded control and dense *Rhododendron* data that were available for analysis.