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RESEARCH ARTICLE

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Understorey plant community composition reflects invasion history decades after invasive Rhododendron has been removed

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Abstract

1. A growing awareness of the destructive effects of non-native invasive species has led to a massive increase in removal programmes around the world. However, little is generally known about what happens to sites following the removal of the invasives and the implicit assumption that the native community will return, unaided, to pre-invasion conditions is often left untested.
2. We assessed recovery of the native understorey plant community following removal of the non-native invasive *Rhododendron ponticum* L. from Scottish Atlantic oak woodland. We recorded understorey community composition in sites covering a gradient of increasing *R. ponticum* density, and across a separate series of sites covering a chronosequence of time since *R. ponticum* removal. We then compared both of these series to the target community found in uninvaded sites. We also analysed differences in soil chemistry between the sites to test for chemical legacy effects of invasion in the soil.
3. Native understorey cover declined as *R. ponticum* density increased, with bryophytes dropping to less than a third of the cover present in uninvaded sites and forbs and grasses being completely extirpated under dense stands.
4. Cleared sites showed no evidence of returning to the target community, even after 30 years of recovery, and instead formed a bryophyte-dominated "novel community," containing few of the typical oak woodland vascular plants.
5. Contrary to expectation, soil pH, C:N ratio and nutrient concentrations (N, P, K, Ca and Mg) were not affected by the invasion of *R. ponticum*, and chemical legacy effects in the soil were not responsible for the failure of the native community to revert to pre-invasion conditions. Instead, we hypothesise that the rapid formation of a bryophyte mat, coupled with the often substantial distances to potential seed sources, hindered vascular plant recolonisation.
6. *Synthesis and applications*. Clear evidence of invasion history can be detected in the understorey plant community even decades after the successful removal of the invasive *Rhododendron ponticum* L. This finding demonstrates that native communities may be unable to recover effectively of their own accord following invasive species removal, and will require further management interventions in order to achieve restoration goals.

KEYWORDS
Atlantic oak woodland, bryophytes, community ecology, invasive species, legacy effects, non-native, restoration, rhododendron, understorey plant community

1 | INTRODUCTION

Non-native invasive species represent a major threat to biodiversity in almost every biome on Earth (Corbin & D'Antonio, 2012; Mooney, 2005). Large-scale eradication programmes targeting problematic invasives have, therefore, been implemented in many regions to combat these destructive effects (Reid, Morin, Downey, French, & Virtue, 2009; Scalera, Genovesi, Essl, & Rabitsch, 2012). While many of these schemes have been successful in achieving their immediate goal of reducing invasive population densities, the implicit assumption that native communities will then return to pre-invasion conditions is often left untested (Levine et al., 2003; Reid et al., 2009). Indeed, in the few cases where communities have been monitored following control efforts, the target invasive is often replaced by other invasive species, or a highly reduced subset of natives (Buckley, Bolker, & Rees, 2007; Corbin & D'Antonio, 2012; Reid et al., 2009). Recolonisation by native species may be a slow process, however, and long-term studies are extremely rare.

In some cases, native species may be unable to recolonise, even long after the invasive species has been removed. This can happen if the invasive species brought about persistent changes to the biotic or abiotic environment that do not automatically reverse following invasive species removal. These lasting changes are known as "legacy effects," and there is increasing evidence for their importance in hindering restoration efforts in a variety of invaded ecosystems (Corbin & D'Antonio, 2012; Ehrenfeld, 2010). The presence of legacy effects can lead to the creation of a "novel community" that bears little resemblance to the desired pre-invasion community (Hobbs, Higgs, & Hall, 2013; Seastedt, Hobbs, & Suding, 2008). Persistent legacy effects often emerge following plant invasions that result in drastically altered abundances of native species (Corbin & D'Antonio, 2012). For example, if the invasion has a disproportionate impact on certain taxonomic groups then they may form a much smaller proportion of the native community following invasive species clearance than they do in pristine, uninvaded sites. Effective recovery in these cases will depend on the availability of a suitable source community from which desired native species can recolonise, and there is likely to be a considerable lag period before the native community regains its pre-invasion composition, if, in fact, this composition is ever recovered (Corbin & D'Antonio, 2012). Indeed, if a certain subset of native species or taxonomic groups comes to rapidly dominate the community following invasive species removal, then they may create a barrier to recolonisation by species or groups that were slower to recover due to all the suitable germination sites already being filled. In this case, an "alternate stable state" may be reached whereby the novel community forming following invasive species removal is highly resistant to recovering the full complement of native species found in pristine, uninvaded plots (Suding, Gross, & Houseman, 2004).

In addition to these potential legacies in native community composition, an increasing number of studies have demonstrated the capacity of invasive plant species to exert legacy effects via changes in soil and litter chemistry (Corbin & D'Antonio, 2012; Ehrenfeld, 2010). For example, invasive species have been shown to cause lasting changes in soil pH, soil moisture, carbon (C), nitrogen (N) and cation concentrations, and the presence of monoterpenes and polyphenols in litter (Corbin & D'Antonio, 2012; Ehrenfeld, 2010; Levine et al., 2003; Liao et al., 2008). If these changes make the environment inhospitable to many native species, they may prevent the desired native community from getting re-established, even in the presence of suitable source populations (Hobbs et al., 2013; Seastedt et al., 2008). Effective restoration in the presence of such soil legacy effects is likely to require intensive management interventions such as soil mixing or the application of appropriate mitigation treatments in addition to eradicating the invasive plants (Firn, House, & Buckley, 2010; Suding et al., 2004).

Rhododendron ponticum is one such invasive plant that appears likely to exert both biotic and abiotic legacy effects on the native community by (1) forming dense, impenetrable stands that effectively exclude native species from large areas (Cross, 1975) and (2) exuding toxic polyphenols that reduce nutrient availability for native species and have the potential to persist in the soil long after the removal of the invasive plants themselves (Cross, 1975; Rotherham, 1983). While the presence of polyphenols in *R. ponticum* plant tissue and in the surrounding soil has been demonstrated, the impacts on native plants have never been tested in the field, and the importance of legacy effects of any type have never been evaluated (Rotherham, 1983).

Rhododendron ponticum was introduced to the UK in 1763 and planted widely as an ornamental plant in gardens, and as game cover on shooting estates (Cross, 1975; Dehnen-Schmutz, Perrings, & Williamson, 2004). It quickly spread from these source populations to become naturalised across large areas of woodland and open hillside and is now recognised as one of the most problematic invasive species in the UK (Dehnen-Schmutz et al., 2004; Edwards, 2006). One of the habitat types most at risk from invasive *R. ponticum* is the Atlantic oak woodland of Western Scotland, where it has been identified as posing a major threat to native communities (Edwards, 2006; Long & Williams, 2007). This habitat is represented in EC Habitat Directive Annex I as "old sessile oakwoods with *Ilex* and *Blechnum*" and is of high conservation importance. In recent years it has been subject to extensive removal efforts, but budgetary constraints and the prioritisation of resources to further control efforts has precluded the subsequent monitoring of sites to determine whether native communities have been successfully restored (Dehnen-Schmutz et al., 2004).

The purpose of this research was to assess the long-term impact of invasive *R. ponticum* on the native plant community in Scottish

Atlantic oak woodlands. We used a series of sites spanning a gradient of increasing *R. ponticum* density to investigate how the understorey community changed during invasion and to ascertain whether certain native plant species or taxonomic groups were better able to survive the invasion. We also studied a separate series of sites spanning a temporal gradient (chronosequence) of between 1 and 30 years of recovery following *R. ponticum* clearance to determine whether the plant community returned to pre-invasion conditions following the removal of invasive stands. We additionally measured components of soil chemistry across both gradients to test for the presence of chemical legacy effects in the soil that could hinder site recovery. The inclusion of sites spanning three decades of recovery following invasive species removal represented an important advance over the majority of existing studies, which typically consider recovery across only one or two seasons and offered an unprecedented opportunity to assess the recovery of native communities across ecologically relevant timescales (Corbin & D'Antonio, 2012; Reid et al., 2009).

Our specific questions were: (1) did certain taxonomic groups within the understorey community (forbs, grasses, bryophytes, ferns or woody species) decline more severely than others as *R. ponticum* increased in density?; (2) did all taxonomic groups recover effectively following *R. ponticum* clearance and did the understorey community composition recover to resemble that found in uninvaded control plots?; and (3) did *R. ponticum* exert a strong chemical legacy effect on the soil?

2 | MATERIALS AND METHODS

2.1 | Data collection

All fieldwork was conducted in Atlantic oak woodlands on the west coast of Scotland in Argyll, Kintyre and Lochaber, between 55°76′N and 56°90′N, an area of *c.* 120 km by 70 km (see Figure S1). The tree community in these woodlands principally contained oak (*Quercus pertraea* [Mattuschka] and *Quercus robur* [Mattuschka]), rowan (*Sorbus acuparia* L.), hazel (*Corylus avellana* L.), birch (*Betula pendula* [Roth] and *Betula pubescens* Ehrh.) and ash (*Fraxinus excelsior* L.).

Two separate studies were established to assess the long- and short-term impacts of invasion on the understorey plant community. Study 1 assessed the impact of the initial *R. ponticum* invasion, and Study 2 assessed recovery following *R. ponticum* removal. For Study 1, conducted in summer 2013, we identified and sampled 56 plots across the study area that were subject to different densities of *R. ponticum* (site locations are listed in Table S1). These plots ranged from uninvaded areas (used as "control" plots to give baseline data on the composition and structure of the uninvaded community) to high-density *R. ponticum* thickets (up to 3,000 bushes per ha). Plots were chosen to be as similar as possible to reduce variability not associated with their history of *Rhododendron* invasion. All plots consisted of ancient semi-natural woodland and were located more than 100 m from any ravines, rocky outcrops or plantation forestry and none were subject to active management of the tree community (i.e. no harvesting, coppicing or removal of dead wood).

Potential plots 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. Plots were chosen based on availability and also to ensure the even distribution of plots with different *Rhododendron* densities throughout the study area. This study design therefore conformed to the "natural experiment" paradigm described by Diamond (1983), whereby plot locations for experimental treatments (in this case different *Rhododendron* densities) 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 *Rhododendron* in an ideally designed field trial). While plots were selected based on availability, following the field season, each plot was assigned to one of 10 spatial blocks based on their geographic location, with each block containing plots covering a range of *R. ponticum* densities (see Table S1). These geographic blocks were included in the statistical analyses in order to account for much of the spatial variation inherent in a study of this type.

To quantify understorey community composition at each plot, we established a 20 m by 20 m perimeter and deployed nine 1-m^2 quadrats in a 10 m by 10 m grid formation (Figure S2). At each quadrat, we measured the distance to the nearest *R. ponticum* bush in each of the four compass quadrants, and used these distances to calculate the overall *R. ponticum* density for the site (using the "point-centred quarter" method of Cottam & Curtis, 1956). We then recorded the per cent cover of every understorey plant species (including ferns, bryophytes and tree seedlings) in each quadrat and averaged abundances across the nine quadrats to determine plot-level understorey community composition. After recording understorey community composition, we extracted a 5-cm diameter soil core to 10-cm depth at each quadrat location. These were stored at 4°C until the end of the sampling period, then samples were bulked for each plot, dried and C:N ratios were calculated from the total N and C content, determined by an automated Dumas combustion procedure (Pella & Colombo, 1973) using a Flash 2000 elemental analyser (Thermo Scientific). An additional soil sample was taken at each quadrat and its pH was determined later the same day using a portable pH meter (Hanna Instruments HI99121) in a mix of 20-ml soil to 80-ml de-ionised water, which was mixed and then left to settle for 5 min before taking pH readings. In order to obtain a more detailed understanding of how soil chemistry changed as *R. ponticum* increased in density, we additionally deployed plant root simulator probes (WesternAg, Saskatoon, Canada) at a subset of 20 sites with different *R. ponticum* densities to reveal changes in NO_3, NH_4, P, K, Ca and Mg (see Table S1 for nutrient probe site locations). Four sets of probes were deployed in each plot—one in each plot corner—then results were averaged for the plot. The probes were inserted vertically into the soil up to a depth of 10 cm and left for 8 weeks to accumulate nutrients, and then returned to WesternAg laboratories for analysis. These probes use ion exchange resins to accumulate nutrients in a similar manner to nutrient absorption by plant roots, and they therefore reveal the nutrient status of the soil as encountered by plants (Qian & Schoenau, 2002).

For Study 2, conducted in summer 2014, we identified and sampled a chronosequence of 37 plots that were previously infested with high-density *R. ponticum* stands (i.e. with closed canopy cover across the plot area), but which had been cleared at different points in time between 1984 and 2014 (Figure S1 and Table S2). We also surveyed six additional plots with dense *R. ponticum* thickets and six pristine, uninvaded plots for comparison with the cleared plots. We used the same methods to identify plots as in Study 1, and plots were once again assigned to one of 10 spatial blocks based on their geographic locations. To ensure that plots would be comparable, we only used locations that were cleared by cutting the *R. ponticum* bushes at the stump and applying herbicide (usually triclopyr or glyphosate; Edwards, 2006), with follow-up applications of foliar spray as necessary in subsequent years. This combination of techniques represents the most common method of control in Scotland (Edwards, 2006). If control efforts are not maintained then *R. ponticum* quickly regenerates to form dense stands. Since we were interested in the process of native species' recolonisation following the removal of an invasive species, and not in the process of invasive regeneration, we restricted our plots to areas where *R. ponticum* control efforts were maintained. These subsequent control efforts were restricted to the removal of *R. ponticum* and did not include the removal of other invasive species. We assessed community composition, pH and soil C:N ratios using the methods in Study 1, but did not deploy soil probes at these sites.

2.2 | Statistical analysis

The community composition data were used to calculate total species richness summed over all nine 1-m^2 quadrats in each plot, along with the mean overall vegetation cover averaged across the nine quadrats. The overall community composition for each plot was also broken down into five taxonomic groups: forbs, grasses, bryophytes, ferns and woody plants; and the average proportional cover and total cover for each group in each plot was calculated, along with the total species richness for each group across the whole plot.

For Study 1 analyses, *R. ponticum* density was $\log_e$ transformed and used as the explanatory variable (fixed effect) using the lme model formulation of the nlme package (Pinheiro, Bates, DebRoy, & Sarkar, 2014) in R statistical software (version 3.1.2; R Core Team, 2014). Spatial block was included as a random effect in all models to account for any variation in the results caused by geographic location, and no interactions were included between the fixed and random effects. These models account for the slightly unbalanced design present in our study, with a different number of plots falling into each block (Patterson & Thompson, 1971; see Table S1). These lme models were used to assess the effects of increasing *R. ponticum* density on the (1) species richness and (2) vegetation cover of the whole community. Similar models (using the same model formulation, but different response data) were then constructed and used to assess the effects of increasing *R. ponticum* density on the (1) species richness, (2) vegetation cover and (3) proportional cover of each taxonomic group separately (i.e. a separate model for forbs, grasses, bryophytes, ferns and woody species). The uninvaded plots were removed from all these analyses since these plots represent a qualitative difference from plots containing different densities of *R. ponticum*, giving a sample size of $n = 51$ plots distributed across 10 spatial blocks. For all analyses, the explanatory variable, *R. ponticum* density, was fitted as both a linear and a quadratic term, with the quadratic term subsequently being removed from the model if it was not significant at $p < .05$.

CANOCO 5 statistical software (Ter Braak & Šmilauer, 2012) was then used to perform partial-redundancy analysis (partial-RDA; using spatial block as a random effect [covariate in the language of CANOCO 5]) in order to reveal how changes to *R. poncitum* density impacted overall community composition. Linear methods (rather than unimodel methods) were used since the data covered only a short gradient in community composition (Šmilauer & Lepš, 2014). Data for each plot were standardised by plot norm so that the analysis would reveal changes in the proportion of each species and not be unduly influenced by changes in total vegetation cover between plots (Šmilauer & Lepš, 2014). Permutation tests (using 9,999 permutations) were used to test the significance of all constrained axes, but since only one explanatory variable was used in each analysis, this gave the same results as a test on only the first constrained axis.

Study 2 analyses used the same model formulations as in Study 1, but used time since *R. ponticum* clearance (rather than *R. ponticum* density) as the fixed explanatory variable. Paralleling Study 1, models tested for the effect of time since clearance on the (1) species richness, (2) vegetation cover and (3) proportional cover of the whole community and of each taxonomic group separately. The uninvaded plots were once again removed from these analyses since these plots represent a qualitative difference from plots where *R. ponticum* had been cleared and the dense *Rhododendron* sites were included as "time 0" plots since the community composition found under a dense thicket will be the community that is present immediately after the bushes have been cleared. This gave a sample size of $n = 43$ plots distributed across 10 spatial blocks. In an additional analysis, 16 plots that were cleared 10–20 years ago were lumped together and considered as a single level of a factor, with high-density *R. ponticum* plots ($n = 16$ plots) and pristine control and very low-density plots ($n = 16$ plots) from both years being used for comparison as the other two levels of the factor. Mixed effects models were then used to investigate how *Rhododendron* site type (uninvaded, cleared or dense) impacted per cent cover, proportional cover and species richness for the whole community and for each taxonomic group in each set of plots. Tukey's HSD post hoc comparisons from this analysis were then conducted to reveal whether the cleared plots more closely resembled high-density plots or uninvaded plots—i.e. whether they were recovering effectively 10–20 years after *R. ponticum* removal.

A partial-RDA was then constructed to test whether the overall community composition changed with increasing time since *R. ponticum* clearance. This analysis again used spatial block as a random effect (covariate), standardised the data by plot norm and used

9,999 permutations. A second partial-RDA was then performed where time since clearance was split into discrete levels of a factor by lumping plots together into groups covering 5-year intervals. These were then compared to plots with high *R. ponticum* cover and to pristine control plots using a classified plot diagram (Ter Braak & Šmilauer, 2012) to illustrate how the plots of different types were distributed in multivariate space. The RDA constrained the analysis so that the maximum amount of variation was accounted for by the explanatory variables, without constraining the analysis to treat years in a consecutive order. If the plots were shown to follow a logical order in the classified plot diagram, therefore, this would reveal that their community composition changed in a predictable way through time.

The impacts of increasing *R. ponticum* density and increasing time since *R. ponticum* removal on soil pH, total C and N concentrations, and C:N ratio, were investigated using a series of lme mixed effects models using the nlme package in R (Pinheiro et al., 2014), including spatial block as a random effect. The effect of increasing *R. ponticum* density on NO_3, NH_4, P, K, Ca and Mg was also assessed using mixed models. The explanatory variables were log transformed where necessary to achieve a normal distribution of residuals, determined by visually checking graphs of their distribution.

3 | RESULTS

> *Question 1: Did certain taxonomic groups within the understorey community (forbs, grasses, bryophytes, ferns or woody species) decline more severely than others as* R. ponticum *increased in density?*

As *R. ponticum* density increased, species richness ($F_{1,40} = 12.26$, $p = .001$) and understorey vegetation cover ($F_{1,40} = 77.83$, $p < .001$) decreased, with very little native vegetation remaining at high *R. ponticum* densities (Figure S3). The total cover of forbs ($F_{1,40} = 29.49$, $p < .001$), grasses ($F_{1,40} = 42.95$, $p < .001$), bryophytes ($F_{1,40} = 18.77$, $p < .001$) and ferns ($F_{1,40} = 4.13$, $p = .049$) decreased in plots with higher *R. ponticum* density, while there was no significant effect on the cover of woody species ($F_{1,40} = 0.47$, $p = .499$) (Figure 1, row 1). When looking at the cover of each taxonomic group as a proportion of the total cover, however, bryophytes showed a proportional increase within the understorey community ($F_{1,40} = 19.31$, $p < .001$), while forbs ($F_{1,40} = 7.24$, $p = .010$) and grasses ($F_{1,40} = 14.90$, $p < .001$) showed a proportional decrease. There was no significant change in the proportional abundance of ferns ($F_{1,40} = 0.72$, $p = .403$) or woody species

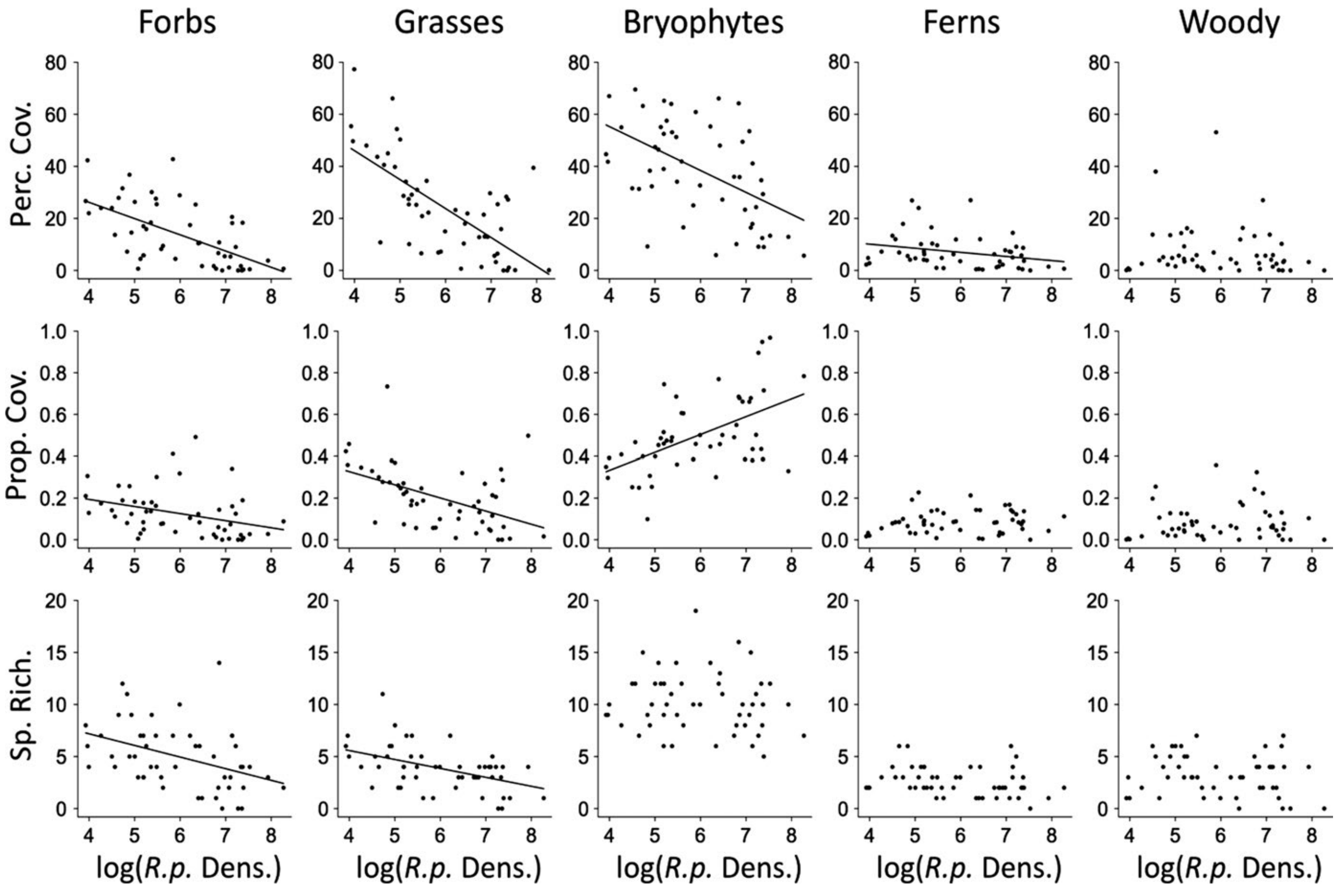

FIGURE 1 The effect of increasing *Rhododendron ponticum* density ($\log_e$[bushes per ha +1]) on the per cent cover (row 1), proportional cover (row 2) and species richness (row 3) of forbs, grasses, bryophytes, ferns and woody species (*n* = 51). Species richness is the total over all nine quadrats in each plot, whereas per cent cover and proportional cover are averaged across the nine quadrats. Regression lines (the average for all blocks) are presented where significant at the $p < .05$ level

($F_{1,40} = 0.37$, $p = .546$) (Figure 1, row 2). The species richness of forbs ($F_{1,40} = 9.94$, $p = .003$) and grasses ($F_{1,40} = 16.00$, $p < .001$) also decreased as *R. ponticum* density increased, while there was no significant change in bryophyte species richness, which remained high ($F_{1,40} = 0.48$, $p = .493$), or in fern ($F_{1,40} = 3.56$, $p = .067$) and woody ($F_{1,40} = 0.98$, $p = .329$) species richness, which remained low (Figure 1, row 3). The results of the partial-RDA supported these patterns, revealing a significant change in community composition as *R. ponticum* increased in density (test on all constrained axes: $F = 1.9$, $p = .029$). Most species were negatively correlated with *R. ponticum* density, apart from a few common bryophyte species such as *Thuidium tamariscinum* and *Kindbergia praelonga*, which showed a weak positive correlation (Figure 2).

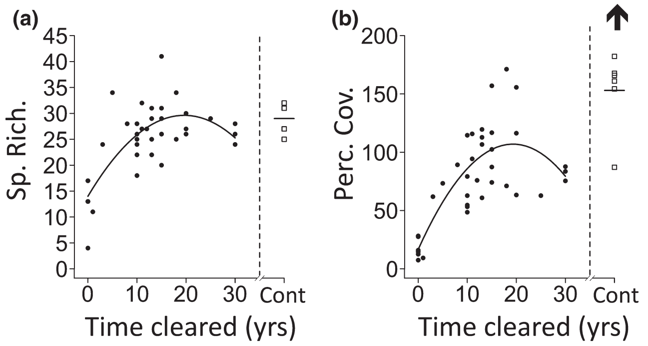

FIGURE 3 The effect of increasing time since *Rhododendron ponticum* removal on (a) understorey plant species richness and (b) vegetation cover (per cent cover). Regression lines are the average for all blocks ($n = 43$). Uninvaded control plots are also plotted for comparison, and the mean of these values is indicated with a horizontal bar. The arrow indicates that vegetation cover in these control plots is significantly higher than plots cleared 10–20 years ago, whereas there is no significant difference in species richness

> *Question 2: Did all taxonomic groups recover effectively following* R. ponticum *clearance and did the understorey community composition recover to resemble that found in uninvaded control plots?*

Species richness ($F_{1,28} = 25.06$, $p < .001$) and understorey vegetation cover ($F_{1,28} = 26.97$, $p < .001$) both increased with time since *R. ponticum* clearance (Figure 3). Tukey's post hoc comparisons of plots that were cleared 10–20 years ago with high current *R. ponticum* density plots and with uninvaded control plots revealed that species richness in cleared plots was significantly higher than in high-density plots ($t_{1,39} = 6.21$, $p < .001$), but did not differ significantly from the species richness found in uninvaded control plots ($t_{1,39} = 1.18$, $p = .47$). The understorey vegetation cover in cleared sites, however, remained significantly lower than that in the pristine controls ($t_{1,39} = 6.21$, $p < .001$), although it did increase significantly from the cover found in high-density plots ($t_{1,39} = 8.15$, $p < .001$).

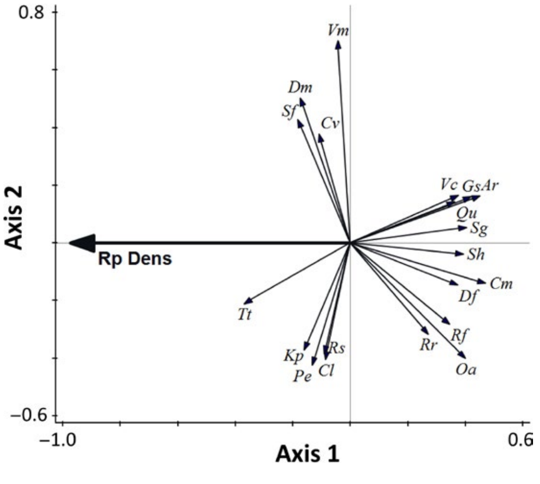

FIGURE 2 Results from a partial-RDA using logged *Rhododendron ponticum* density as the only explanatory variable and spatial block as a random effect ($n = 51$ plots). The 30 best-fitting species are plotted (*Ar = Ajuga reptans*; *Cl = Circaea lutetiana*; *Cm = Conopodium majus*; *Cv = Calluna vulgaris*; *Df = Dryopteris filix-mas*; *Dm = Dicranum majus*; *Gs = Galium saxatile*; *Kp = Kindbergia praelonga*; *Oa = Oxalis acetosella*; *Pe = Pellia epiphylla*; *Qu = Quercus* spp.; *Rf = Ranunculus ficaria*; *Rr = Ranunculus repens*; *Rs = Rubus fruticosus*; *Sf = Sphagnum fallax*; *Sg = Scapania gracilis*; *Sh = Stellaria holostea*; *Tt = Thuidium tamariscinum*; *Vc = Vicia cracca*; *Vm = Vaccinium myrtillus*) [Colour figure can be viewed at wileyonlinelibrary.com]

The total cover of forbs ($F_{1,28} = 1.42$, $p = .244$) and grasses ($F_{1,28} = 3.57$, $p = .069$) did not change significantly with time since the *R. ponticum* clearance (Figure 4). Indeed, Tukey's post hoc comparisons revealed that the cover of forbs ($t_{1,39} = 7.49$, $p < .001$) and grasses ($t_{1,39} = 6.25$, $p < .001$) in plots cleared 10–20 years ago remained significantly lower than that found in uninvaded control plots (Figure 4; row 1). Bryophyte total cover, however, showed a significant increase with time since *R. ponticum* clearance ($F_{1,28} = 38.45$, $p < .001$), and plots that were cleared 10–20 years ago were indistinguishable from uninvaded control plots in this respect ($t_{1,39} = -1.44$, $p = .33$). The proportional cover of forbs ($F_{1,28} = 0.613$, $p = .440$), grasses ($F_{1,28} = 2.52$, $p = .123$) or bryophytes ($F_{1,28} = 1.12$, $p = .300$) did not change with time since *R. ponticum* clearance, with the proportion of forbs ($t_{1,39} = 5.04$, $p < .001$) and grasses ($t_{1,39} = 4.40$, $p < .001$) remaining significantly lower, and the proportion of bryophytes ($t_{1,39} = -5.29$, $p < .001$) remaining significantly higher, in plots cleared 10–20 years ago than in uninvaded controls (Figure 4, row 2). The species richness of forbs ($F_{1,28} = 5.82$, $p = .023$) and grasses ($F_{1,28} = 20.23$, $p < .001$) increased slightly, albeit significantly, with time since *R. ponticum* clearance, but the species richness in plots cleared 10–20 years ago remained significantly lower than that in uninvaded control plots (forbs: $t_{1,39} = 7.14$, $p < .001$, grasses: $t_{1,39} = 3.67$, $p < .001$). The species richness of bryophytes, by contrast, increased dramatically with time since *R. ponticum* clearance ($F_{1,28} = 14.11$, $p < .001$), and ended up significantly higher in plots cleared 10–20 years ago than in uninvaded control plots ($t_{1,39} = 4.09$, $p < .001$; Figure 4, row 3). While ferns and woody species showed some significant changes with time since *R. ponticum* clearance, these changes were of a very small magnitude and are unlikely to be biologically significant due to their small effect size (Figure 4).

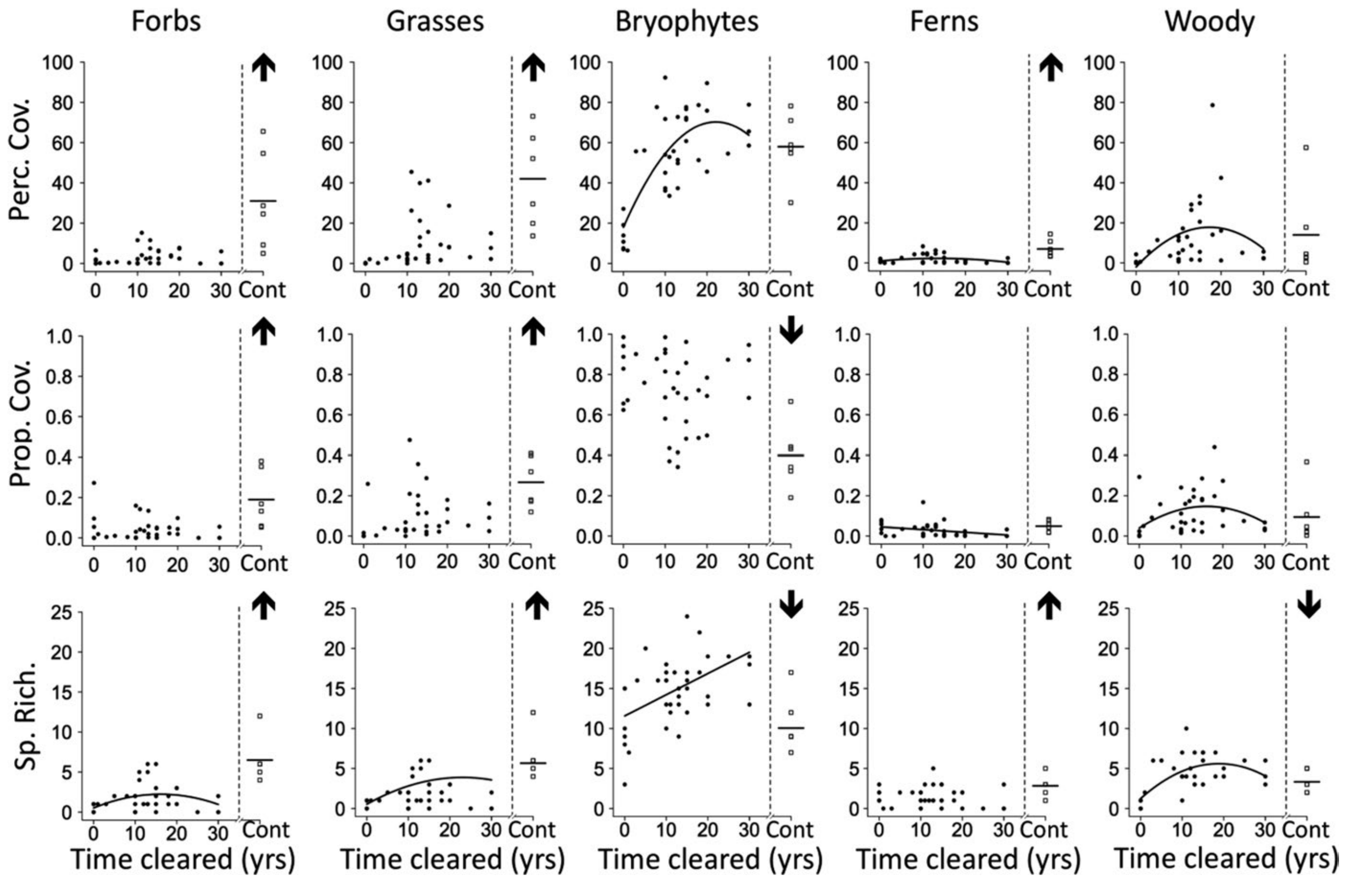

FIGURE 4 Results from mixed models showing the effect of time since *Rhododendron ponticum* clearance on the per cent cover (row 1), proportional cover (row 2) and species richness (row 3) of forbs, grasses, bryophytes, ferns and woody species ($n = 43$). The regression line (the average for all blocks) is only plotted where significant at the $p < .05$ level. Uninvaded control plots are plotted for comparison, with their mean value indicated by a horizontal bar. Arrows show the relationship between these control plots and the group of plots that were cleared 10–20 years ago. Arrows are only featured where the relationship between time and the response variable is significant; arrows pointing up denote that control plots have significantly higher values than the cleared plots; arrows pointing down denote that control plots have a significantly lower value than the cleared plots; and a lack of arrow denotes the lack of a significant difference

Partial-redundancy analysis revealed that there was a significant change in community composition through time ($F = 4.7$, $p = .001$), with all but a few species (such as *K. praelonga* and *Isothecium myosuroides*) being positively correlated with time since *R. ponticum* removal (Figure 5). Visual inspection of the classified plot diagram, resulting from the partial-RDA which included time as a factor, however, revealed that these changes were not proceeding towards the community composition found in pristine control plots, and were instead following their own divergent trajectory (Figure 6).

> *Question 3: Did* R. ponticum *exert a strong chemical legacy effect on the soil?*

There was no significant change in pH ($F_{1,40} = 0.52$; $p = .47$), or any of the other measured soil properties (C:N ratio [$F_{1,33} = 2.12$; $p = .15$], P [$F_{1,18} = 0.84$; $p = .37$], K [$F_{1,18} = 0.17$; $p = .68$], Ca [$F_{1,18} = 2.03$; $p = .17$], Mg [$F_{1,18} = 3.34$; $p = .12$]), as *R. ponticum* density increased (Figure S4). There was also no significant change in pH ($F_{1,37} = 2.39$; $p = .13$) or C:N ratio ($F_{1,34} = 0.80$, $p = .37$) with increasing time since *R. ponticum* clearance (Figure S5).

4 | DISCUSSION

Our results revealed that understorey plant community composition did not return to its pre-invasion state, even decades after the removal of invasive *R. ponticum* stands. Instead, a novel community was formed, which appeared to be the result of changes in community composition occurring during the invasion, rather than being driven by any lasting impacts of invasion on soil chemistry. Namely, invasion favoured a bryophyte-dominated community, which quickly recolonised following *R. ponticum* removal at the expense of forbs and grasses. This novel community appeared to be maintaining an "alternate stable state" (Suding et al., 2004), with little evidence of forbs or grasses returning even after up to 30 years of recovery.

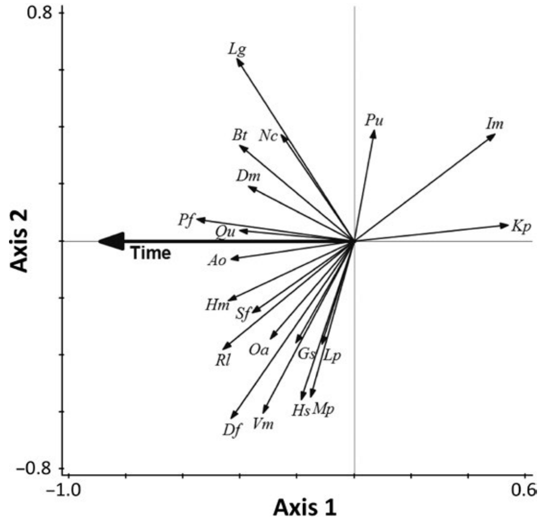

FIGURE 5 Results from partial-RDA, using time since *Rhododendron ponticum* removal as the only explanatory variable and spatial block as a random effect (*n* = 31 plots). The 20 best-fitting species are plotted (*Ao* = *Anthoxanthum odoratum*; *Bt* = *Bazzania trilobata*; *Df* = *Deschampsia flexuosa*; *Dm* = *Dicranum majus*; *Gs* = *Galium saxatile*; *Hm* = *Holcus mollis*; *Hs* = *Hylocomium splendens*; *Im* = *Isothecium myosuroides*; *Kp* = *Kindbergia praelonga*; *Lg* = *Leucobryum glaucum*; *Lp* = *Lonicera periclymen*; *Mp* = *Melampyrum pratense*; *Nc* = *Nowelia curvifolia*; *Oa* = *Oxalis acetosella*; *Pf* = *Pollitrichastrum formosum*; *Pu* = *Plagiomnium undulatum*; *Qu* = *Quercus* spp.; *Rl* = *Rhytidiadelphus loreus*; *Sf* = *Sphagnum fallax*; *Vm* = *Vaccinium myrtillus*)

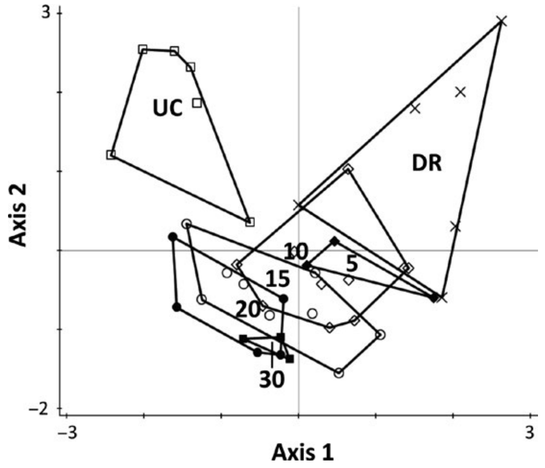

FIGURE 6 Classified plot diagram from a partial-RDA coding time since *Rhododendron ponticum* removal as levels of a factor and spatial block as a random effect (*n* = 37 plots). UC = uninvaded control plots (open squares); DR = dense *R. ponticum* plots (i.e. "time 0"; diagonal crosses); 5–30 = number of years since *R. ponticum* removal (5 = filled diamonds; 10 = open diamonds; 15 = open circles; 20 = filled circles; 30 = filled squares). Plots 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 plots at the top left of the diagram

> *Question 1: Did certain taxonomic groups within the understorey community (forbs, grasses, bryophytes, ferns or woody species) decline more severely than others as* R. ponticum *increased in density?*

Invasion was revealed to have a disproportionate effect on certain taxonomic groups, with forbs and grasses showing a proportional decline and bryophytes showing a proportional increase within the understorey community (although all groups showed an absolute decrease in per cent cover with increasing *R. ponticum* density). Furthermore, bryophytes were able to maintain the same overall species richness in dense *R. ponticum* stands as in uninvaded woodland, while forbs and grasses were all but extirpated in heavily invaded areas. These findings complement previous research showing that invasive plants can have differential effects on different taxonomic groups within a site (Corbin & D'Antonio, 2012). For example, the different responses of vascular plants and bryophytes to invasion that we detected here are also apparent following the invasion of Sitka spruce (*Picea stichensis*) in European coastal heathlands (Saure, Vandvik, Hassel, & Vetaas, 2014).

> *Question 2: Did all taxonomic groups recover effectively following* R. ponticum *clearance and did the understorey community composition recover to resemble that found in uninvaded control plots?*

Once the invasive *R. ponticum* had been removed, overall species richness quickly returned to similar values to those found in uninvaded control plots, while total per cent cover only recovered to about two-thirds of that found in the controls after 30 years. A more detailed look at which species responded to removal revealed that the recovery in species richness was entirely driven by bryophytes, which actually gained more species during the post-clearance recolonisation process than were present in uninvaded controls. This increase in bryophyte diversity was almost certainly aided by reduced competition with the vascular plants which, being completely excluded from dense *R. ponticum* thickets, were much slower to recolonise following *R. ponticum* removal. Overall vegetation cover therefore never fully recovered, since plots failed to regain grass and forb cover to supplement the bryophyte cover.

Although overall species richness did return to pre-invasion levels following removal of the invasive species, the proportional cover of each of the taxonomic groups remained similar to that found under dense *R. ponticum* thickets. RDA revealed that while the community composition of plots changed in a consistent way through time, it was proceeding towards a novel community composition, and showed no signs of reconverging on the community composition found in uninvaded control plots. This finding supports recent papers on invasion theory suggesting that many sites may require further post-clearance management interventions, such as re-seeding with native species, in order to restore pre-invasion communities (Corbin & D'Antonio, 2012; Suding et al., 2004).

There was quite a lot of variation in the results for sites with the same number of years of recovery following *R. ponticum* removal. While all sites had been covered with dense *R. ponticum* stands prior to clearance, the total extent of the stands and the length of invasion may have differed between sites. Unfortunately, detailed site histories were unavailable for most sites due to a lack of record keeping at the time of invasion, which in all cases occurred many decades ago. Also, while all sites were selected to be as similar as possible with regard to tree species composition, management regime and other features such as a lack of ravines or rocky outcrops, sites will undoubtedly have differed with respect to other unmeasured characteristics. Since we were limited to using available sites, rather than being able to introduce and clear *R. ponticum* in a perfectly replicated field trial (which would have taken many decades), it is inevitable that this will have introduced variation into our results. Understanding the additional factors that may accelerate or decelerate the rate of site recovery represents an interesting avenue of future research.

> *Question 3: Did* R. ponticum *exert a strong chemical legacy effect on the soil?*

We found little support for the presence of legacy effects in the soil in our system and did not detect any changes in soil chemistry either during the invasion or during the recovery period after *R. ponticum* removal. This was surprising, since previous research has suggested that *Rhododendron* species acidify the soil, increase C:N ratios and reduce the availability of various nutrients (Horton, Clinton, Walker, Beier, & Nilsen, 2009; Rotherham, 1983; Wurzburger & Hendrick, 2007). This previous research was mostly conducted for sister species on other continents, however, or for plants growing in laboratory conditions (Nilsen et al., 1999; Rotherham, 1983). It therefore seems likely that we did not detect any changes in our study since soils in oak woodlands are already comparatively nutrient poor and possess a low pH (Cross, Perrin, & Little, 2010). This is encouraging in that it suggests that *R. ponticum* may not be as damaging to the environment in oak woodlands as compared to other invaded ecosystems. This also highlights the fact that legacy effects can be highly context dependent, and illustrates that an invasive species may alter ecosystems in different ways depending on the local environment (Corbin & D'Antonio, 2012; Ross, Johnson, & Hewitt, 2003).

It is, of course, possible that *R. ponticum* exerted a soil legacy effect on some unmeasured aspect of the system which lay out with the scope of this study, for example by altering the mycorrhizal community, as occurs with other ericaceous species (Hogberg, Hogberg, & Myrold, 2007; Kohout et al., 2011). Additional research will be necessary to elucidate any impacts on these additional aspects of the soil environment. However, further research by our group has revealed that re-seeding with native species represents a viable restoration strategy following *R. ponticum* removal (Maclean, 2016). This evidence that native plants can grow in soil that was previously subject to dense *R. ponticum* invasion suggests that any legacy effects in the soil do not present a significant barrier to recolonisation by native plants.

4.2 | Synthesis

If changes to soil chemistry did not play an important role in this system then an alternative mechanism must be responsible for the failure of native communities to fully recover even decades after the invasive bushes had been removed. Since mature *R. ponticum* forms dense, evergreen stands that transmit little light to the understorey throughout the year, it is likely that competition for light was responsible for excluding most native species (Cross, 1975; Long & Williams, 2007; Rotherham, 1983). Greatly reduced light transmission to ground level would impact vascular plants more than bryophytes, reflecting the patterns seen in our data, and would be particularly detrimental to the many woodland species that depend on high irradiance at the forest floor in early spring before the trees are in leaf (Clinton, 2003; Cross, 1975). Since impacts on light transmission to ground level are immediately reversed once the bushes are removed, these effects can have played no part in the failure of forbs and grasses to recover in the years following *R. ponticum* removal. Instead it seems likely that decades of invasion reduced the local seed bank in addition to extirpating the adult plant populations, so preventing rapid germination and recolonisation from seed once light levels had been restored (Gioria & Pyšek, 2016; Maclean, 2016). Instead of regenerating from the seed bank, plants would have to recolonise from neighbouring populations, which may be several kilometres away—a process that could take many decades (Reid et al., 2009; Seabloom et al., 2003; Suding et al., 2004). Recolonisation could be further hampered by increased habitat fragmentation, which in the study region is partly driven by the replacement of native woodland with plantation forests that lack a diverse ground flora (Long & Williams, 2007).

Once seeds of native species arrived at recovering sites, they would face a further barrier from the bryophyte layer that we have revealed forms rapidly in cleared sites. The presence of a bryophyte layer has been demonstrated to cause a significant barrier to the germination and survival of vascular plant seeds in many other environments including New Jersey Pinelands, Swedish birch-heath-woodlands and under laboratory conditions (Sedia & Ehrenfeld, 2003; Soudzilovskaia et al., 2011). This rapid formation of a bryophyte layer may lead to the creation of an "alternate stable state" in cleared sites whereby the bryophyte layer maintains itself over the long term, preventing recolonisation by vascular plants (Firn et al., 2010; Suding et al., 2004).

5 | CONCLUSIONS

We have revealed that native plant communities showed no sign of returning to pre-invasion conditions after up to 30 years of recovery following *R. ponticum* removal. A lack of observed legacy effects on the soil suggested that, following a review of local conservation objectives, restoration efforts should focus on aiding the arrival and establishment of forbs and grasses, and need not seek to alter the condition of the soil (Corbin & D'Antonio, 2012;

Suding et al., 2004). Indeed, preliminary research by our group has revealed that management techniques focused on manipulating the understorey community, such as bryophyte removal or seed addition, are effective in achieving restoration goals, whereas management techniques seeking to alter soil chemistry, such as the addition of activated carbon or fertilisation, are not successful (Maclean, 2016).

This study has highlighted the long-term destructive effects of invasive species, which can persist long after the invasives themselves have been removed. It has revealed that site recovery cannot be assumed to occur naturally following invasive species removal and has emphasised that further management may often be necessary to achieve restoration goals.

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AUTHORS' CONTRIBUTIONS

All authors conceived the ideas, designed the methodology, contributed critically to drafts and gave final approval for publication; and J.E.M. collected and analysed the data and led the writing of the manuscript.

DATA ACCESSIBILITY

Data are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.t4j7k (Maclean, 2017).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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