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Exclusion of large herbivores: Long-term changes within the plant community

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ABSTRACT

Semi-natural woodlands are a globally important relict ecosystem for biodiversity, which are threatened through a range of anthropogenically induced changes, including overgrazing by large herbivores. Fencing to conserve biodiversity is increasingly used as a management tool, so the long-term impacts of large herbivore removal requires investigation. The objective of this research is to investigate the effect of large herbivore exclusion on vegetation, through time, using empirical long-term vegetation data collected over ~40 years. The responses of ground flora communities to this removal will be assessed, and it is predicted that a change in woodland vegetation will occur through time. Plant community composition was surveyed in a network of 7 large-herbivore exclosures, within protected temperate oak woodland in Ireland, at intervals up to 41 years. Ground flora species abundance was quantified and time since fencing was used to standardise the survey data, with three time groups being derived from this to assess beta diversity changes through time. With total removal of large herbivores from the oak woodland ecosystem, this study has identified significant changes in ground flora composition and abundance, and a general homogenisation of the vegetation community with increasing time since large herbivore removal. Large-scale long-term fencing of oak woodlands should be replaced by large herbivore management programmes, in order to ensure the conservation of diverse woodland ecosystems.

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1. Introduction

Semi-natural woodlands are a globally important ecosystem (Klenner et al., 2009). At a European scale, 45% of the land area is forested, although only ~26% of this (4% excluding the Russian Federation) is classified as natural (undisturbed by man) and 70% (87% excluding the Russian Federation) as semi-natural (Forest Europe et al., 2011). The functioning of these woodland ecosystems are being impacted through a range of anthropogenically induced vegetation changes (Rackham, 2008), including climate change (e.g., Rackham, 2008; Munson et al., 2012), invasive species (e.g., Mack et al., 2000; Rackham, 2008; Santos et al., 2011), and overgrazing (e.g., Côté et al., 2004; Rackham, 2008). Large herbivore overabundance can impact greatly on the woodland ecosystem and has been shown to drive change in an ecosystem (Fuller and Gill, 2001; Côté et al., 2004) with cascading effects on a range of biotic and abiotic components such as invertebrates (Pollard and Cooke, 1994; Allombert et al., 2005; Bugalho et al., 2011), birds (McShea and Rappole, 2000), small mammals (Buesching et al., 2011; Bush et al., 2012), vegetation (Côté et al., 2004), soil (Mofidi

et al., 2012), terrestrial carbon storage (Tanentzap and Coomes, 2012) and ecosystem functioning (Rooney and Waller, 2003). A European Union report stated that overgrazing is among the most important anthropogenic impacts associated with the decline in forest biodiversity (Slingenberg et al., 2009).

Woodland ecosystem dynamics are long-term processes, which are usually studied either empirically at short-term (within a decade) or historically at long-term (within centuries and millennia) scales. Being able to investigate long-term vegetation community data allows for improved understanding of the ecosystem (Silvertown et al., 2010) and has become an increasingly important tool for biodiversity research (Magurran et al., 2010). It is particularly useful for understanding the effects of anthropogenic impacts on plant communities, such as those caused by deer grazing, as it can also provide powerful insight into how deer drive changes within plant communities (Côté et al., 2004). The longer a study is, the more valuable it becomes, allowing for the detection of cumulative or slow-acting impacts (Silvertown et al., 2010). The impact of the removal of deer on aspects of tree regeneration has been covered extensively in temperate native woodlands (Perrin et al., 2006; Bobiec et al., 2011; Tanentzap et al., 2011). However, there has been less focus on ground flora changes with large herbivore removal, particularly over longer time-scales.

Fencing to conserve resources is not a new concept and is one which has developed dual purposes; keeping something out, and

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keeping something in (Hardin, 1968; Hayward and Kerley, 2009). Fencing for biodiversity conservation is a more contemporary concept, which may ultimately be an acknowledgement of our failure to successfully coexist with biodiversity (Hayward and Kerley, 2009). Long-term fencing to exclude large herbivores, in particular, has been adopted as a defence against over-grazing and has become a method used to implement conservation objectives such as tree regeneration (NPWS, 2005a,b). However, initial costs of fencing are high, fences may not be totally effective, maintenance will be required, and there may be a reduction of tourism value in the area (Pérez and Pacheco, 2006). Also, it has been noted that only short-term fencing to achieve management aims may be appropriate (Hester et al., 2000).

Ireland has comparatively low land area of semi-natural woodland relative to the European context, at less than 2% cover, of which oak dominated woods are among the most common (Perrin et al., 2008). Much of these woods have been found to be grazed by large herbivores such as deer and feral goats (Perrin et al., 2008). Although no native deer species have survived from the last glacial cold stage to present day, Ireland was once home not only to the red deer (*Cervus elaphus* Linnaeus, 1758) but also the giant Irish deer (*Megaloceros giganteus* Blumenbach, 1799) and reindeer (*Rangifer tarandus* Linnaeus, 1758) (Woodman et al., 1997). New evidence suggests that red deer were re-introduced in the Neolithic period (Carden et al., 2012) after a period of extinction, while Japanese sika deer (*Cervus nippon nippon* Temminck, 1838) have been introduced in more recent times. The most common woodland deer species now found in Ireland, red deer and sika deer, have increased in range by 565% and 353%, respectively between 1978 and 2008 (Carden et al., 2010). Other herbivores such as wild boar (*Sus scrofa* Linnaeus, 1758), and domestic cattle, sheep, pigs and goats have had a long history in the Irish landscape (Woodman et al., 1997; Mitchell and Ryan, 2003; Carden et al., 2012). This indicates that large herbivore grazing, at varying intensities, has been a part of Irish woodlands for thousands of years (Mitchell, 2005).

The combination of low cover of semi-natural oak woodland habitat and recent dramatic increases in wild herbivores makes Ireland an ideal location to study the management option of long-term herbivore removal, as the conservation status of this oak habitat has been designated as unfavourable (NPWS, 2008). This unfavourable status was given because the structure and functions (including features such as typical species, low-branched trees, and many ferns, mosses, lichens, and evergreen shrubs) necessary for the long-term maintenance of semi-natural oak woodland did not exist and were likely not to exist for the foreseeable future (NPWS, 2008). Although the results of the long-term data used here have already been partially reported from a few individual exclosures (Bleasdale and Conaghan, 1996; Kelly, 2000; Perrin et al., 2006, 2011), this study is unique as it is the first to unify the analysis of long-term exclosure data in order to examine trends at a wider temporal and spatial scale.

The objective of this research is to investigate the effect of large herbivore exclusion on vegetation, through time, using empirical long-term vegetation data collected over ~40 years. The responses of ground flora communities to this removal will be assessed, and it is predicted that a change in woodland vegetation will occur through time.

2. Materials and methods

2.1. Study sites

The study sites are located within protected ancient oak woodlands in three National Parks in Ireland: Killarney National Park, Co. Kerry; Glenveagh National Park, Co. Donegal; and Wicklow

Mountains National Park, Co. Wicklow, located between 52°0'–55°3' N and 6°18'–9°35'W (Fig. 1). In addition to national designations, these woodlands are protected as Special Areas of Conservation (SAC) under the European Union's Habitats Directive (E.U., 1992) as they contain representative areas of old sessile oak with *Ilex aquifolium* L. (holly) and *Blechnum spicant* (L.) Roth (hard fern) (Annex 1 EU code 91A0) (nomenclature follows Stace (2010)).

Quantitative data on the large herbivore communities at the three study sites at the time of fencing is largely non-existent. Where quantitative data have been collected, translation into herbivore density is often meaningless (cf. Putman et al., 2011a,b) as the landscape is highly fragmented, large herbivores can move freely in and out of the National Parks, and large woodland exclosures displace deer habitat. A qualitative assessment of historical grazing levels (20+ years) (as detailed by Forestry Commission Scotland, 2013), adjacent to the long-term fenced plots used in this study, indicated high levels of historic herbivore impact at all control plots, excluding one plot, which indicated low historic grazing impacts; likely due to the influence of a regional road (single carriageway with two lanes) located 10 m from the plot (Newman, 2013). High historic grazing levels were identified using indicators such as: vegetation forming a low sward; dominance of grasses and bryophytes; absent or limited understorey; and a prominent browse line (Forestry Commission Scotland, 2013). Areas with low historic grazing levels were characterised by indicators including: dense *Vaccinium myrtillus* L.; frequent *Rubus fruticosus* agg. L. and *Lonicera periclymenum* L.; and an understorey of tree species with low growing branches (Forestry Commission Scotland, 2013).

A detailed paired comparison of the vegetation between long-term fenced plots and adjacent contemporary control (grazed) areas is described by Newman, 2013.

Mean annual rainfall (between 1961 and 1990) at the 3 study sites was in excess of 1600 mm, while the mean daily min of the coldest month and the mean daily max of the warmest month were 2.8 °C and 16.1 °C, respectively (available from <http://www.met.ie>). The eastern half of the country is drier than the west; however, the coastal distribution of mountains results in oceanic conditions still being found in eastern counties (e.g., Wicklow and Antrim) (Ratcliffe, 1968). The predominant soil type at the sites is podzolic, with a current (2011) log mean pH (\pm SE) of 3.96 ± 0.1 (top 10 cm) (M. Newman, unpublished data). The study sites are in upland areas, although the woodland study plots ranged in altitude between 35 and 175 m above sea level.

2.2. Experimental design, data collection and standardisation

The data used for this study were collected over a 41 years period (1969–2011) from within seven deer exclosures established in the three National Parks between 1969 and 1988 (Table 1). Historic data are only available from within the exclosure and, consequently, there are no control data available. The cover of each vascular plant species (excluding tree species), occurring as part of the woodland ground flora (i.e., ≤ 2 m in height), was sub-sampled in varying sizes of sub-plot with varying degrees of replication (Table 2). The cover of species within a plot were averaged over the sub-plot replicate records. Species cover was collected using the Braun-Blanquet, Domin, and percent scales (Kent, 2010). In order for meaningful comparisons to be made, all cover data were converted to percent using the Domin 2.6 (Currall, 1987) method from values recorded in Domin scale, and the median percent value of each of the ranges in Braun-Blanquet scale. The Domin 2.6 conversion uses a simple function ($\text{cover} = (\text{Domin score})^{2.6}/4$) to provide a closer approximation to the functional relationship between Domin scores and percent cover over the entire Domin range (Currall, 1987).

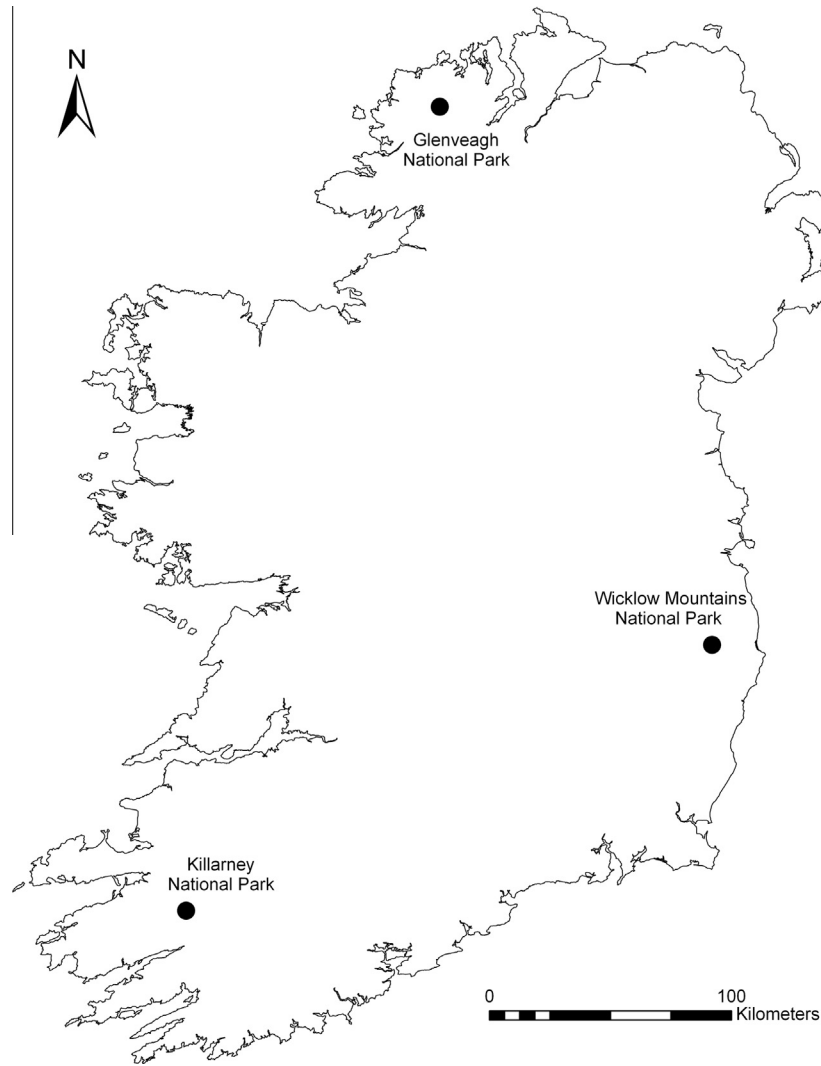


Fig. 1. Map of Ireland showing study sites.

Table 1
Study enclosures.

Exclosure code	Exclosure size (m ²)	Year fenced	National Park
K1	1090	1969	Killarney
K2	5560	1972	Killarney
W1	400	1970	Wicklow
W2	400	1970	Wicklow
W3	400	1970	Wicklow
G1	~26,000 ^a	1988	Glenveagh
G2	~27,000 ^a	1975	Glenveagh

^a Large area of exclosure extended into non-woodland habitat, wooded area ~11,000 m². First letter of exclosure code indicated National Park location.

As there is variation in the year in which the exclosures were established and surveyed, a standardisation variable of time since fencing (years) has been used. This has been used to sequentially order sample point by time since fencing instead of year of survey, resulting in 33 sample points (Table 2).

2.3. Data analysis

Species composition of each sample point was analysed using a non-metric multidimensional scaling (NMS) ordination of aver-

aged species abundance data in PC-ORD 6.08 (McCune and Mefford, 2011). This ordination technique was used to view the relationships among plots through time by reducing the dimensionality of the data space (McCune and Grace, 2002). The ordination was run using the Sørensen (Bray-Curtis) distance matrix, with a maximum of 500 iterations (250 with real data and 250 with randomised data), an orthogonal rotation, and a Monte Carlo randomisation test, for a data matrix of 33 plots and 55 plant species.

In order to test for a significant difference in vegetation composition over time, a permutational multivariate analysis of variance (PerMANOVA) (Anderson, 2001a) was conducted. This procedure provides a multivariate equivalent to the *F*-ratio, calculated through a distance or dissimilarity matrix by partitioning the total sum of squares and expectations of mean squares, according to the nature of the experimental design (Anderson, 2001a, 2008). A *p*-value, based on permutations, is then calculated (Anderson, 2001b; Anderson and ter Braak, 2003). The test was performed in PERMANOVA+1.0.3, an add-on function to PRIMER 6.1.13 (PRIMER-E, 2009). This test was carried out with time since fencing (TSF) as a continuous co-variable and site (National Park) as a random factor in a crossed design, using a Sørensen (Bray-Curtis) distance matrix on a total of 9999 permutation of residuals under a reduced model, with type III (partial) sums of squares.

Table 2
Plots surveyed, survey year, time since fencing, time group, and replication.

Survey plot	Year surveyed	TSF	Time group	Sub-plot replication
G1-1 ^a	1996	8	1	1 × 4 m ²
G1-2 ^a	1996	8	1	1 × 200 m ²
G1-3 ^a	1996	8	1	1 × 4 m ²
G1 ^a	2011	23	2	20 × 1 m ²
G2-1 ^b	1987	12	1	1 × 24 m ²
G2-1 ^b	1996	21	2	1 × 24 m ²
G2-2 ^b	1996	21	2	1 × 4 m ²
G2 ^b	2011	36	3	20 × 1 m ²
K1	1969	0	1	9 × 1 m ²
K1	1974	5	1	10 × 1 m ²
K1	1980	11	1	15 × 1 m ²
K1	1985	16	2	15 × 1 m ²
K1	1993	24	2	15 × 1 m ²
K1	1997	28	2	15 × 1 m ²
K1	2001	32	3	20 × 1 m ²
K1	2010	41	3	20 × 1 m ²
K2	1972	0	1	10 × 8 m ²
K2	1973	1	1	10 × 8 m ²
K2	1981	9	1	10 × 8 m ²
K2	1988	16	2	10 × 8 m ²
K2	1994	22	2	10 × 8 m ²
K2	2007	35	3	12 × 1 m ²
K2	2011	39	3	20 × 1 m ²
W1	1976	6	1	50 × 1 m ²
W1	1980	10	1	50 × 1 m ²
W1	2002	32	3	50 × 1 m ²
W1	2010	40	3	20 × 1 m ²
W2	1976	6	1	50 × 1 m ²
W2	1980	10	1	50 × 1 m ²
W2	2002	32	3	50 × 1 m ²
W2	2010	40	3	20 × 1 m ²
W3	1967	6	1	50 × 1 m ²
W3	1980	10	1	50 × 1 m ²

TSF = time since fencing.

^a Plot located within G1 enclosure.

^b Plot located within G2 enclosure. First letter of enclosure code indicates National Park location.

Average multiple-site dissimilarity measures were used to assess changes to vegetation community turnover and nestedness through time. In order to compare changes in diversity through time, the data points were divided into three *a priori* age groups. These groups were delimited by gaps in the frequency histogram of survey points on a time since fencing scale. The three natural groups in the data represent the time since fencing groups of: time 1 (0–12 years, $n = 16$), time 2 (16–28 years, $n = 8$), and time 3 (32–41 years, $n = 9$). Sørensen and Simpson, with their many variations, are some of the most used measures of beta diversity (Baselga, 2010). Issues relating to the dependence of beta diversity measures on species richness (see Anderson et al., 2011) are not a concern here, as preliminary analysis indicated that species richness varies little between time groups. Here, the multi-site dissimilarity measures (based on Baselga, 2010) of Simpsons beta (β_{SIM} – species turnover) and Sørensen beta (β_{SOR} – species turnover and nestedness – subsets of the same species occurring among sites) are used to highlight dissimilarities in species turnover and nestedness among time groups. The Sørensen (Bray-Curtis) matrix calculated for the ordination analysis has also been used to compare species abundance and time groups. This measure is similar to β_{SOR} but also takes plant abundance into account. The β_{SIM} and β_{SOR} diversity measures were calculated using the *ecodist* package (Goslee and Urban, 2007) in R (R Core Team, 2012), and the Sørensen (Bray-Curtis) measure was calculated in PC-ORD 6.08 (McCune and Mefford, 2011).

Differences among the time groups and diversity measures were analysed using a General Linear Model (GLM), with time group as a fixed factor and site (National Park) as a random factor,

with a Tukey HSD post hoc comparison test (Hsu, 1996) in SPSS (2010). To ensure comparability between time groups in the analysis and compliance with the assumptions of GLM, the Levene's test of homogeneity was carried out in SPSS (2010). Log₁₀ transformations were carried out where necessary.

To analyse the contribution of individual species abundances to differences between time groups, a similarity percentage routine (SIMPER) was carried out in PRIMER 6.1.13 (PRIMER-E, 2009). The Sørensen (Bray-Curtis) distance matrix was used to decompose dissimilarities within and between time groups (Clarke and Gorley, 2006). A two way crossed design using time group and site was used to allow for the selection of species which contribute to the different times occurring in all Parks.

3. Results

3.1. Community composition, diversity, and heterogeneity

The NMS output of sample points exhibits some grouping by site (National Park) but, with increased TSF, all plots move towards the centre of ordination space (Fig. 2A). Plots recorded closer to the time of fencing (i.e., low TSF) exhibit the widest dispersion, with the vast majority of the plots recorded within the first 12 years of fencing positioned on the periphery of the ordination. A similar trend is seen with the trajectory of resurveyed plots through time (Fig. 2B), illustrating that, with resurvey through time, plots do not all go in the same direction but do mostly trend towards a central end point. Plots at the periphery of the ordination are characterised by *Oxalis acetosella* L., *B. spicant*, *Anthoxanthum odoratum* L. and *Agrostis capillaris* L., while plots at the centre are characterised by *Luzula sylvatica* (Huds.) Gaudin, *R. fruticosus* agg., *L. periclymenum* and *V. myrtillus*. Analysis of the plant community composition and time since fencing (TSF), using PerMANOVA, indicates that community composition differs significantly with TSF ($p < 0.0001$), among sites ($p < 0.0001$), and also with the interaction between TSF and site ($p = 0.0021$). When species presence/absence was tested instead of abundance with PerMANOVA, community composition differed significantly with TSF ($p = 0.01$) and site ($p = 0.001$), but the interaction effect was not significant.

The beta diversity results show a similar pattern to the ordination, where an increase in community composition similarity is seen through time (Fig. 3). Sørensen's distance indicated that plots from the three time groups were not significantly different, but there is a decreasing trend with time towards similarity in terms of species turnover and nestedness, however, the interaction between time group and site was significant ($p = 0.001$). Sørensen's beta diversity (β_{SOR}) shows that all three time groups are significantly different from each other, with an increase in similarity among plots with time. Simpson's beta diversity (β_{SIM}) indicated that plots from times 2 and 3 are significantly more similar to each other than to time 1, in terms of species turnover.

3.2. Species abundance changes

Analysis of species abundance dissimilarities over time has highlighted some characteristic differences between the time groups (Table 3). Group dissimilarity is greatest between times 1 and 3, while times 2 and 3 are most similar. The abundance of *L. sylvatica* or *V. myrtillus* contribute greatest to group dissimilarities in each time comparison, while the abundance of *L. sylvatica* and *Pteridium aquilinum* (L.) Kuhn are characteristic of dissimilarity in all time comparisons.

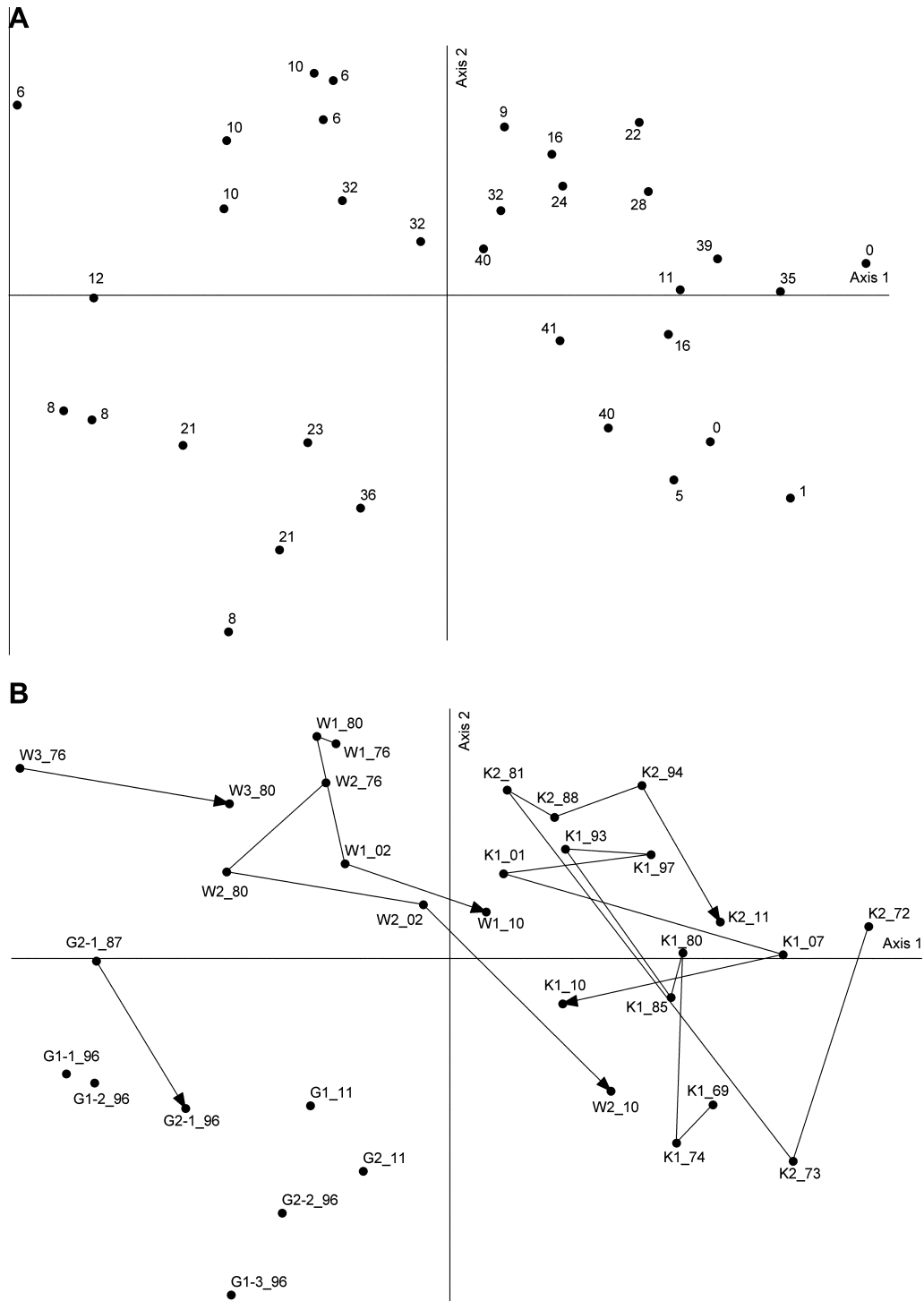


Fig. 2. NMS ordinations of average species abundance per plot, displaying (A) time since fencing (TSF) in years, and (B) plot code with survey year, and successional vectors. Successional vectors link the trajectory of plots through time; plots without vectors are once off survey plots. The most suitable ordination was a 2-dimensional solution, with a final stress was 15.78 and an instability of <0.00001. The r^2 of axis 1 and 2 were 52.8% and 21.2%.

4. Discussion

The results of this study have shown that species abundance and assemblages change with time since large herbivores exclusion. A homogenisation of the ground flora is seen when comparing time groups, with the abundance of four key species accounting for the differences between these time groups.

Plant community composition and abundance were shown to change with time since large herbivore exclusion. Although the

composition and abundance of species is changing at all sites, with TSF, not all sites are responding in the same way. This may be explained visually by studying the ordination plot (Fig. 2B). It is clear that vegetation plots are moving in ordination space through time, and also that the plots from some sites are moving more than others. Although the direction of movement in ordination space differs, plots trend towards the centre with increased TSF. Analysis of the species presence/absence matrix gave similar results to the analysis of species abundance. However, all sites responded in a

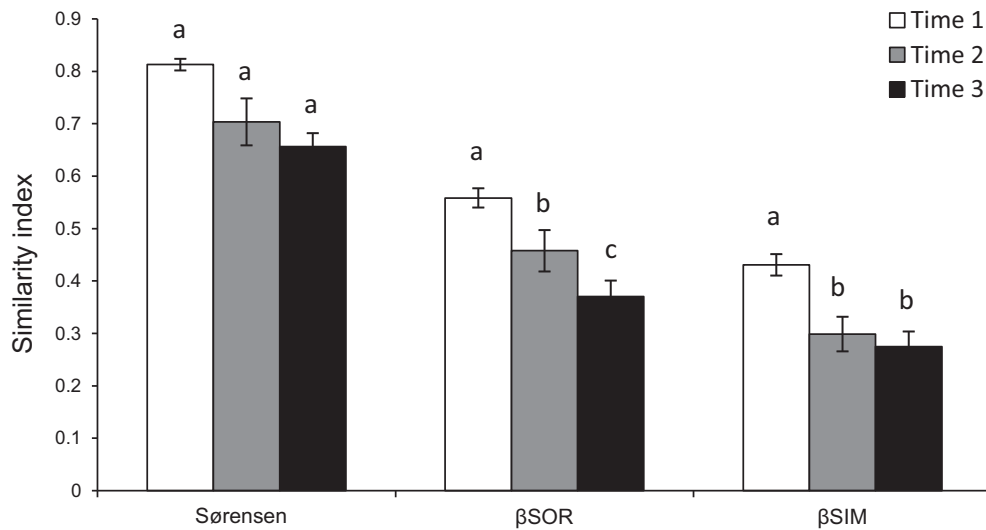


Fig. 3. Comparison of average dissimilarity measures (\pm se) among time groups, where 0 = complete similarity and 1 = complete dissimilarity. Significant differences (Tukey post hoc, $p < 0.05$) between time groups within each dissimilarity measure indicated using different lowercase letters. Time 1 = 0–12 years ($n = 16$), time 2 = 16–28 years ($n = 8$), and time 3 = 32–41 years ($n = 9$).

Table 3
Time group dissimilarity and species abundance dissimilarities between time groups. Time 1 = 0–12 years ($n = 16$), time 2 = 16–28 years ($n = 8$), and time 3 = 32–41 years ($n = 9$).

Time group comparison	Mean group dissimilarity	Species	Mean abundance (%) per time group		Contribution to dissimilarity (%)
1 vs. 2	65.4		1	2	
		<i>Luzula sylvatica</i>	17.74	18.31	39.31
		<i>Hedera helix</i>	0.17	3.03	7.56
		<i>Pteridium aquilinum</i>	9.51	1.95	5.92
1 vs. 3	69.64		1	3	
		<i>Vaccinium myrtillus</i>	16.84	13.68	17.56
		<i>Luzula sylvatica</i>	17.74	21.74	17.16
		<i>Pteridium aquilinum</i>	9.51	4.99	8.84
2 vs. 3	52.55		2	3	
		<i>Luzula sylvatica</i>	18.31	21.74	40.25
		<i>Vaccinium myrtillus</i>	6.09	13.68	23.64
		<i>Pteridium aquilinum</i>	1.95	4.99	6.76

similar way, indicating that species turnover is happening in the same way at all sites. The species which characterise plots at the centre of the ordination space (*L. sylvatica*, *R. fruticosus* agg., *L. periclymenum* and *V. myrtillus*) may do so because of their sensitivity to large herbivore browsing/grazing, which is discussed in more detail later.

The role played by large herbivores in maintaining the heterogeneity of an ecosystem has been previously noted (Hester et al., 2000; Vera, 2000), and changes in temperate woodland vegetation composition with time following removal of grazing have been identified (Putman et al., 1989; Price et al., 2010). Time lags in the response of species density to time since large herbivore removal have been noted, with 14 years being the time before a significant difference was detected (Price et al., 2010), a trend reiterated by a study of deer reductions in New Zealand woodlands (Tanentzap et al., 2012). These general vegetation changes have been described as the recovery and development of tall-growing browse-sensitive species after 12 (Anderson and Katz, 1993) and 32 (Perrin et al., 2011) years. However, after 8 years of deer exclusion, Webster et al. (2005) found no recovery of browse-sensitive species, illustrating the different conclusions which can be drawn depending on the time scale of such experiments and highlighting the value of long-term datasets. Having datasets which extend for multiple decades, as the one presented here, allows the tracking of vegetation change and the identification of trends on a larger temporal scale. A potential drawback of working with long-term data-

sets is that experimental design principles, which are paramount now, may not have been as important decades ago. In this case, control plots were not established when the experiment began. It could be argued that the wider landscape is changing in the same way over time as in the exclosures, however, a comparison of these exclosures with contemporary adjacent controls has shown that significant differences, in the vegetation composition and cover, are present between exclosures (ungrazed) and control (grazed) plots (Newman, 2013).

Using beta diversity as a proxy for plot dissimilarity, an increase in vegetation composition homogenisation is seen with increased time since fencing. This indicates that woodland vegetation is becoming more similar with time when large herbivores are excluded, possibly due to increased dominance of certain species when grazing disturbance is removed.

The beta diversity measures illustrated that homogenisation of the ground flora was occurring through increasing time groups. More specifically, a reduction in turnover (β_{SOR}) of plant species among plots at each increasing time group. From the time group analysis it appears that turnover and species abundance is not significantly different among the groups, although the decreasing trend with increasing time group can also be seen here. The proportion of species shared among plots within a time group (β_{SIM}), decreased significantly between 16 and 41 years since fencing, compared to recently fenced plots (0–12 years). This is an important issue for biodiversity conservation as the results indicate a

potential reduction in the number of plant species found in areas where large herbivore grazing has been removed for long periods (e.g., >12 years). An increase in community homogeneity was also noted in previous studies on some of the Killarney research sites. Species richness and Simpson's diversity index in the K2 plot peaked after 10 years of exclusion, trending downwards thereafter, with the mean number of vascular plant species and total number of angiosperm herbs falling below what they were prior to fencing, after 26 years (Kelly, 2000). Looking at 32 years of deer exclusion data for the K1 plot, Perrin et al. (2011) noted that there appeared to be an initial increase in species diversity, followed by a long-term decline.

It is clear that changes are occurring in the vegetation with increasing time since fencing, but what species are driving this change? Of the four key species identified as the greatest contributors to species abundance difference between the time groups, two species (*L. sylvatica* and *P. aquilinum*) contribute to the differences between all the group comparisons. The mean abundance of *L. sylvatica* was shown to increase with time, a finding supported by other studies of the plots in Killarney National Park after 26 years (Kelly, 2000) and 32 years (Perrin et al., 2011) of exclusion. The dominance of *L. sylvatica* following cessation of grazing was also noted by Mitchell and Kirby (1990). This species may not respond to large herbivore removal in the same way as other graminoids because reductions in graminoids were noted after 16 years in woodland exclosures in Wisconsin (Rooney, 2009) and after 22 years in England (Putman et al., 1989). The decline was also noted in the Scottish uplands after 9 years of large herbivore removal (Miller et al., 2010). The increased abundance of graminoids in grazed areas may reflect the adaptation of this life-form to grazing pressure (McNaughton, 1984), as graminoids have been identified as the main summer food source for enclosed red deer (Sherlock and Fairley, 1993). The increasing dominance of *L. sylvatica* with large herbivore removal may be due to its sensitivity to grazing (Rodwell, 1991; Kirby, 2001). This species may also be out-competing other graminoids, as indicated by the reduction in graminoid species richness seen when these long-term plots were compared to grazed areas (Newman, 2013).

The abundance of the climber *Hedera helix* L. was shown to be one the main differentiating species between time group 1 and 2, with an increasing cover when large herbivores were removed. This increase is likely due to the absence of herbivores, as this species can be considered grazing sensitive. This finding is supported by an increase in frequency of *H. helix* with time since fencing in an English woodland (Putman et al., 1989), and also by the decreased cover of climbers (*H. helix* and *L. periclymenum*) noted when exclosed plots were compared with grazed plots in Ireland (Newman, 2013). Few shrub species were recorded in this study; however, *V. myrtillus* has been identified as an important species differentiating species composition through time, showing a reduction in abundance from time 1 to 2, with a subsequent rebound with increased time since fencing. This initial reduction may be counterintuitive as previous studies described the species as browse sensitive and noted increased abundance when grazing was absent (Onaindia et al., 2004; Perrin et al., 2011). The abundance of the fern, *P. aquilinum*, shows a similar trend as *V. myrtillus*, where a decline from time 1 to 2 was followed by a slight rebound in time 3. *P. aquilinum*, the only fern species recorded from a long-term woodland deer exclosure, showed a decreasing trend in frequency after 22 years (Putman et al., 1989). Ferns may be negatively impacted by large herbivore exclusion as a declining trend in overall fern abundance was noted after 32 years of deer exclusion by Perrin et al. (2011), while the loss of the locally frequent (Page, 1997) Tunbridge filmy-fern (*Hymenophyllum tunbrigense* (L.) Sm.) was recorded after 26 years of herbivore exclusion in Killarney (Kelly, 2000). This

may be a result of increased competition from rebounding browse sensitive plant species.

5. Conclusion

With total removal of large herbivores from the oak woodland ecosystem, this study has described significant changes in ground flora composition and abundance, and a general homogenisation of the vegetation community with increasing time since large herbivore removal. In temperate oak woodlands which have evolved with large herbivores, complete removal of herbivores may cause more long-term damage (e.g., reduction in vegetation community heterogeneity) than it would prevent. Removal is undesirable other than for short-term objectives to be completed (Hester et al., 2000), because large herbivores perform integral ecosystem functions, such as disturbance and driving succession through selective herbivory, within woodlands (cf. Vera, 2000). Short-term fencing, directed at increasing tree regeneration or biodiversity maintenance for example, could still be used with the knowledge that ground flora community homogenisation may take place after 12 years. It can therefore be concluded that the findings of this research, combined with those of others (e.g., Kelly, 2000; Perrin et al., 2011), suggest a general homogenisation of temperate oak woodlands will occur with total large herbivore removal. It is recommended that large-scale long-term fencing of oak woodlands be replaced by large herbivore management programmes, in order to ensure the conservation of diverse native woodland ecosystems. These management programmes should be implemented through adaptive management where large herbivore impacts are monitored and adjusted, through localised culling, to achieve specific long-term management objectives such as landscape-level heterogeneity.

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