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Long-term deer exclusion in yew-wood and oakwood habitats in southwest Ireland: Changes in ground flora and species diversity

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ABSTRACT

Changes in ground flora were monitored over a 32-year period in deer exclosures in a yew-wood and a neighbouring oakwood in Killarney National Park, southwest Ireland; both woods are Annex I habitats under the European Habitats Directive. Comparison was made with unfenced plots adjacent to each of the exclosures. During the period of the study, both woods were heavily grazed by introduced sika deer (*Cervus nippon*). In the yew-wood exclosures, total ground flora cover increased markedly during the period of deer exclusion, the main species to increase in abundance being *Rubus fruticosus* agg. and *Hedera helix*. Herbaceous species increased initially in frequency but subsequently declined; herbaceous species had higher total cover in unfenced plots than in fenced plots at the end of the study. In the oakwood, *Luzula sylvatica* and *Vaccinium myrtillus* expanded their cover in one exclosure with cover in ferns declining, but in other exclosures where dense holly thickets developed, it was instead *R. fruticosus* and *H. helix* that became more abundant within the fences than outside. Overall, long-term fencing has caused a shift from vegetation characterised by woodland specialist to woodland generalist species and there are indications of a long-term decline in diversity. We conclude that chronic heavy grazing in these woodlands has strongly influenced the overall abundance and composition of the ground flora, but that complete exclusion of grazing is also undesirable due to potential declines in diversity of woodland specialists.

1. Introduction

Grazing animals can have significant impacts on the ground flora of semi-natural woodlands in several ways (Mitchell and Kirby, 1990; Kirby, 2001; Watkinson et al., 2001). Abundance and composition of the ground flora can be affected through the decline of palatable species and the associated promotion of unpalatable or grazing-tolerant plants (e.g. Putman et al., 1989; Latham and Blackstock, 1998). Trampling by large herbivores can damage woodland plants and may promote the spread of ruderal species (e.g. Kirby and Thomas, 2000). Nutrient distribution within woodlands can be altered by herbivores' patterns in dunging and urination. Long-term heavy grazing can also affect the species richness and diversity of woodland communities (e.g. Kelly, 2000) although, as reviewed by Kirby (2001), the nature of this impact can be variable. Grazing is thus a significant force in determining woodland dynamics and biodiversity. It is consequently a critical factor in conservation management of temperate woodland (Vera, 2000). The general consensus is that fencing to control excessive grazing which leads to the complete exclusion of grazing is detrimental and that some level of grazing is beneficial (e.g. Cooper and McCann, 2011; Hester et al., 2000; Kirby, 2001; Watkinson et al., 2001); this conclusion also concurs with proposed scenarios for natural woodland grazing systems (Vera, 2000). In this paper we test this assumption by investigating the impact of the complete exclusion of grazing from temperate woodlands of high conservation importance.

The challenge in any investigation of woodland dynamics is the availability of data that cover sufficiently long time intervals to explore the processes involved adequately. Space-for-time chronosequences are thus commonly used in such studies (e.g. Price et al., 2010). Long-term monitoring datasets from any ecosystem are rare but highly valued for their contribution to exploring ecological processes (Magurran et al., 2010; Prach and Walker, 2011; Silvertown et al., 2010).

Woodland dominated by *Taxus baccata* (yew)[1] is one of the rarest of European stand types, being largely restricted to the southeast of England and the west of Ireland, and thus has been granted priority conservation status under Annex I of the EU Habitats Directive (Anon., 2007). Reenadinna Wood in the Killarney National Park, Co. Kerry is the largest extant area of this habitat in Ireland, comprising yew and yew-hazel woodland over limestone pavement. The vegetation of the wood has been described by Kelly (1981) and the

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[1] Botanical nomenclature in this paper follows Stace (2010).

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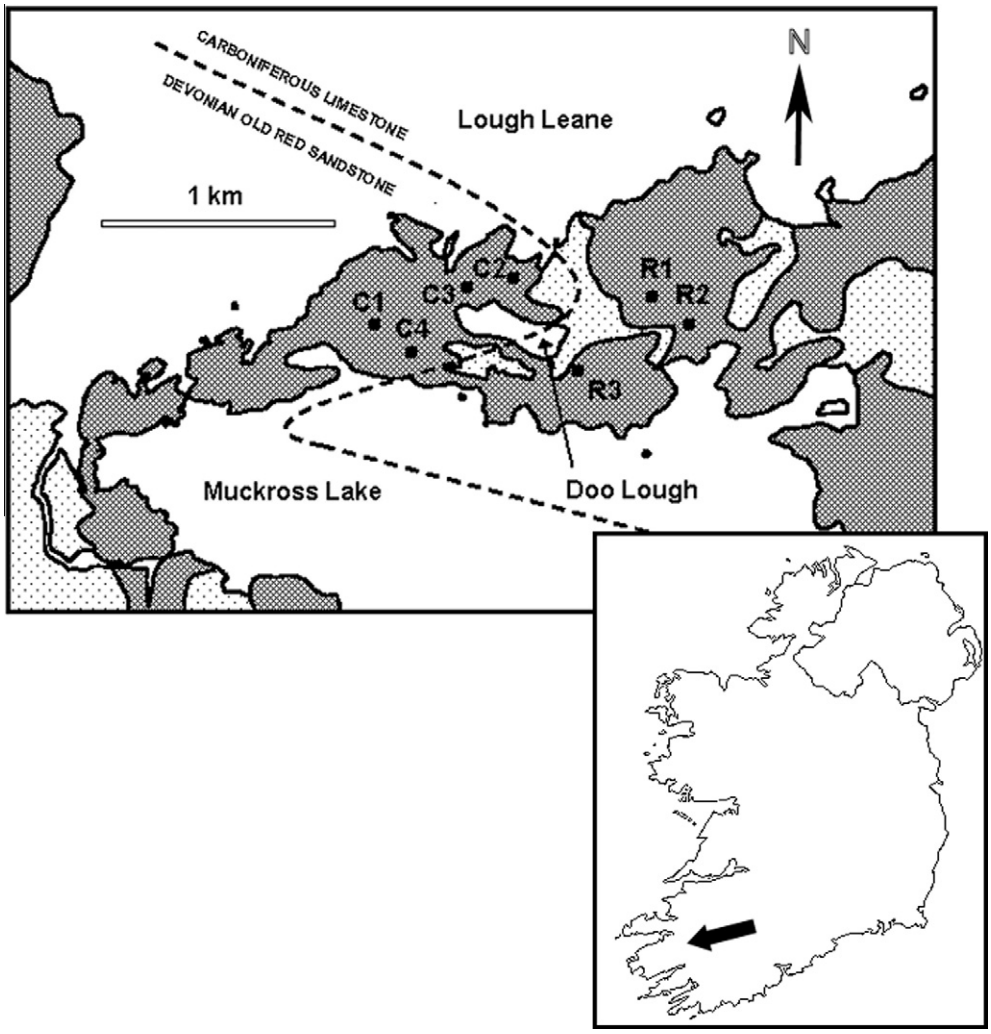

Fig. 1. Map of the Muckross Peninsula, Killarney National Park, showing the location of the deer exclosures. The dashed line indicates the geological boundary. Heavy shading indicates wooded areas, light shading indicates non-wooded terrestrial habitats (grassland, fen and bog). The arrow in the smaller map shows the location of the study site within Ireland.

palaeoecology has been investigated by Mitchell (1990). The central management issue concerning this site is heavy grazing, partly by native *Cervus elaphus* (red deer) but largely by non-native *Cervus nippon* (sika deer) that were introduced to the area in 1865 and have bred extremely successfully (Whitehead, 1964). In recent decades they have been present at high densities within the lowland woodlands of the park (Higgins et al., 1996). In 1969, a long-term deer exclusion experiment was initiated to investigate the impact that grazing was having on the ecology of Reenadinna and the neighbouring acidophilous oakwood of Camillan. The effects on seedling and sapling abundance and associated changes in stand structure have been reported by Perrin et al. (2006).

The main aim of the present paper is to investigate how chronic heavy deer grazing has affected the composition and diversity of the vascular ground flora within these woodlands.

2. Methodology

2.1. Study area

The study was conducted in the woodlands of the Muckross Peninsula in Killarney National Park, southwest Ireland (Fig. 1) between 1969 and 2001. The peninsula is divided by a geological boundary, separating Carboniferous Limestone to the east from Devonian Old Red Sandstone to the west. The limestone area supports Reenadinna Wood (longitude 9° 30′, latitude 52° 1′), a *T. baccata*-dominated woodland, about 38 ha in size[2] and located on a series of outcropping limestone reefs. Soil is largely skeletal, with a pH in the grykes of around 6.8. Kelly (1981) classified the plant community as a facies of the *Corylo–Fraxinetum* association (Braun-Blanquet and Tüxen, 1952). The canopy is low (6–14 m in height) and in most areas no appreciable understorey is present. *Fraxinus excelsior* and *Corylus avellana* are frequent, especially where pockets of soil have accumulated, and occasionally *C. avellana* replaces *T. baccata* as the canopy dominant. The field layer is typically very sparse, but a luxuriant bryophyte carpet covers the surface of the karst limestone, dominated by *Thamnobryum alopecurum*, *Eurhynchium striatum* and *Thuidium tamariscinum*. The outcrops are fringed by areas of wet woodland dominated by a mixture of *Betula pubescens*, *F. excelsior* and *Salix cinerea* ssp. *oleifolia*. Recent work has classified this site as ancient woodland (Perrin and Daly, 2010), although the current stands do not appear remarkably old; using ring counts on 20 specimens killed by bark-stripping, Watts (1984) dated the oldest yew, a very large specimen, to about the 1780s.

The sandstone area supports Camillan Wood (longitude 9° 32′, latitude 52° 1′), a *Quercus petraea*-dominated woodland of about

[2] This area revises that presented in Perrin et al. (2006).

Table 1
Location, canopy openness, vegetation type and area of fenced and unfenced plots on the Muckross Peninsula, with date of fenced plot establishment.

Site	Location	Canopy	Vegetation	Fenced plot area (m^2)	Fenced plot established	Unfenced plot area (m^2)
R1	Reenadinna	Closed	*Taxus baccata* woodland	888	1969–70	600
R2	Reenadinna	Closed	*Taxus baccata - Corylus avellana* woodland	764	1969–70	600
R3	Reenadinna	Semi-open	*Taxus baccata* scrub woodland	1036	1969–70	600
C1	Camillan	Closed	*Quercus petraea - Ilex aquifolium* woodland	1090	1969–70	600
C2	Camillan	Semi-open	*Quercus petraea - Ilex aquifolium* woodland	959	1974	600
C3	Camillan	Semi-open	*Quercus petraea - Betula pubescens* woodland	260	1974	260
C4	Camillan	Closed	*Quercus petraea - Ilex aquifolium* woodland	225*	1974–75	225

* Indicates that this was a plot within a larger exclosure.

34 ha in size[3]. The soil is podzolised, with a mor humus of pH around 4.5. The oak canopy is 13–25 m in height with an evergreen understorey (5–10 m in height) of *Ilex aquifolium*. Scattered individuals of *B. pubescens* and *Sorbus aucuparia* are frequent and *Arbutus unedo* is common around the woodland margins. The vegetation has been classified as belonging to the *Blechno–Quercetum* association typical of acidophilous oakwoods in upland and western Ireland (Kelly, 1981). The age structure of the wood has been investigated by O'Sullivan and Kelly (2006), who found establishment dates for the current stands ranging from 1800s to 1940s, although the site itself has again been deemed ancient woodland (Perrin and Daly, 2010).

During the course of the study, naturalised *C. nippon* were resident throughout these woods. Population estimates are not available for the whole period, but Larner (1977) recorded densities on the Muckross Peninsula of 0.51 animals ha^{-1} in 1970 and 0.82 animals ha^{-1} in 1975. Higgins et al. (1996) reported lower densities of 0.18 animals ha^{-1} in 1991 and 0.22 animals ha^{-1} in 1996 for a larger area of the Muckross estate which includes the peninsula. The native *C. elaphus* population in this area is much lower and has a relatively minor impact on the vegetation.

The climate of the area is extreme oceanic, with cool summers and mild winters. For the period of the study, 1969–2001, the mean maximum yearly temperature was 25.2 °C, the mean minimum yearly temperature −5.0 °C, the mean number of frost days 26 $year^{-1}$ and the mean rainfall 1676 mm $year^{-1}$ (Met Éireann, unpublished data for Killarney town 6 km NNE of the peninsula).

2.2. Exclosure establishment

Four deer-proof exclosures were established in the winter of 1969–70 (Table 1). Exclosures R1–R3 were erected on limestone outcrops in Reenadinna and situated to cover a representative range of yew-wood stand types. Exclosure C1 was established in Camillan, where three further exclosures (C2–C4) were added in 1974–75. Exclosures C2 and C3 fenced off areas that had been cleared of *Rhododendron ponticum* in 1972. Exclosure C4 was a very large exclosure encompassing a range of habitats. The location of all exclosures is shown in Fig. 1.

Exclosure fences were approximately 2 m high, composed of wire stock netting topped with barbed wire and maintained throughout the course of the study. Outside the exclosures, there were no physical barriers to animal movement along the peninsula throughout the period of this study.

The fenced plots were left unmanaged except for the removal of invasive exotics (in line with National Park policy). In the Reenadinna exclosures, there were no significant impacts of invasive species: control consisted of the removal of three *R. ponticum* bushes from exclosure R1 in the mid-1980s and the occasional removal of *Fagus sylvatica* seedlings. In Camillan, regeneration of *R. ponticum* was frequent but was removed at intervals from all exclosures; at no stage since fencing was *R. ponticum* cover allowed to become extensive. Without active control of *R. ponticum*, the experiment would have produced dramatically different results in Camillan, with the almost complete elimination of the field layer (Cross, 1981; Kelly, 1981; Higgins, 2008). Effects in Reenadinna would have been localized only and probably non-significant, within the timeframe of this study.

2.3. Data collection

A base-line survey of the vascular ground flora in exclosures R1–R3 and C1 was conducted prior to fencing in 1969, and these exclosures were subsequently resurveyed at irregular intervals until 1997 (Table 2). Restricted random sampling with 1 m × 1 m quadrats was employed, with new random co-ordinates being used for each survey. Percentage cover estimates were recorded for all vascular plant species within the field layer. To facilitate analysis,

Table 2
Surveys of ground flora in exclosures R1–R3 and C1, 1969–1997.

Year	Exclosures surveyed	No. of quadrats
1969	R1	8
	R2	12
	R3	10
	C1	9
1974	R1–R3, C1	10 per exclosure
1980	R1–R3, C1	15 per exclosure
1985	R1–R3, C1	15 per exclosure
1992	R3	15
1993	C1	15
1994	R1–R2	15 per exclosure
1997	C1	15

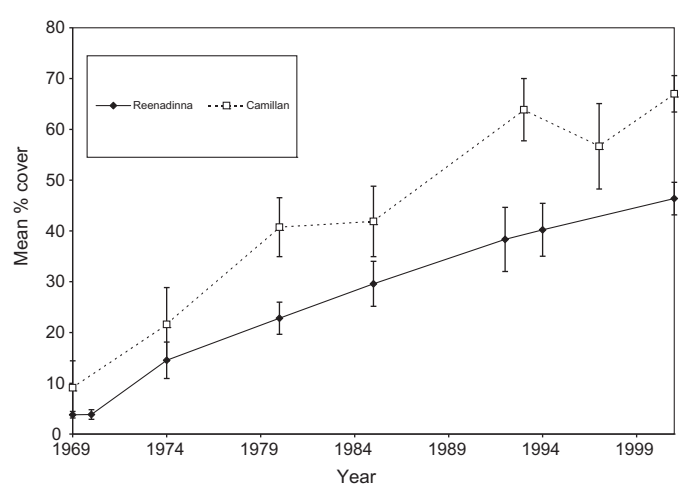

Fig. 2. Change in total ground flora cover within the Reenadinna deer exclosures (R1–R3) and Camillan deer exclosure (C1) 1969–2001.

[3] This area revises that presented in Perrin et al. (2006).

the 1992 data for exclosure R3 and the 1994 data for exclosures R1 and R2 were all treated as estimates for vegetation in 1993. Baseline data are not available for exclosures C2–C4.

In summer 2001, to permit a comparison of grazed and ungrazed woodland, an unfenced plot was established adjacent to each exclosure (Table 1). To avoid edge effects and paths worn by deer around exclosures, unfenced plots were positioned 2–3 m away from the fenceline. Vascular ground flora in all fenced and unfenced plots was again surveyed using a restricted random sampling method. In both woods $n = 60$ per treatment (fenced and unfenced); for R1–R3 and C1–C2, $n = 20$ per treatment whilst for C3–C4, $n = 10$ per treatment. The percentage cover of bryophytes was also recorded and the maximum height of *Rubus fruticosus* agg. in Reenadinna and *Vaccinium myrtillus* and *L. sylvatica* in Camillan exclosure C1 was measured in each quadrat in which they were present. These three species were chosen because they can form relatively tall components of the ground flora and it was hypothesised they would respond to the exclusion of grazing. A comprehensive survey inside exclosure C4 was not practical because of its large size and heterogeneous structure, so a 15 m × 15 m sub-plot was established in woodland inside the fencing at the western end of the exclosure. Exotic species in unfenced controls were managed as inside the exclosures.

2.4. Data analysis

Univariate statistical analysis was conducted using Statistica 7 (StatSoft Inc., Tulsa) and SPSS 11 (SPSS Inc., Chicago). Where data

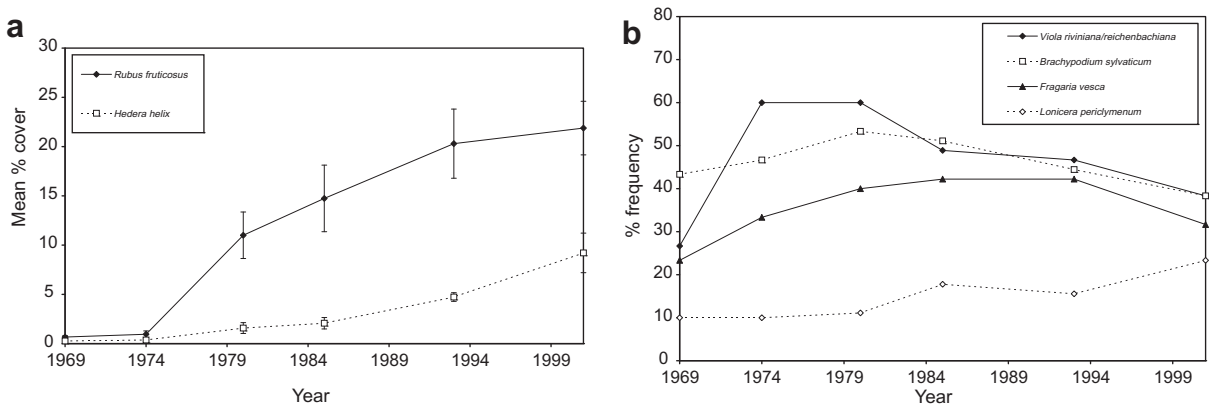

Fig. 3. Changes in main ground flora species within the Reenadinna deer exclosures (R1–R3) 1969–2001: (a) abundance (b) frequency. Vertical bars indicate ± standard error.

Table 3
Comparison of ground flora and other cover variables within fenced and unfenced plots R1–R3 in Reenadinna, 2001 ($n = 60$ per treatment). Differences in percent cover analysed using Mann–Whitney *U* test but mean values are shown because medians tend to zero. Differences in frequency analysed using Fisher's exact test.

	Woodiness	Specialism	Frequency (%)		*P*	Cover (%)		*P*
			Fenced	Unfenced		Fenced	Unfenced	
Grazing-sensitive species								
Hedera helix	W	G	68.3	18.3	***	9.2	0.14	***
Lonicera periclymenum	W	S	23.3	5.0	**	1.8	0.1	**
Rubia peregrina	SW	S	26.7	10.0	*	1.1	0.1	**
Rubus fruticosus	W	G	78.3	40.0	***	21.9	0.6	***
Solidago virgaurea	H	N	15.0	1.7	*	0.2	0.1	*
Grazing-tolerant species								
Hypericum pulchrum	H	N	0.0	8.3	n.s.	0.0	0.1	*
Oxalis acetosella	H	G	0.0	10.0	*	0.0	0.2	*
Potentilla sterilis	H	S	0.0	15.0	**	0.0	0.1	**
Sanicula europaea	H	S	6.7	21.7	***	0.3	1.5	*
Veronica chamaedrys	H	G	0.0	10.0	*	0.0	0.1	*
Viola riviniana/reichenbachiana	H	G/S	38.3	61.7	**	0.5	2.0	***
Other species								
Brachypodium sylvaticum	H	S	38.3	48.3	n.s.	0.3	1.1	n.s.
Carex flacca	H	N	3.3	11.7	n.s.	0.1	1.1	n.s.
Carex pulicaris	H	N	6.7	11.7	n.s.	0.2	2.6	n.s.
Carex sylvatica	H	S	8.3	1.7	n.s.	0.1	0.1	n.s.
Fragaria vesca	H	G	31.7	21.7	n.s.	1.3	0.4	n.s.
Polystichum setiferum	H	S	5.0	3.3	n.s.	0.6	0.3	n.s.
Potentilla erecta	H	N	0.0	5.0	n.s.	0.0	0.1	n.s.
Succisa pratensis	H	N	3.3	5.0	n.s.	0.1	0.2	n.s.
Teucrium scorodonia	H	G	15.0	5.0	n.s.	0.7	0.4	n.s.
Total vascular ground flora			96.7	96.7	n.s.	46.4	11.7	***
Total bryophytes			100.0	100.0	n.s.	87.6	82.1	***

n.s., not significant. Under woodiness: W, woody; SW, semi-woody and H, herbaceous. Under specialism: S, woodland specialist; G, woodland generalist and N, non-woodland. Only non-tree species with frequency ⩾5% in at least one treatment are tabulated.
*** $P < 0.001$.
** $P < 0.01$.
* $P < 0.05$.

defied normalization, Mann–Whitney U tests were employed in place of ANOVA. Fisher's exact test was used to compare frequencies. Species richness and Simpson's index were used to examine species diversity. The complement form of Simpson's index (D) was used where S = species richness and p_i is the fraction of all organisms which belong to the i-th species:

$$D = 1 - \sum_{1}^{S} p_i^2$$

Where quadrats contained no vascular species, a value of zero was used. Simpson's index is regarded as preferable to the widely used Shannon index by Magurran (2004).

Multivariate analysis on the 2001 data was conducted using PCOrd 5 (MjM Software, Gleneden Beach, Oregon). Non-metric multidimensional scaling (NMS) ordination was used to examine the community level differences in vegetation between treatments and woodlands. NMS has been found better suited to ecological community data than other techniques such as detrended correspondence analysis (DCA; e.g. Minchin, 1987; Legendre and Legendre, 1998; McCune and Grace, 2002). Five quadrats were omitted due to absence of any vascular species and species occurring in 2 or fewer quadrats were excluded, resulting in a matrix of 235 quadrats and 36 species. The following parameters were used: Sørensen (Bray–Curtis) distance measure, 250 runs with real data, 100 runs with randomized data, stability criterion of 1×10^{-7} standard deviations in stress over last 15 iterations, and a maximum number of iterations of 500. Varimax rotation around the centroid was employed and a species overlay was plotted using weighted average scores.

Habitat preferences for species were examined using the Broad Habitats Classification of Hill et al. (2004). Species that are listed by Hill et al. (2004) only for woodland habitat were denoted as woodland specialists. Species that are listed for both woodland and non-woodland habitats were denoted as woodland generalists and species that are not listed for woodland habitat as non-woodland species. Mean indices for each of these three categories were calculated for each quadrat, weighted by the abundance of each species-level record. Similar indices were calculated for Ellenberg indicators as modified by Hill et al. (2004). These weighted indices were used to create a vector overlay for the ordination.

Data from 2001 for exclosures C2–C4 were analysed separately from those for exclosure C1, because vigorous regeneration of *I. aquifolium* occurred in exclosures C2–C4, in contrast to exclosure C1 where holly regeneration was poor (data presented in Perrin et al., 2006).

Table 4
Mean maximum height (cm) of selected species ± standard error in fenced and unfenced plots in 2001. Analysed with one-way ANOVA.

	Mean maximum height (cm)		P
	Fenced	Unfenced	
Reenadinna (R1–R3)			
Rubus fruticosus	37.0 ± 3.4 (n = 47)	10.0 ± 2.4 (n = 24)	<0.001
Camillan (C1)			
Vaccinium myrtillus	50.5 ± 8.1 (n = 17)	23.3 ± 3.3 (n = 17)	0.013
Luzula sylvatica	40.3 ± 3.9 (n = 18)	25.9 ± 3.8 (n = 15)	0.004

3. Results

3.1. Species abundance and frequency

The total cover of ground flora increased markedly over time in both woodlands (Fig. 2). In Reenadinna, the most significant spe-

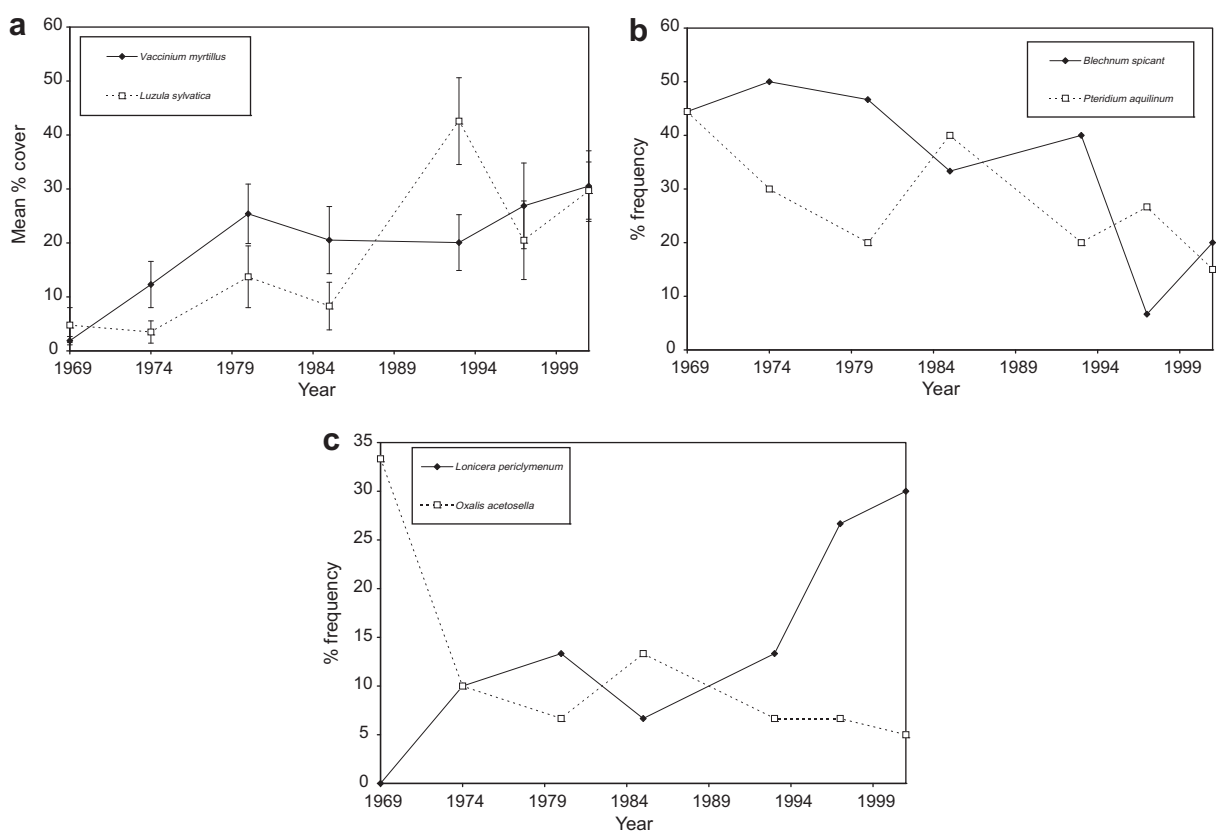

Fig. 4. Changes in main ground flora species within the Camillan deer exclosure (C1) 1969–2001: (a) abundance, (b) and (c) frequency. Vertical bars indicate ± standard error.

cies changes following fencing were gradual increases in the abundance of the woody plants *R. fruticosus* and *Hedera helix* (Fig. 3a), from less than 1% for both in 1969, to 22% and 9% in 2001, respectively. No other species achieved cover of greater than 2.5% during this period, so frequency of occurrence within the survey quadrats was used to examine more accurately trends for the four next most abundant taxa (Fig. 3b). *Viola riviniana/reichenbachiana* increased rapidly in frequency following fencing, but subsequently declined; both these *Viola* species were frequent in this wood but they could not be assessed separately during summer fieldwork. *Brachypodium sylvaticum* and *Fragaria vesca* displayed similar but less marked changes in frequency, whilst *Lonicera periclymenum* increased gradually throughout the study period with no decline. These changes are largely reflected in the comparison of fenced and unfenced plots in 2001 (Table 3), with woody species being more abundant within the exclosures and several herbaceous species (e.g. *V. riviniana/reichenbachiana*, *Potentilla sterilis* and *Sanicula europaea*) more abundant outside the exclosures. Total vascular plant cover and bryophyte cover were significantly greater within the exclosures. Mean maximum height of *R. fruticosus* was significantly higher within the fenced plots (Table 4).

In Camillan, sequential data were only recorded for exclosure C1. The most significant changes following fencing were increases in the abundance of the *V. myrtillus* and *L. sylvatica* (Fig. 4a), from 2% and 5% in 1969 to 31% and 30% in 2001, respectively. No other species achieved cover greater than 4.5%, so again frequency was used to examine the trends of the four next most abundant species (Fig. 4b and c). *Oxalis acetosella* showed a rapid decline after fencing; two ferns, *Blechnum spicant* and *Pteridium aquilinum*, also declined overall during this period. As in Reenadinna, *L. periclymenum* increased gradually in frequency following fencing. These changes are largely reflected in the 2001 data for exclosure C1 (Table 5), where within the fenced plot, *H. helix* and *L. sylvatica* were more significantly more abundant and *L. periclymenum* was significantly more frequent, leading to total vascular plant cover being greater. Whilst not quite statistically significant, cover of *V. myrtillus* was nearly twice as high within the fence as without. *B. spicant* and *O. acetosella* were more frequent in the unfenced plot.

Table 5
Comparison of ground flora and other cover variables within fenced and unfenced plots C1 in Camillan, 2001 ($n = 20$ per treatment). Differences in percent cover analysed using Mann–Whitney *U* test but mean values are shown because medians tend to zero. Differences in frequency analysed using Fisher's exact test.

	Woodiness	Specialism	Frequency (%)		*P*	Cover (%)		*P*
			Fenced	Unfenced		Fenced	Unfenced	
Grazing-sensitive species								
Hedera helix	W	G	75.0	40.0	n.s.	6.5	0.5	**
Lonicera periclymenum	W	S	30.0	0.0	*	3.9	0.0	n.s.
Luzula sylvatica	H	G	90.0	70.0	n.s.	29.7	13.0	*
Other species								
Blechnum spicant	H	G	20.0	40.0	n.s.	2.5	2.0	n.s.
Oxalis acetosella	H	G	5.0	25.0	n.s.	0.1	0.4	n.s.
Pteridium aquilinum	H	G	15.0	20.0	n.s.	1.3	6.5	n.s.
Rubus fruticosus	W	G	10.0	0.0	n.s.	1.3	0.0	n.s.
Vaccinium myrtillus	W	N	85.0	90.0	n.s.	30.6	15.5	n.s.
Total vascular ground flora			100.0	100.0	n.s.	67.0	37.0	***
Total bryophytes			100.0	100.0	n.s.	23.8	19.9	n.s.

n.s., not significant. Under woodiness: W, woody and H, herbaceous. Under specialism: S, woodland specialist; G, woodland generalist and N, non-woodland. Only non-tree species with frequency ⩾5% in at least one treatment are tabulated.
*** $P < 0.001$.
** $P < 0.01$.
* $P < 0.05$.

Table 6
Comparison of ground flora and other cover variables within fenced and unfenced plots C2–C4 in Camillan, 2001 ($n = 40$ per treatment). Differences in percent cover analysed using Mann–Whitney *U* test but mean values are shown because medians tend to zero. Differences in frequency analysed using Fisher's exact test.

	Woodiness	Specialism	Frequency (%)		*P*	Cover (%)		*P*
			Fenced	Unfenced		Fenced	Unfenced	
Grazing-sensitive species								
Hedera helix	W	G	85.0	80.0	n.s.	17.1	1.1	***
Rubus fruticosus	W	G	32.5	2.5	***	4.3	<0.1	*
Other species								
Brachypodium sylvaticum	H	S	0.0	10.0	n.s.	0.0	0.2	n.s.
Blechnum spicant	H	G	15.0	7.5	n.s.	1.3	3.0	n.s.
Dryopteris dilatata	H	G	2.5	7.5	n.s.	<0.1	0.1	n.s.
Lonicera periclymenum	W	S	5.0	7.5	n.s.	1.0	0.1	n.s.
Oxalis acetosella	H	G	12.5	17.5	n.s.	0.1	0.3	n.s.
Pteridium aquilinum	H	G	5.0	12.5	n.s.	0.3	3.8	n.s.
Vaccinium myrtillus	W	N	5.0	5.0	n.s.	0.1	0.5	n.s.
Total vascular ground flora			97.5	100.0	n.s.	49.9	21.7	***
Total bryophytes			45.0	100.0	***	3.2	36.1	***

n.s., not significant. Under woodiness: W, woody and H, herbaceous. Under specialism: S, woodland specialist; G, woodland generalist and N, non-woodland. Only non-tree species with frequency ⩾5% in at least one treatment are tabulated.
*** $P < 0.001$.
* $P < 0.05$.

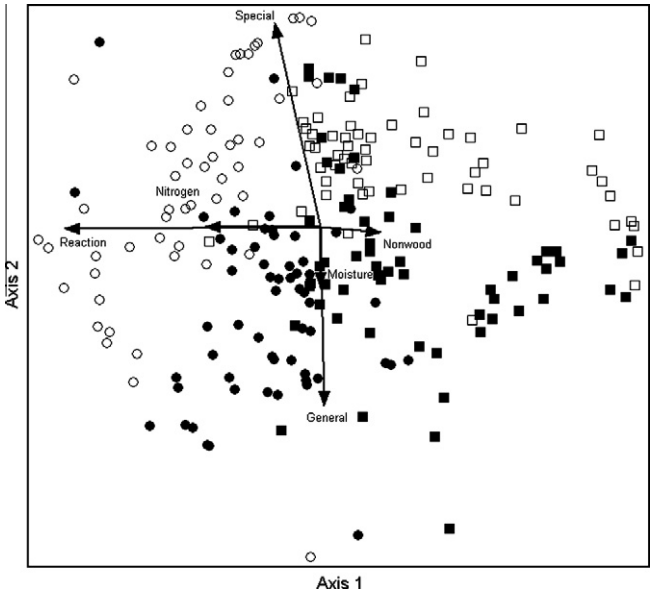

Fig. 5. Non-metric multidimensional scaling ordination of quadrats recorded in 2001. Symbols indicate treatment and location of quadrats: open circles = Reenadinna unfenced; closed circles = Reenadinna fenced; open squares = Camillan unfenced; closed squares = Camillan fenced. Vectors indicate correlation of indices with axes for indices where $r^2 > 0.1$. Reaction, Moisture and Nitrogen denote Ellenberg indicator values. Special, General and Nonwood denote woodland specialists, woodland generalists and non-woodland species, respectively.

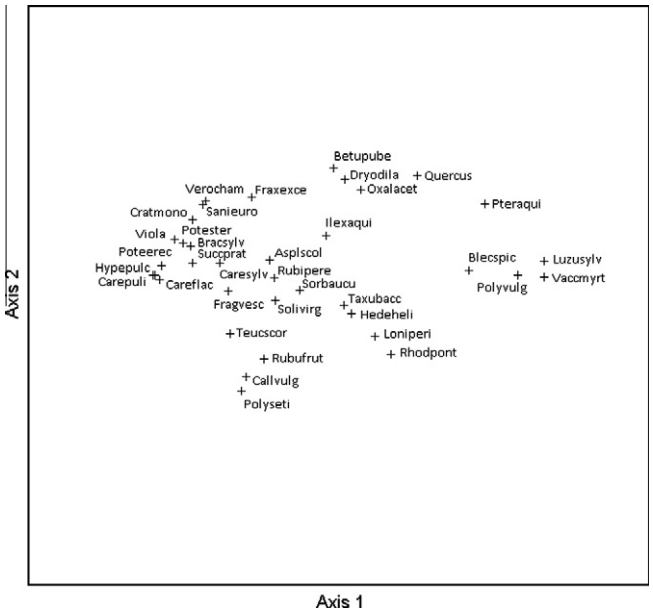

Fig. 6. Species overlay for NMS ordination based on weighted averaging. Abbreviations as follows: Betupube, *Betula pubescens*; Blecspic, *Blechnum spicant*; Bracsylv, *Brachypodium sylvaticum*; Callvulg, *Calluna vulgaris*; Careflac, *Carex flacca*; Carepuli, *Carex pulicaris*; Caresylv, *Carex sylvatica*; Cratmono, *Crataegus monogyna*; Dryodila, *Dryopteris dilatata*; Fragvesc, *Fragaria vesca*; Fraxexce, *Fraxinus excelsior*; Hedeheli, *Hedera helix*; Hypepulc, *Hypercium pulchrum*; Ilexaqui, *Ilex aquifolium*; Loniperi, *Lonicera periclymenum*; Luzusylv, *Luzula sylvatica*; Oxalacet, *Oxalis acetosella*; Phylscol, *Asplenium scolopendrium*; Polyseti, *Polystichum setiferum*; Polyvulg, *Polypodium vulgare* agg.; Poteerec, *Potentilla erecta*; Potester, *Potentilla sterilis*; Pteraqui, *Pteridium aquilinum*; Quercus, *Quercus petraea*; Rhodpont, *Rhododendron ponticum*; Rubipere, *Rubia peregrina*; Rubufrut, *Rubus fruticosus* agg.; Sanieuro, *Sanicula europaea*; Solivirg, *Solidago virgaurea*; Sorbaucu, *Sorbus aucuparia*; Succprat, *Succisa pratensis*; Taxubacc, *Taxus baccata*; Teucscor, *Teucrium scorodonia*; Vaccmyrt, *Vaccinium myrtillus*; Verocham, *Veronica chamaedrys*; Viola, *Viola riviniana/reichenbachiana*.

Total vascular plant cover was lower in fenced plots C2–C4 (mean of 49.9%) where holly had regenerated more vigorously than in fenced plot C1 (mean of 67.0%). Instead of *L. sylvatica* and *V. myrtillus*, the main ground flora components here were *H. helix* and *R. fruticosus* which were significantly more abundant than in the unfenced plots (Table 6).

3.2. Community analysis

A statistically significant two-dimensional solution for the NMS ordination was found (Figs. 5 and 6). The two axes represent 36% of variation in the original matrix and stress on the solution was 26, which is rather high but may be deemed acceptable given the large sample size (McCune and Grace, 2002). Axis 1 represents a gradient of edaphic conditions, with the base-rich quadrats from more fertile soils in Reenadinna being found at the lower end of the axis and the quadrats from acidic soils in Camillan at the higher end of the axis. Axis 2 clearly distinguishes between treatments, with fenced plots being found towards the lower end of the axis and unfenced plots towards the top of the axis. Axis 2 was also correlated with a difference in species' ecology, with unfenced plots being characterised by herbaceous woodland specialist species (e.g. *P. sterilis* and *S. europaea*) and fenced plots being characterised by woody woodland generalist species (e.g. *R. fruticosus* and *H. helix*). Of the four groupings indicated in Fig. 5, the fenced and unfenced plots in Reenadinna and the unfenced plots in Camillan form relatively discrete clusters of quadrats. The exceptions are the quadrats from fenced plots in Camillan, which are more dispersed, due to the major variation in vegetation development among the four exclosures (see above).

Changes in diversity measures between 1969 and 2001 are shown in Fig. 7. In both woods there was an initial rise in species richness followed by a decline, although this decline was minor in Reenadinna. Simpson's index indicates an overall decline in diversity over the period of the experiment in both woods. Analysis of diversity measures for 2001 data (Table 7) show some indication of lower diversity within the fenced plots.

4. Discussion

4.1. Methodological considerations

There are limitations to the inferences that can be made from exclosure experiments due in part to the restraints that practicality and expense normally place on experimental design. As reviewed by Stohlgren et al. (1999), caveats on inferences may stem from subjective placement and small size of exclosures, low numbers of replicate exclosures and consequently common involvement of pseudoreplication *sensu* Hurlbert (1984), and also from the relatively small area actually sampled during recording. With these limitations borne in mind, we focus here on the major results of the present experiment. Strictly speaking, exclosure experiments actually inform us about recovery from grazing rather than the vegetation that would occur in the absence of grazing (Rooney and Waller, 2003). Whilst exclosure experiments (including the present one) typically only examine the effects of the presence or absence of grazing animals, grazing pressure in natural systems is actually a continual variable and the responses of vegetation elements to this may be non-linear in nature (Hester et al., 2000; Rooney and Waller, 2003). Manipulation and measurement of wild deer populations is naturally more difficult than with domestic herbivores. Interpretation of the present dataset is partly hindered by a lack of accurate data on the deer densities during the 32 years of the experiment; there are indications from the data that grazing levels in the study sites declined during this period.

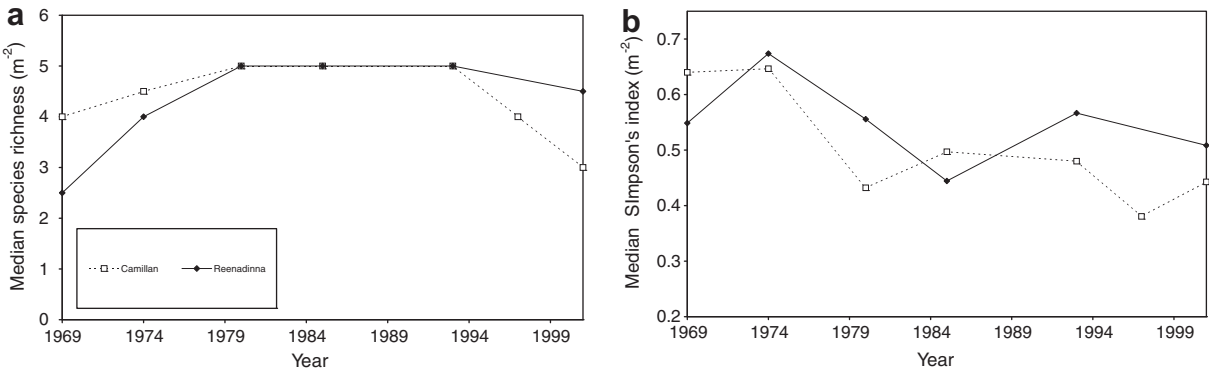

Fig. 7. Changes in species diversity within the deer exclosures 1969–2001: (a) species richness, (b) Simpson's index. Reenadinna data are for exclosures R1–R3, Camillan data are for C1 only.

Table 7
Comparison of diversity measures between fenced and unfenced plots in Reenadinna and Camillan in 2001. Values shown are medians analysed with Mann–Whitney *U* test.

	n per treatment	Species richness		*P*	Simpson's index		*P*
		Fenced	Unfenced		Fenced	Unfenced	
R1–R3	60	4.5	4.0	0.560	0.51	0.62	0.073
C1	20	3.0	4.0	0.368	0.49	0.53	0.601
C2–C4	40	3.0	4.0	0.004	0.28	0.38	0.049

4.2. Vegetation changes

The evidence of change within the exclosures is striking, with the development of a field layer dominated by tall-growing, palatable species. Given that control plots were not monitored over time along with the exclosures, could factors other than fencing be involved? Slight increases in canopy cover occurred in the exclosures over the period 1981–2001, reflected by a mean increase in total basal area of 4.84% for the Reenadinna exclosures and of 0.60% for Camillan exclosure C1 (Perrin et al., 2006). These increases in shading would be expected to have a slight negative effect on field layer cover, and possibly on diversity; such effects – if any – have clearly been overwhelmingly countered by the effects of fencing. Changes in climate over the timescale of the study are likely to be insignificant.

The main ground flora species to benefit in Reenadinna were *R. fruticosus*, *H. helix* and *L. periclymenum*. *R. fruticosus* is clearly highly susceptible to browsing, despite its thorns. Higher abundance of these species in fenced woodland has also been found in several other studies (e.g. Cooper and McCann, 2011; Latham and Blackstock, 1998; Putman et al., 1989). Kirby and Woodell (1998) reported that *R. fruticosus* spread rapidly in fenced areas in a wide range of woodland types in England. The decline in *R. fruticosus* in various unfenced stand types at Brigsteer Wood, Cumbria, including a yew-dominated stand, was attributed to the increase in roe deer (*Capreolus capreolus*) abundance by Barkham (1992). In Northern Ireland, McEvoy et al. (2006) found cover of *R. fruticosus* was greater in ungrazed woodlands; they also found *L. periclymenum* and *H. helix* to be indicators for ungrazed woodland.

Increases in these woody species are generally accompanied by decreases and losses of herbaceous species (Putman, 1994). In Reenadinna, release from grazing resulted in an initial increase in frequency of some herbaceous species, but these plants appear to have been gradually outcompeted by the expanding woody species. For example, by 2001 the unpalatable *O. acetosella* (Putman et al., 1989) had become virtually restricted to grazed plots. Cooper and McCann (2011) found that this species declined in their cattle exclosure in Reilly Wood, Co. Fermanagh over a 10-year period. Van Uytvanck and Hoffmann (2009) reported that large *Rubus* thickets had a negative impact on both the flowering and cover of the woodland specialist *Anemone nemorosa*.

Perhaps the most noteworthy feature of the current field layer in the yew-wood exclosures is its total cover: a mean of 46%, compared with 12% in the contemporaneous grazed plots, and only 4% in the exclosure plots prior to fencing. An extreme sparseness of the field layer is reported as a characteristic of yew-woods in Britain (Rodwell, 1991). In Reenadinna, however, it was clearly grazing pressure and not shade that was primarily responsible for the extreme paucity of the field layer.

The development of the field layer in Camillan was site-dependent, as evidenced by the more heterogeneous dataset with clear differences between the field layer that developed in exclosure C1 and that in exclosures C2–C4. In C1 there was a marked increase in cover of *V. myrtillus* and *L. sylvatica*. Spread of *V. myrtillus* was also noticeable in sheep exclosures in Yarncliff Wood, Yorkshire (Pigott, 1983). Baines et al. (1994) found that *V. myrtillus* cover did not differ between grazed and ungrazed woodland, but that grazed plants were only half as tall, due to removal of leading shoots by deer. *L. sylvatica* is also reported as being sensitive to grazing (e.g. Cooper and McCann, 2011; McEvoy et al., 2006). Barkham (1978) reported that there was considerable regrowth of this species in the exclosure in Wistman's Wood, Dartmoor, established in 1965, whilst at the grazed site of Black Tor Copse, also on Dartmoor, it was restricted to areas of steeply sloping, unstable clitter, which were inaccessible to animals.

The expansion of these vigorous woodland plants in the absence of grazing may have a negative impact on less competitive vascular species, as demonstrated in Camillan by the declines in *B. spicant*, *P. aquilinum* and *O. acetosella*. *P. aquilinum* also declined in abundance in the exclosures of Cooper and McCann (2011). The loss of *Hymenophyllum tunbrigense* and several angiosperm herbs from the exclosure in Tomies oakwood, also in the Killarney National Park, was ascribed by Kelly (2000) to increased competition from *L. sylvatica* and *Ilex* saplings. Mitchell and Kirby (1990) commented that dominance of *L. sylvatica* following cessation of grazing could reduce ground flora diversity. Judging from the decline in cover value, bryophytes have also clearly suffered beneath the shade of the taller vegetation in Camillan exclosures C2–C4. Kirby et al. (1994) commented that in two woodland nature reserves in Wales (Coed y Rhygen and Coed Ganllywyd), initial plans to eliminate sheep grazing had to be modified to allow a controlled level of grazing in order to conserve rare Atlantic bryophytes.

4.3. Diversity and management

Exclusion of deer appears to have resulted in initial increases in measures of diversity, followed by a long-term decline, so that diversity at the conclusion of the study is generally lower within the exclosures than outside them; however, trends and comparisons are rather weak. Kelly (2000) found more striking results in a woodland exclosure in the nearby oakwood of Tomies, where vascular plant richness increased substantially after fencing but was followed by a gradual decline. As in Camillan, the decline in Tomies Wood was ascribed to increased cover in a small number of competitive but relatively grazing-sensitive species. McEvoy et al. (2006) similarly found greater species richness in grazed woods than in ungrazed woodlands. Cooper and McCann (2011) found the decline in species richness in cattle exclosures in woodland in Northern Ireland was mainly a function of the loss of ruderal species. In the present study, the decline in diversity was accompanied by a shift in dominance from woodland specialist species to woodland generalist species – a potentially undesirable trend. Corney et al. (2008) found increased deer browsing was one factor resulting in an increase in grass species and a loss of woodland herbs in Wytham Woods, England. It appears that the rate of change in diversity is higher in Camillan than in Reenadinna. The skeletal soil over the karst limestone terrain probably limits the ability of taller-growing species to achieve competitive exclusion of lower-growing species.

Whilst complete exclusion of grazing animals has been shown to be beneficial in terms of natural regeneration for certain species within the Killarney woodlands (Kelly, 2002; Perrin et al., 2006), long-term fencing of the woodlands may be undesirable if the management objectives are to achieve high levels of ground flora diversity. These findings are particularly pertinent as widespread fencing of woodland in Killarney occurred soon after the conclusion of this study. Fencing may also have the impact of increasing grazing pressure onto neighbouring habitats that are also of conservation value.

Hester et al. (2000) recommended that fencing only be used as a short-term measure in heavily degraded woodlands and rotational exclosure was one of the recommendations by Mitchell and Kirby (1990) for grazed upland woodlands. Ideally, such fences should be removed once a sufficient density of saplings of each target species has exceeded the maximum browse height of the main herbivores; for both *C. elaphus* and *C. nippon* this height is 1.8 m according to Mayle (1999). As shown in Perrin et al. (2006), the success and rate of natural regeneration vary considerably between woodland types and even between stands within the same woodland, making it difficult to give guidelines. It follows that regular monitoring of natural regeneration and ground flora within woodlands fenced for management (as opposed to experimental purposes) is required to ensure that fences are not left *in situ* for longer than necessary. The present study and that of Perrin et al. (2006) suggest that fencing under canopy may be an inappropriate tool for promoting regeneration of *Quercus petraea* in oakwoods and *T. baccata* in yew-woods, as declines in ground flora diversity may occur before sufficient regeneration of target species has occurred; the mean heights of regeneration for these species were much lower than 1.8 m after 32 years. Further research is needed to investigate the effects in Irish woodlands of deer grazing at low and moderate densities, such that critical thresholds of grazing intensity (cf. Hester et al., 2000) can be identified.

5. Conclusions

This 32-year experiment has demonstrated that deer grazing has a major influence on the ground flora of woodlands in the Killarney National Park. Exclusion of grazers primarily benefits competitive, grazing-sensitive species, such as *R. fruticosus*, *H. helix*, *L. periclymenum*, *L. sylvatica*, *V. myrtillus* and *I. aquifolium* which gradually outcompete herbaceous woodland specialist species. In the long-term, grazing exclusion may result in declines in vegetation diversity.

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