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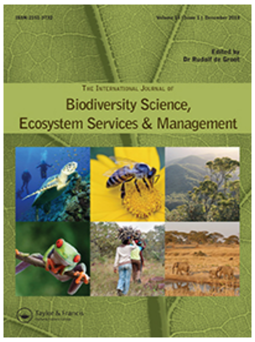

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Ecosystem service responses to rewilding: first-order estimates from 27 years of rewilding in the Scottish Highlands

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ABSTRACT

Rewilding as a conservation strategy is gaining increasing scientific, political and public attention, yet empirical evaluations of its impacts remain scarce, especially with regards to ecosystem services. We provide evidence of the change in three ecosystem services (timber [provisioning], pollination [regulating], and aesthetics [cultural]) from up to 27 years of a moorland rewilding strategy in the Scottish Highlands using a chronosequence of rewilded plots and adjacent controls. These services were assessed in the field and using online surveys. We found that rewilding increased aboveground woody biomass and restored natural tree recruitment processes, although the latter only emerged after at least 15 years of rewilding. Rewilding caused a linear increase in perceived aesthetic quality over the first 27 years, but had no effect on pollination visitation rates. Thus, we conclude that rewilding can be used for ecosystem service recovery in moorland landscapes, but that results vary depending on the preferred service.

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Introduction

Rewilding is an emerging conservation and ecological restoration strategy that is gaining increasing attention from the public, policymakers and the conservation community (Monbiot 2013; Navarro and Pereira 2015; Jepson 2016; Svenning et al. 2016; Wentworth and Alison 2016). Broadly defined as 'the passive management of ecological succession with the goal of restoring natural ecosystem processes and reducing human control of landscapes…[where] intervention may be required in the early restoration stages' (Navarro and Pereira 2015), rewilding captures a range of different intervention types and target ecological baselines (Fernández et al. 2017). While the end-goal of rewilding activities often vary (Pettorelli et al. 2018), most share a focus on the restoration of natural ecosystem processes to facilitate the establishment of self-sustaining ecosystems. Rewilding is often promoted as a solution to two major conservation challenges: first, rewilding can be used to reverse defaunation and restore biodiversity in degraded systems (Navarro and Pereira 2015; van der Zanden et al. 2017); second, it is perceived by some stakeholders to have the potential to restore the societal connection with nature by harnessing the public engagement generated by charismatic megafauna and autonomous natural systems (Rewilding Europe 2015; Jepson 2016). Furthermore, rewilding is considered a low-cost alternative to agriculture on marginal lands which are otherwise managed economically inefficiently, or abandoned entirely (Merckx and Pereira 2015; Navarro and Pereira 2015). Nevertheless, rewilding remains controversial (Nogués-Bravo et al. 2016; Rubenstein and Rubenstein 2016), not least because of a notable lack of empirical evidence addressing its impacts (e.g. on biodiversity) (Svenning et al. 2016; Pettorelli et al. 2018).

The specific type of rewilding activity applicable in a given region varies considerably due to socio-political and land use differences (Pettorelli et al. 2018). Importantly, in areas with lower population densities and the potential for restoration of large spatial extents, rewilding might emphasise landscape-scale processes such as natural disturbance regimes or large animal reinroductions (Fernández et al. 2017). For example, opportunities for rewilding based around the restoration of the ecological function of large animals, so-called trophic rewilding, might be relatively more abundant in areas undergoing high rates of agricultural abandonment and thus where risks of livestock predation are comparatively low (e.g. Treves et al. 2004). However, opportunities for the restoration of landscape-scale processes are far more restricted in other regions, such as the UK (Sandom and Wynne-Jones 2018). This is evidenced by efforts to support trophic rewilding through

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Supplemental data for this article cam be accessed here.

predator reintroduction in Scotland thus far achieving limited political support (Wilson 2004; Wentworth and Alison 2016). In such places, many rewilding initiatives are currently operating at small spatial scales, and instead of focusing on landscape-scale processes their focus is on restoring bottom-up ecological processes such as succession that can allow for the 'autonomous' development of natural systems whilst minimising human intervention (Sandom and Wynne-Jones 2018). Nevertheless, they often represent the first stages of ambitious rewilding projects occurring over far larger spatial scales.

In Scotland, efforts are under way to rewild landscapes through the restoration of threatened Caledonian pinewoods. While pine forests are thought to have once covered much of Scotland (Froyd and Bennett 2006), they have declined dramatically in the last 250 years, as a result of timber extraction and increases in deer and livestock densities (Hobbs 2009). A number of recent initiatives intend to reverse this decline and restore functional, self-regulating native forests (Carrifran Wildwood 2008; Hobbs 2009; Brown et al. 2011; Trees for Life 2018). The recovery of the late successional pinewood ecosystem is impaired by both reductions in seed sources and by high deer densities which have severely negatively impacted on the process of natural recruitment (Miller et al. 1998; Côté et al. 2004; Hobbs 2009). As a result, rewilding strategies applied in the Scottish Highlands often focus on restoring natural recruitment processes and suppressing the artificially high levels of herbivory constraining forest regrowth in moorland landscapes (Hobbs 2009).

Whilst empirical evaluations of the ecological and socio-economic impacts of rewilding remain scarce, one area that remains particularly under-addressed is the impact of rewilding on ecosystem service delivery. Although theorised to improve the delivery of some, particularly regulating, ecosystem services (Cerqueira et al. 2015; van der Zanden et al. 2017), a Web of Science search conducted on 1/8/17 with search terms 'rewilding AND "ecosystem services"' yielded just 14 papers from the last 20 years. Following a wider review, we found four papers have compared the site-level provision of multiple ecosystem services between rewilding or passive land management strategies and alternative land uses, and these have all demonstrated trade-offs between services (Table 1). Navarro and Pereira (2015) conducted a qualitative assessment of the ecosystem services delivered by rewilding relative to intensive and extensive agriculture and commercial forestry, and concluded that rewilding is the most effective land use for the provision of regulating services, falls closely behind extensive agriculture in the delivery of cultural/recreational services, and performs least well with regards to provisioning services. Birch et al. (2010) evaluated the

Table 1. Results of papers comparing ecosystem services delivered by rewilding land management relative to alternative baseline land management strategies/land uses. ↑/-/↓ correspond to an increase/no change/decrease in ecosystem services respectively. All papers listed assess the total level of ecosystem service delivery except Birch et al. (2010) which assesses the net present value of ecosystem service changes including restoration costs.

Study	Study area	Baseline land use	Food (inc. livestock)	Fibre (inc. timber)	Energy	Freshwater	Flood protection	Recreation (inc. tourism)	Aesthetics	Carbon sequestration	Soil protection	Biodiversity
Hodder et al. 2014	Knepp Estate, UK	Arable and livestock farm	–	↑	↑	–	↑	↑	–	↑		
	Wild Ennerdale, UK	Mixed use landscape including plantation forestry	–	–	↑	–	↑	–	↑	↑		
	Great Fen, UK	Lowland fen and arable farming	↑	↑	↑	–	↑	↑	↑	↑		
Cordingley et al. 2016	Dorset, UK	Lowland heathland		↑				↓	↑	↑		↓
Birch et al. 2010	Río Negro/Neuquén, Argentina	Dryland forest	–	↑				–		↑		
	Valparaíso region, Chile	Dryland forest	↓	↑				↑		↑		
Navarro and Pereira 2015	Qualitative assessment	Extensive agriculture	↓	↓		↑	↑	–	↓	↑	↑	↑

net present values of changes in ecosystem services in South American dry forests under alternative restoration scenarios, and found that passive restoration led to positive net present values for all services assessed in the study (carbon sequestration, non-timber forest products, timber, tourism) except livestock production, even after restoration costs were accounted for. Hodder et al. (2014) evaluated the change in ecosystem services at three UK rewilding projects under the implementation of landscape-scale management, and identified that the landscape-scale rewilding approach led to ecosystem service levels that either matched or exceeded those delivered by the baseline land management scenario for every service. Finally, Cordingley et al. (2016) evaluated the changes in ecosystem services delivered by the passive management of lowland heath in the southern UK relative to alternative management scenarios and found that passive management delivered the highest levels of timber, carbon sequestration, and aesthetic quality, but the lowest levels of recreational and biodiversity benefits. Whilst some of the differences in outcomes outlined in these studies can be attributed to definitional differences (e.g. Navarro and Pereira (2015) assume that rewilding delivers no timber services because it is fundamentally non-extractive, whilst the other studies calculate the option value associated with timber), it is hard to make generalised conclusions due to the limited sample size. Thus, further empirical data encompassing all ecosystem service types (i.e. provisioning, regulating and cultural) are urgently needed.

In an attempt to address this data deficiency and further develop the evidence base for the ecosystem services delivered by rewilding, this study assesses changes in three ecosystem services in a chronosequence of eight rewilding exclosures in the Scottish Highlands erected from 1990 to 2016 and their adjacent controls. We aim to provide first-order estimates of the impact of rewilding on ecosystem service proxies using on-the-ground data. This is one of the first empirical, field-based studies to investigate the impact of rewilding on at least one ecosystem service for all three dimensions (provisioning, regulating and cultural), and, to the best of our knowledge, the first to assess the impact of what is explicitly considered a rewilding intervention on pollinator visitation.

Methods

Study site

The study was conducted north of Loch Beinn a' Mheadhoin (57.16°N, 4.57°W) and in Dundreggan Conservation Estate (57.11°N, 4.45°W) in neighbouring valleys in the Scottish Highlands (Figure 1). The area contains one of Scotland's largest remaining ancient Caledonian pinewood fragments (Froyd and Bennett 2006). Eight rewilding exclosures covering a sum of 964 ha have been erected over the last 27 years by the UK Forestry Commission and the charity Trees for Life (www.treesforlife.org.uk). For reference, by current total area this is medium-sized UK rewilding initiative comparable in size to other well-known projects such as the Knepp Estate [1416 ha (https://www.kneppestate.co.uk/)] and Carrifran Wildwood [300 ha (http://www.carrifran.org.uk/about/what-we-have-achieved/)], and additionally the charity owns approximately a further 9000 ha with plans for expanding rewilding management (https://treesforlife.org.uk/work/dundreggan/). All of the deer exclosures were erected on wet moorland and bog and wet heathland communities dominated by heather, grasses, bog myrtle and sphagnum and other mosses, with few or no trees present within the boundaries. In each case, exclosures underwent a native tree-planting treatment soon after establishment, where seedlings were planted on site, occasionally followed a few years later by supplementary planting (Supplementary material, Table S1). Planting included a mix of native species known to play important roles in Caledonian pinewood ecosystems, including Scots Pine (*Pinus syvestris*), silver and downy birch (*Betula pendula/pubescens*), rowan (*Sorbus aucuparia*), juniper (*Juniperus communis*) and hazel (*Corylus avellana*). The predominant planting technique used was mounding (digging up and overturning a patch of earth before planting a seedling in the exposed sub-surface soil), and seedlings were planted at mean densities of approximately 1034 ± 399 (std. dev) stems per hectare. Paired control sites were selected directly adjacent to each of the exclosure sites which were as similar in altitude and aspect to the exclosure sites as possible.

Ecosystem service evaluation

We assessed a provisioning, regulating and cultural ecosystem service, specifically, timber (via aboveground woody biomass), pollination (via visitation rates) and aesthetic quality. All sampling occurred in June and July, 2017.

Provisioning service – timber

We measured aboveground woody biomass at 12 random locations within each exclosure, and six within each adjacent control, equally stratifying the sample above and below the mean contour line for the site. At each random location, we set up a 20x20m plot. In each plot, we identified each stem over 4cm diameter-at-breast-height (DBH; henceforth referred to as 'trees') to species level and recorded the DBH. In addition, we recorded the number and species of stems with height > 50cm and DBH < 4cm

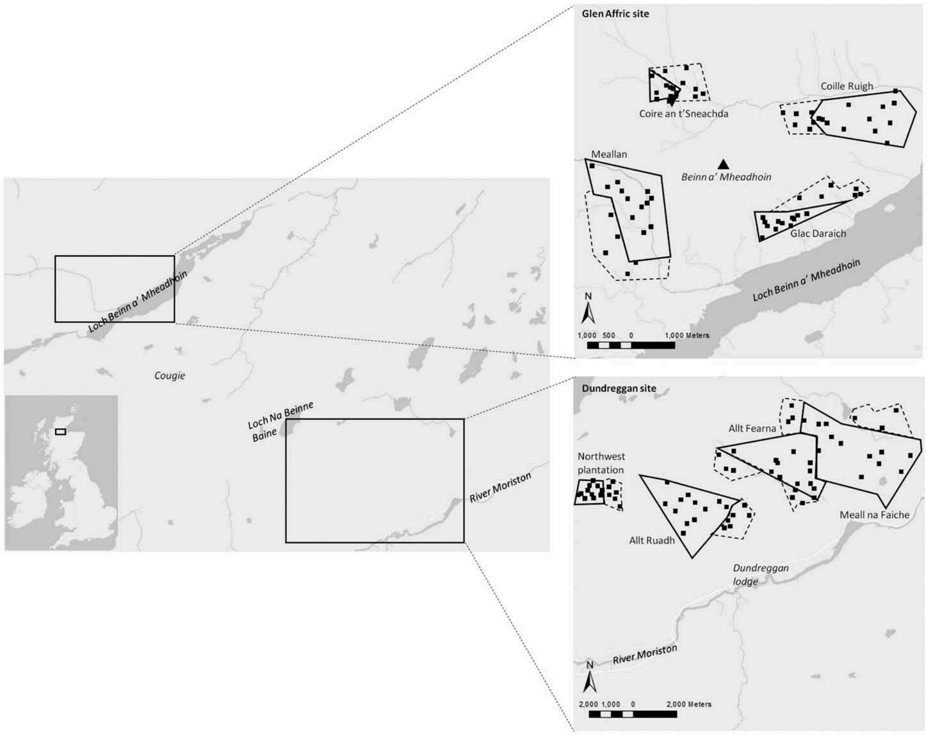

Figure 1. Map of the study area and location of the study sites. Unbroken lines represent the outlines of the exclosures. Dashed lines represent the boundaries of the sites chosen as adjacent controls. Black squares represent the locations of individual sample plots.

(henceforth 'saplings'). We also conducted a 1x20m transect along a randomly-selected edge of the plot and recorded the number of stems < 50cm tall (henceforth 'seedlings'), as well as the number of deer pellet groups in the transect (providing an indication of deer density; e.g. Marques et al. 2001; Valente et al. 2017). We visually assessed flowering plant species richness and the percentage of different ground-cover types in a 1x1m quadrat in each of the four corners of the plot. In total, we sampled 5.76 ha across all plots.

We derived estimates of aboveground woody biomass from the collected diameter and/or height data using allometric equations available in the Global Allometree database where possible (http://globallometree.org/, Henry et al. 2013; Supplementary material, Table S2). We favoured species specific allometric equations from the UK (2/11 species), although if these were lacking then equations from northern Europe were sought (6/11 species) before North American equations were used (1/11 species). When species-specific equations from all three geographic regions were absent, then we used equations for a proxy species in the same genus, following the same hierarchy (2/11 species representing 5.8% of stems in dataset). We excluded all trees with a current DBH of > 20cm from the analysis (< 1% of stems in dataset) because their establishment likely preceeded the exclosure construction and could not be confidently attributed to the rewilding intervention. Due to our focus on potential timber production, we used equations for deriving woody biomass rather than all aboveground biomass where available, but for six species (10.7% of stems) only equations for deriving total aboveground biomass were available.

We then estimated the volume of timber delivered by each site by converting the biomass of each tree into volume using species-specific wood-density data provided in the Global Wood Density Database (Chave et al. 2009; Zanne et al. 2009), again using proxy species from the same genus where required (3.7% of stems) (Supplementary material, Table S2). We used biomass-volume conversion factors from Europe where available (9/11 species), but for two species conversion factors from the US and China were used.

Following the methodology of Newton et al. (2012), monetary estimates of coniferous timber option values were calculated by multiplying the coniferous wood volume by the Coniferous Standing Sales price for the UK in 2017, £19.05 m^{-3} (Forestry Commission 2017), and for broadleaf timber by multiplying the broadleaf volume by the average cost of hardwood firewood logs, £47 m^{-3} (D. Halliday, Forestry Commission, personal communication). We valued each stem individually instead of adopting the cumulative yield approach adopted by other attempts to value forest provisioning services because the low growth rates and planting densities associated with the rewilding interventions would be unlikely to be managed in the same manner as commercial forestry (Newton et al. 2012; K. Hay, Forestry Commission, personal communication). All trees with a DBH < 7cm were omitted from the timber volume calculation in line with guidance from the Forestry Commission (Forestry Commission 2016). The sum of the value for each of the plots from each site was then used to derive a mean per-hectare value of provisioning services for each site.

In order to distinguish between biomass attributable to the growth of planted stems versus natural regeneration, we calculated the expected diameter of trees planted during the coniferous and broadleaf planting phases for each site using tree growth equations for Scottish heather moorland derived from Palmer and Truscott (2003) (Equation 1; Supplementary material, Figures S1-S2).

$$diameter = 0.0053^{*}age^{2} + 0.0661^{*}age + 0.0048 \quad (1)$$

Based on observations (D. Gilbert, Trees for Life, personal communication), we assumed an average diameter for seedlings of 1cm, and for saplings of 2.5cm. Thus, we were able to allocate each stem as a result of either planting or natural regeneration by comparing the measured diameter with the expected values for each site from the projected growth of planted seedlings and saplings. Stems with smaller size properties than the expected value were assumed to have established after the planting phase and therefore to be a result of natural regeneration.

Regulating service – pollination

We conducted two days of pollinator surveys in the centre of each site and control. Between the hours of 1200 and 1630, we visually assessed all of the potential pollinators passing within 1m of the experiment for half an hour. Each site and control was sampled within 30 min of each other to ensure environmental characteristics were as similar as possible. Whilst the distance between the site and control sampling points varied between sites (from 500m at Coire an t'Sneachda to 2km at Meall na Faiche) depending on the size of the rewilding exclosures, for none of the sites were the pollinator survey points sufficiently far away from paired controls to be considered completely independent at the landscape scale (Ricketts et al. 2008). As a result, our measurements were likely to be conservative estimates of the difference in pollinator visitation rates between rewilding sites and controls because of spillover effects. However, our results can be considered to reflect local-scale site-selection effects on pollination visitation [i.e. based on visual and olfactory cues (Lazaro and Totland 2010)]. We also conducted a pollinator assessment using cameras directed at baited artificial flowers, but visitation rates for this method were low (Supplementary materials).

Cultural service – aesthetic quality

Photos were taken at each site and used in an online survey to assess visual quality. At each plot, we took multiple photographs of the site using a Lumix DMC-G3 camera. In order to minimise variability in aesthetic value attributable to non-natural features, human-associated features (e.g. fences, pylons) were framed out of the photos where possible. Photos were taken from a height of approximately 1m so that local vegetation was clearly visible, and the horizon position was normalised to always appear in the top third of the frame to avoid impacting responses (Svobodova et al. 2014). Each site was visited and photographed on two separate dates and weather was almost uniformly overcast. Based on the methods of Arriaza et al. (2004), we created five different 4 × 4 grids of images by selecting one ecologically representative photo from each site and adjacent control and placing it at a random location in the grid. Photos were edited so that each scene was square for easy comparability and numbered 1–16. All photos were enhanced using Google photos' 'auto enhance' feature to increase visual clarity of the photos as well as some of the colour balance lost due to the overcast weather.

Using Survey Monkey, grids were presented in a random order (https://www.surveymonkey.com/). Participants were asked to rank their four favourite and least favourite photos in each grid, and each photo was then given a representative score (i.e. a score from + 4 to −4). In line with other research into landscape aesthetic preferences (e.g. van der Zanden et al. 2018), they were further asked to provide three adjectives describing their most and least favourite photos, and after the first 80 participants, a list of the most popular adjectives used was compiled and participants were given a choice from the existing set of adjectives alongside an opportunity to continue presenting their own.

The survey was distributed by targeting: (a) academics (via an email invitation sent to members of the Scottish Rural College [SRUC, 109 participants]); (b) farming-associated stakeholders (via posts on the Farming Online Twitter page [https://twitter.com/farmingonline?lang=en, 21 participants] and the Crofting, Farming and Gamekeeping in the Highlands Facebook group [https://www.facebook.com/groups/347861621914508/, 12 participants]); (c) outdoor-recreation-associated participants (via posts on the Rewild Scotland Twitter page [https://twitter.com/RewildScotland?lang=en, 87 participants] and the Scottish Hill Walking and Wild Camping [https://www.facebook.com/groups/shwwc/about/, 48 participants] and Highland Scenery [https://www.facebook.com/groups/highlandscenery/about/, 43 participants] Facebook groups); and (d) urban residents (via the Edinburgh Meadows share [https://www.facebook.com/groups/TheMeadowsShare/, 7 participants]

Facebook group). The survey was framed as a study on aesthetic preferences, and rewilding was not mentioned in order to minimise participants' implicit bias. All survey responses were collected between 5 and 20 July 2017.

Statistical analyses

The impacts of the time since the initiation of the rewilding intervention on all ecosystem services were tested using linear regression models using R version 3.3.2 (R Core Team 2016). For timber, the data showed high levels of heteroscedasticity. Thus, we ln-transformed 1+ the dependent variable (above-ground biomass) and used robust Huber-White standard errors to account for residual heteroskedasticity. The explanatory variables in our model included: altitude, time since the initial rewilding intervention (with control sites assigned a zero value), mean percentage cover of sphagnum and other mosses, the total number of stems in the plot (a proxy for initial planting effort), site as a categorical variable, and an interaction term between the time since the initial rewilding intervention and the number of trees in the plot. To test whether or not natural regeneration was occurring as a result of the rewilding intervention, we applied the same modelling procedure as above using the biomass associated with natural regeneration per plot as the dependent variable. We also tested whether the rewilding intervention was successfully reducing deer presence in the exclosures by conducting a t-test on the number of deer pellets per plot in exclosures versus controls.

For pollination, our model contained the explanatory variables altitude, mean percentage flowering plant cover, mean plant species richness, years since the rewilding intervention, mean number of stems per hectare, and an interaction between the mean number of stems and the time since the rewilding intervention.

For aesthetic quality, a scale of landscape attributes featuring in the set of photos was compiled based on the criteria set out in Arriaza et al. (2004), and each photo used in the survey scored for each category (Table 2). Variables were ordered in a way that presented a continuous scale so that the directionality of the effect of each landscape attribute on visual preferences could be assessed. If two landscape features on the same variable were present in a single photo, the value representing the 'higher' feature was selected (e.g. if both a river and lake were presented, the photo would be allocated a 2 for that landscape attribute). Our linear regression model tested the impact of landscape attributes and time since rewilding against the mean visual quality score assigned to each photo by participants. We acknowledge that our stakeholder sampling approach is non-random and thus there is potential for self-selection bias in our sample, so in order to evaluate this we separated our sample of participants into their respective stakeholder groups, and plotted the mean visual quality score given to photos from each rewilding age class by participant group. As a result of the low number of urban participants (7), we omitted them from this comparison.

Results

Timber

There was considerable variation in mean above-ground woody biomass between sites, with Glac Daraich (the site rewilded 25 years ago) containing

Table 2. Categorisation of continuous variables representing alternative landscape attributes. Adapted from Arriaza et al. (2004).

Variable	Categories	Description	Dummy variable Scoring
Water present	No water	No water body visible	0
	River	River visible within picture.	1
	Lake	Lake visible	2
Vegetation land cover	0–25%	Percentage of land covered by vegetation	0
	25–50%		1
	50–75%		2
	75–100%		3
Manmade elements	None	Presence of manmade elements.	0
	One element	One manmade element	1
	Two elements	Two manmade elements	2
Horizon	Almost flat	Also included photographs were the horizon was not obviously visable	0
	Some mountains/hilly	Presence of mountains but not main focus of photo	1
	Mountains dominate scene	Mountains are dominant and the main photo focus	2
Internal colour contrast	Low colour contrast	Colours are generally the same shades and hues	0
	High colour contrast	Colours are striking and contrasting	1
Scale effect	No	No elements present to give viewer indication of the size of the lanscape	0
	Yes	Scale effect present (e.g. houses, roads and pylons)	1
Visibility/weather	Clear	Zero or very minimal cloud cover	0
	Mixed	Clouds present but clear sky present	1
	Overcast/raining	Thick cloud, long distance visibility impaired	2
	Misty	Some of the landscape is obstructed by low lying clouds	3

at least double the density and biomass of all other sites (Table 3, Figure 2). The theoretical value of timber services also varied between sites, ranging from 0 at all sites younger than 10 years to £152.00/hectare at Glac Daraich (Table 3). The vast majority of stems in the study were smaller than the 7cm DBH threshold for inclusion in the theoretical value calculation, with just 3.52% of stems large enough for inclusion (143/4065 stems in dataset). All of the value across all sites was derived from trees that were planted, as insufficient time had passed for naturally regenerating trees to reach the diameter threshold.

The model (adjusted $R^2 = 0.64$, $p < 0.001$) describing the ln-transformed aboveground woody biomass included the time since the rewilding intervention and the total number of stems per plot (a proxy for the number of trees planted during the initial restoration intervention) as highly significant explanatory variables (Table S3), and there were also significant site-specific effects on abovegound biomass. Exclosures were successful at reducing deer presence, with significantly fewer deer pellets in exclosure transects than outside (2-sided Student's t-test, rewilded mean = 0.26 ± 0.70, control mean = 0.83 ± 1.21, p = 0.003). Exclosures were also successfully facilitating natural tree regeneration, with time since rewilding emerging as a significant predictor in the model explaining the total naturally regenerated aboveground biomass. However, natural regeneration (i.e. the presence of saplings) was only found on the four oldest sites (Table 3), indicating that it takes more than 7 years of rewilding (the age of the oldest site where natural regeneration was not detected) for natural recruitment processes to begin to establish in the moorland landscape. In the sites where natural regeneration was occurring, there was considerable variation in the percentage of total aboveground biomass attributable to regeneration, rising from 3% at Glac Daraich (25 years old) to 42% at Coille Ruigh (27 years old).

Pollination

85 potential pollinators were surveyed through the visual surveys. Of these observed potential pollinators, 68% were non-syrphid diptera and 19% of the genus *Bombus*. Non-syrphid diptera have been demonstrated to be important pollinators in exposed, high-altitude sites where the presence of alternative insect pollinators is limited (Orford et al. 2015). Our linear regression model indicated there was a weak trend for older rewilded sites with high stem densities to have higher pollinator visitation rates, although this interaction was not significant (p = 0.13; Supplementary material, Table S4). Given the lack of landscape-scale independence between sites and controls (ie. increased pollinator visits in sites may spill over into controls) and the low sample size which both act to reduce the

Table 3. Value of provisioning services and aboveground biomass within the exclosures at each site. Standard errors given in brackets next to values. Meall na Faiche was the only site at which the mean woody biomass/hectare in control sites was non-zero (mean = 35.12, standard error 5.85).

Site	Time since initial intervention	Provisioning service value (£/ha)	Woody biomass (kg/ha)					Mean number of trees (trees/ha)	Mean number of stems (stems/ha)
			Total	Planted	Naturally regenerated	Coniferous	Broadleaf		
Coille Ruigh	27	45.49 (3.74)	1893.27 (109.17)	*1093.30 (89.84)*	*799.97 (28.16)*	*1025.49 (82.19)*	*867.78 (33.50)*	50 (2.80)	1594 (35.60)
Meallan	26	53.74 (2.70)	1935.22 (52.06)	*1734.43 (48.17)*	*200.79 (4.99)*	*877.10 (37.00)*	*1058.12 (43.08)*	150 (4.49)	1240 (27.00)
Glac Daraich	25	152.00 (5.61)	4620.71 (165.04)	*4483.07 (161.63)*	*137.64 (5.83)*	*4522.66 (165.74)*	*98.05 (5.57)*	321 (10.23)	885 (22.97)
Meall na Faiche	15	16.01 (0.85)	1116.14 (43.54)	*1072.95 (42.12)*	*43.18 (1.52)*	*857.25 (30.33)*	*258.88 (14.26)*	158 (5.57)	1085 (26.20)
Northwest plantation	7	0	564.16 (11.74)	*564.16 (11.74)*	0	*12.70 (0.62)*	*551.46 (11.66)*	0	1046 (25.89)
Coire an t'Sneachda	5	0	164.25 (7.95)	*164.25 (7.95)*	0	*0.25 (0.02)*	*164.00 (7.94)*	0	467 (24.90)
Allt Fearna	4	0	468.67 (13.48)	*468.67 (13.48)*	0	*16.19 (1.35)*	*451.82 (13.05)*	0	1285 (37.37)
Allt Ruadh	1	0	95.35 (2.52)	*95.35 (2.52)*	0	*0.39 (0.03)*	*94.96 (2.50)*	0	1338 (36.07)

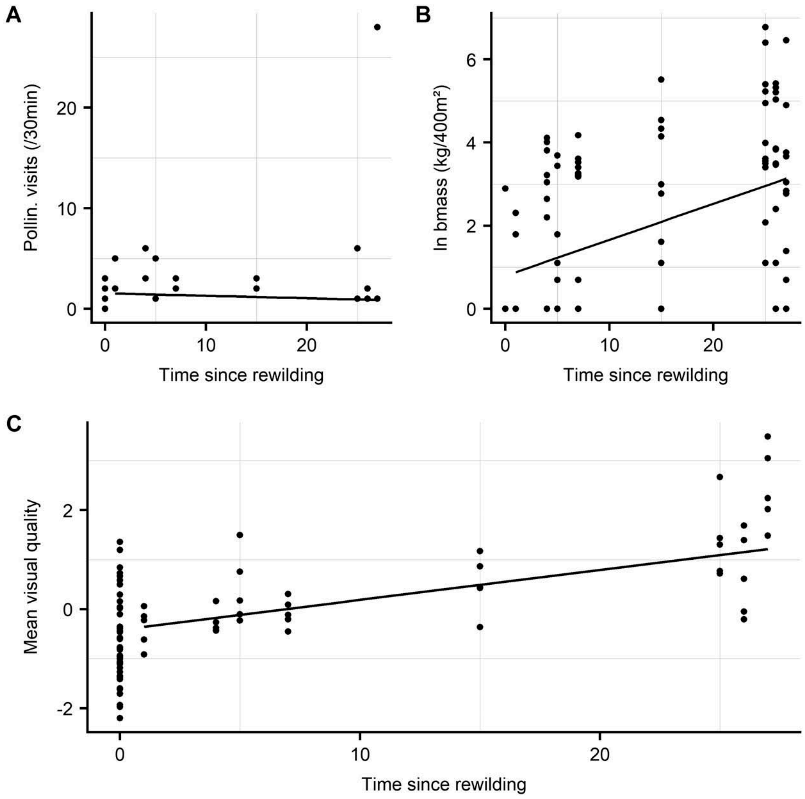

Figure 2. Outputs of linear models describing: A: Predicted pollinator visits as a function of time since rewilding (rewilding was an insignificant predictor of pollination visitation). B: Predicted log aboveground woody biomass as a function of time since rewilding, with all other model variables held at their mean values. C: Predicted photo mean visual quality as a function of time since rewilding, with all other model variables held at their mean values.

statistical significance of this weak trend, we cannot conclusively infer from this that rewilding has no impact on pollinator visitation rates.

Aesthetic quality

The visual quality assessment survey received 328 individual site visits, with 231 respondents completing at least one grid, and 141 (45%) respondents completing the entire survey. Each respondent completed on average 3.6 grids and each grid ranking was completed 154–175 times. Null and duplicate responses were removed based upon submitted email addresses.

Time since rewilding emerged as a significant predictor of photo aesthetic quality in our model (adjusted $R^2 = 0.71$, $p < 0.001$), alongside other landscape features widely recognised to contribute to visual quality, including the presence of water bodies, a mountainous horizon and good visibility (Supplementary material, Table S5). There were limited differences between stakeholder groups with regards to their perceptions of the way that rewilding contributed to visual quality across the rewilding age classes (Figure 3).

Participants' choice of adjectives demonstrated clear differences between rewilded and control sites (Figure 4), with more 'positive' adjectives describing rewilded sites than controls. Similarly, there was a marked change in the adjectives used to describe the rewilded sites along the chronosequence, with more negative adjectives used for younger sites, and more positive ones used for older sites (Figure 4).

Discussion

Understanding the ecosystem services delivered by rewilding is useful to enable the comparison of rewilding with alternative land uses when creating and implementing land use policy. In support of previous studies (Table 1) our results demonstrate that rewilding led to significant increases in timber option value. Our results also show that, over the 27 year chronosequence, rewilding promotes aesthetic quality when applied to moorland habitats. Furthermore, we present the first evidence of the impact of moorland rewilding on pollination, detecting no relationship but under conditions where we would expect a weakened statistical effect, and so this merits further research.

Our results confirm the findings of previous studies in the literature that the rewilding of heathland or moorland systems leads to increases in woody aboveground biomass and concomitant timber value

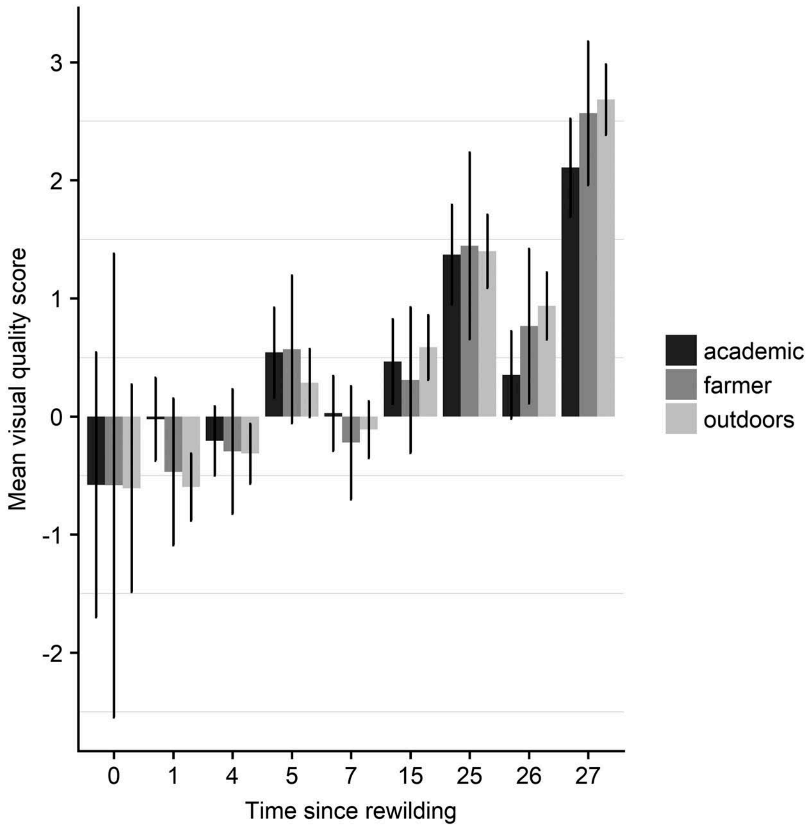

Figure 3. Mean visual quality score assigned by different stakeholder groups to photos representing different rewilding age classes. Lines denote standard errors.

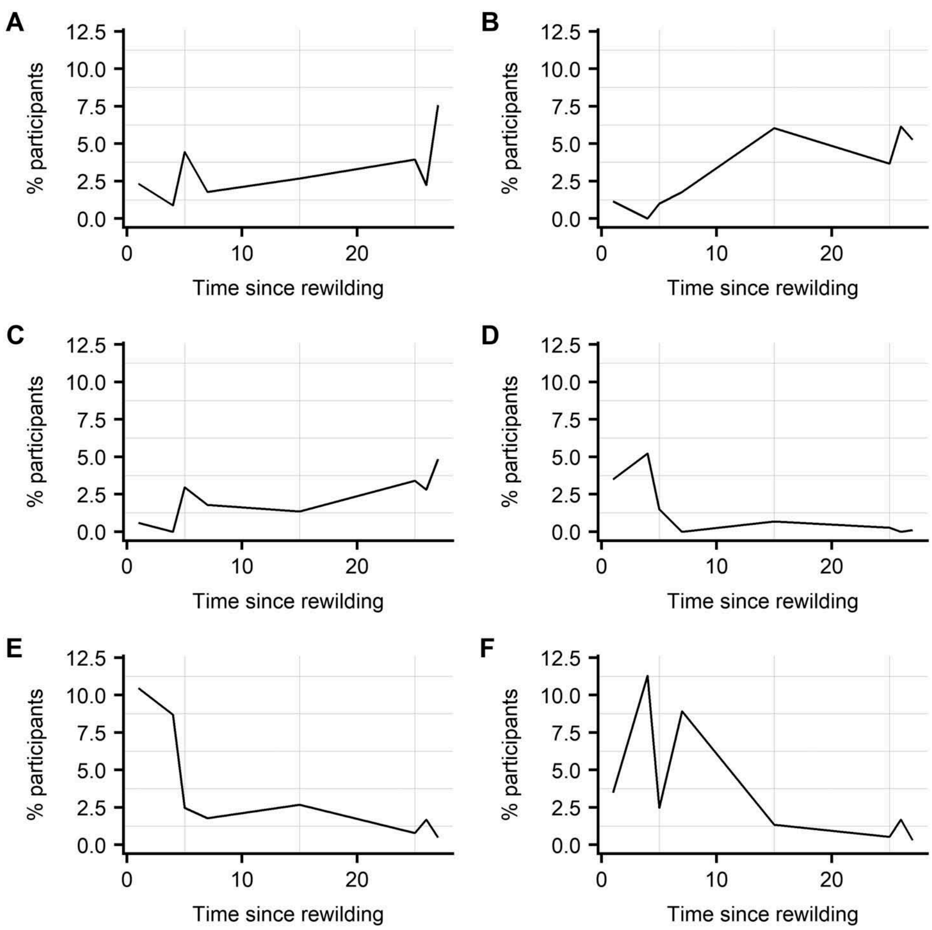

Figure 4. Percentage of participants using adjectives in their descriptions of rewilding plots along the chronosequence: A) Alive; B) Beautiful; C) Wild; D) Uninspiring; E) Boring; F) Bland.

(Hodder et al. 2014; Cordingley et al. 2016). As none of the stems providing timber value in this study resulted from natural regeneration (having not yet reached the required diameter threshold), this increase in timber value is attributable to the active reforestation efforts characterising the early stages of this rewilding project. Thus, the observed recovery of timber services is a result of the specific management strategy used in this rewilding project, and a different rewilding strategy (eg. predator reintroduction) would have been unlikely to cause an equivalent increase in provisioning services. Our results show that the recovery of woody biomass, provisioning services, and natural recruitment processes was slow, with viable timber first emerging after 15 years of growth, and natural regeneration only becoming an important driver of woody biomass (responsible for > 10% of on-site woody biomass) after 26 years of growth. This lag time is consistent with research demonstrating slow tree growth rates on Scottish moorlands (Scott et al. 2000; Palmer and Truscott 2003), attributable in part to waterlogged, low nutrient soils (Forestry Commission 2004). Thus, significant ecosystem function and service responses to rewilding in Scottish moorlands may take decades to occur. How rapidly ecosystem services might recover through rewilding on alternative land cover types remains an avenue for further research.

Our study also empirically evaluated the effectiveness of deer exclosures and assisted planting as a forest regeneration strategy in Scottish moorland landscapes. Our findings are consistent with a large body of work on the impacts of deer exclusion on forest recovery in Scotland, which has demonstrated that whilst exclusion can help promote forest regeneration (Scott et al. 2000; Palmer and Truscott 2003), it is insufficient for promoting forest regrowth in the absence of a local seed source to facilitate colonisation (French et al. 1997; Forestry Commission 2004; Tanentzap et al. 2012). Thus, active restoration strategies (such as planting and deer exclusion) will likely need to be combined if Scotland is to achieve its national policy target of moving from 18% to 21% forest cover by 2032 (Scottish Government 2017a).

The aesthetic value of our sites was significantly and positively affected by the time since the rewilding intervention, and the adjective analysis evidences that this was because sites with greater woody biomass were considered more visually appealing than younger sites in the chronosequence or controls. This suggests that rewilding can be a useful strategy for the aesthetic enhancement of Highlands landscapes. However, it is unlikely that this linear relationship continues indefinitely beyond the 27-year period evaluated in this study. Höchtl et al. (2005) tested for changes in peoples' visual preferences with time by presenting photos of increasingly wooded scenes, and found that respondents preferred sites containing semi-mature woodland. Site preferences initially increased with increasing vegetation maturity, but then declined as mature woodland established, which is consistent with evidence that people have preferences for landscapes characterised by a matrix of alternative habitat types (Junge et al. 2011; Van Berkel and Verburg 2014). Furthermore, whilst this study identifies a positive relationship between reforestation through rewilding and aesthetic beauty, it must be acknowledged that the aesthetic benefits are delivered by more than just the physical characteristics of the habitat type, and are intractably connected to the context and cultural narrative surrounding the rewilding initiative (Prior and Brady 2017; Wynne-Jones et al. 2018).

Interestingly, there appeared to be few differences between groups in their perception of the aesthetic quality driven by rewilding. Previous studies have found that farmers prefer less naturalised landscapes than non-farmers (Junge et al. 2011), and that considerable differences exist between socio-economic groups and different environmental orientations (Bauer et al. 2009; Habron 1998; Fischer and Marshall 2010; Van Berkel and Verburg 2014). Our results indicate that there may be support for moorland rewilding from multiple stakeholders spanning across different sets of environmental attitudes. However, one main difference between the context of this study and these others is that the baseline land use in our study is wild moorland rather than extensive agriculture. Many people have innate preferences for extensively managed agricultural landscapes (Howley et al. 2012), and it is therefore likely that changes in land use from extensive agriculture to rewilding illicit different reactions from those in already unmanaged landscapes, especially from farming-associated stakeholders.

Although our pollination results are not significant, both our low sample size and the lack of landscape-scale independence between sites and adjacent controls would most likely have acted to reduce the statistical significance of a relationship between rewilding and pollinator visitation. A recent meta-analysis demonstrated that pollinators tend to respond positively to ecosystem restoration, even when the restoration intervention is not explicitly designed to benefit pollinators (Tonietto and Larkin 2018). Restoration activities mainly promote pollinators through the restoration of diverse plant communities, increasing the abundance and diversity of pollinators the community can support (Scheper et al. 2013). In this study, rewilding might have been expected to promote pollinator visitation rates by providing greater opportunities for tree-based nesting and reducing pollinator exposure (Kremen et al. 2007). Further research investigating the impact of rewilding on pollination that overcomes the limitations highlighted in our study is needed.

Delivering ecosystem services is just one of the ways that land management strategies deliver societal value, so although it is not the main focus of this work, it is worth briefly discussing the potential economic implications of large-scale rewilding in the Highlands. Dominant alternative land use types in the Highlands include hunting estates and extensive livestock (mostly sheep) grazing in Less Favoured Areas (LFAs), which cover 1.8 million and 3.2 million hectares in Scotland, respectively (MacMillan et al. 2010; Scottish Government 2017b). While both industries are perceived by some stakeholders to play an important cultural and land stewardship role [which is heavily influenced by individual's attitudes and cultural context (MacMillan et al. 2010; Wynne-Jones et al. 2018)], the economic contribution of both land uses is debated. Hunting estates are rarely profitable and are often financially supported through owners' off-site incomes (MacMillan et al. 2010), and despite the vast spatial coverage, are thought to support just 2520 full-time jobs (Edwards and Kenyon 2013). Extensive livestock grazing provides income sources that are particularly valuable for more remote areas with fewer opportunities for alternative employment, but on the other hand they are largely unprofitable in the absence of subsidies, with the mean LFA sheep farm in 2016 making a loss of just under £29,000 without subsidies (Scottish Government 2017b). Rewilding in the UK context does offer alternative economic opportunities. Setting aside the significant potential eco-tourism benefits of species reintroductions (eg. white-tailed eagle on the Isle of Mull (RSPB 2011)), which are not directly relevant to the form of rewilding discussed in the context of this study, rewilding initiatives can create economic opportunities through conservation volunteering schemes [e.g. Trees for Life (https://treesforlife.org.uk/volunteer/)], or wildlife watching focusing on species that have naturally recolonised an area [e.g. recolonisation of Purple Emperor butterflies Apatura iris at the Knepp Estate (https://knepp.co.uk/the-results/)]. Furthermore, rewilding initiatives might generate economic opportunities through restoration-focused agri-environment schemes, and emerging yet controversial conservation finance mechanisms such as biodiversity offsetting and payments for ecosystem services (Navarro et al. 2017).

It is important to highlight what this study does and does not demonstrate to ensure our findings are not extrapolated outside their specific context. This study shows that, for the three ecosystem services addressed, the rewilding management implemented here delivers on average equal or greater ecosystem service value than the surrounding moorland landscapes. This finding is far from trivial, both because it has the potential to inform the optimal allocation of land use over large spatial extents [moorland is Scotland's most common habitat, covering 25% of the landscape (Scottish Natural Heritage 2015)], and because it contributes to ongoing debate regarding the aesthetic value of rewilding relative to alternative land uses (Prior and Brady 2017). However, it should be noted that this finding is not sufficient to draw general conclusions regarding the impact of rewilding on other ecosystem services, or relative to alternative habitat types, and we would expect that the outcomes of our analysis would be sensitive to changes in these factors. For example, this study does not evaluate the relative aesthetic value of rewilding versus extensive agricultural landscapes, which might elicit different results (e.g. Van Berkel and Verburg 2014). Furthermore, the rewilding interventions evaluated in this study comprise only a subset of rewilding management strategies which are adapted to the UK context (Sandom and Wynne-Jones 2018), and thus do not include some of the highly publicised management actions associated with rewilding such as predator reintroduction (Svenning et al. 2016). Thus, this study should be considered an additional piece in a highly incomplete puzzle reflecting the potential ecosystem services delivered by rewilding relative to alternative land uses types.

As such, this study highlights the need for considerable further work investigating rewilding – ecosystem service relationships. Firstly, as indicated above, this study has only analysed the ecosystem service responses resulting from a sub-section of rewilding interventions focused on restoring bottom-up ecosystem processes and facilitating reduced human management. In regions with lower institutional barriers towards restoring large-scale ecological processes such as large animal reintroductions, trophic rewilding is a potential conservation management strategy. While there is strong evidence that large animals played a key role in the functioning of palaeosystems (Malhi et al. 2016; Galetti et al. 2017), the evidence that ecosystem function and services can be restored by refaunation is less well developed (Svenning et al. 2016), and merits significant further attention. Additionally, further research is required to develop a more general overview of the ecosystem services delivered by rewilding relative to alternative land uses, which calls for further empirical studies that incorporate a wider range of ecosystem services and land use types than those addressed here. Furthermore, while rewilding or passive management is seen as a potential mechanism for improving biodiversity and ecosystem service outcomes whilst reducing management costs (Sandom et al. 2013; Rewilding Europe 2015; Wentworth and Alison 2016; Tree 2018), in practice, the up-front costs of rewilding can be high. Our assessment demonstrated quantifiable impacts on ecosystem services but we were unable to conduct a cost-benefit analysis due to data-deficiency.

Cost-benefit analysis has the potential to be an important tool for developing support for nature restoration (Bullock et al. 2011), and so further research into the economics of rewilding is encouraged.

Conclusion

We have conducted one of the first site-based assessments of the change in ecosystem service proxies resulting from a rewilding intervention using a chronosequence and paired controls. Our study found that rewilding promoted both aesthetic and timber value, and had no conclusive effect on pollinator visitation rates. Furthermore, rewilding successfully restored natural tree recruitment processes to the unstructured moorland landscape, although the recovery took at least 15 years to emerge. As a result, this study contributes novel insights into the aesthetic value of rewilding moorland landscapes, and its effectiveness as an ecological restoration strategy in the Scottish highlands. Our study helps develop the sparse evidence base for the impact of rewilding on ecosystem services, and future directions are discussed, including the need for expanding empirical evaluations to incorporate a greater number of ecosystem services, different types of rewilding interventions, and comparison with a greater number of alternative land cover types.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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