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Promoting natural regeneration for the restoration of *Juniperus communis:* a synthesis of knowledge and evidence for conservation practitioners.

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Key words: Juniper; Restoration; Conservation management; Cattle grazing; Scarification; Rotovating; Turf stripping; Soil stripping; Soil fertility; Moss cover; Microsites; Seed viability.

Nomenclature: Stace (2010) for plants; Rodwell (1991–2000) for plant communities; Hill et al. (2006) for mosses

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Abstract

Questions: Natural regeneration is central to plant conservation strategies. Worldwide, many *Juniperus* species are threatened due to their failure to regenerate. We focus on *Juniperus communis* in areas of NW Europe where it is declining and ask: what advice is available to land managers on natural regeneration methods, and when applied, how effective has this been?

Methods: We synthesise knowledge on the efficacy of management interventions and conditions associated with *J. communis* regeneration. In field trials, we test interventions where knowledge is lacking. We assess regeneration of *J. communis,* creation of regeneration microsites and germination of sown seed in response to the interventions.

Results: Although *J. communis* occurs in different habitats, there is consistency in site conditions important for regeneration (unshaded/open, short ground vegetation, disturbed/bare ground, low herbivore pressure). In calcareous grasslands, areas with regeneration are stony/bare or vegetation is short or sparse; in upland acid grasslands and dry heathlands regeneration locations are disturbed areas sometimes with a moss cover. Several interventions (grazing, scarification, turf stripping) can create regeneration conditions. The synthesis identified cattle grazing and ground scarification for further testing on upland acid grasslands. In the resulting field trials, regeneration was rare and recorded on only one cattle grazed site. An exposed moss layer characterised regeneration microsites but there was insufficient evidence that either intervention increased regeneration microsite frequency. Few sown seeds germinated.

Conclusions: Different interventions or intensities of these appear to be required depending on habitat type. Broadly, on calcareous grassland intense scarification or soil stripping is needed, while on dry heathlands light scarification is suitable. On upland acid grassland, cattle grazing and ground scarification do not reliably result in regeneration. Creation of favourable mossy regeneration microsites is unlikely following intervention, unless soil fertility is low. Land use change, increased

climate warming and pollution are pressures acting on *J. communis* and may cause habitat loss and altered site conditions (e.g. soil fertility), making it difficult to create regeneration microsites at all *J. communis* sites. Other constraints on regeneration may operate (e.g. seed predation and low seed viability) and managers should assess population and site potential before undertaking management.

Key words: Grasslands; Heathlands; Juniper; Management intervention; Microsites; Restoration; Seed viability.

Introduction

Self-sustainability in plant populations is a measure of ecological restoration success, with the occurrence of natural regeneration used as an indicator of a functioning ecosystem (Ruiz-Jaen & Aide 2005; Shackelford et al. 2013). Natural regeneration is central to plant conservation strategies and is considered the key process enabling species to adapt to climate change whilst maintaining local, site adapted, genetic resources and avoiding the risks associated with introducing plant material, such as novel pests and pathogens (Koskela et al. 2013; Lefèvre et al. 2013). For conifer species, natural regeneration has been widely and successfully achieved (Matthews 1989).

World wide, conifer species in the genus *Juniperus* show varying success of natural regeneration. For example, the North American species *Juniperus occidentalis* (western juniper) and *J. virginiana* (eastern redcedar) are currently undergoing population expansion whereas challenges to regeneration threatens *J. procera* (African pencilcedar) throughout its geographic range from the Arabian Peninsula to Zimbabwe (Miller et al. 2005; Meneguzzo & Liknes 2015; Negash & Kagnew 2013). More typically, juniper species are a conservation concern in only part of their range, generally due to their failure to regenerate. This is the case for the montane species *J. thurifera* (Spanish juniper, incense juniper) of western Mediterranean regions and North Africa, and *J. communis* (common juniper), which occurs in western and eastern hemispheres, north of the equator (Farjon 2013a, www.iucnredlist.org/details/42255/0, accessed 28 November 2015; Farjon 2013b, www.iucnredlist.org/details/42229/0, accessed 28 November 2015). Although *J. communis* is not threatened with extinction globally in any of its forms (subspecies or varieties) (Farjon & Filer 2013), the species is struggling to survive in some areas, with changes in land use practices and site management identified as a factor driving reduction in plant survival and recruitment (Farjon 2013b).

Within Europe, *J. communis* (represented by the varieties *J. communis* L. var. *communis* and *J. communis* L. var. *saxatilis*) is an important component of designated habitats (calcareous heaths / grasslands, and coastal dunes) as given in Annex 1 of the EU Habitats Directive (92/43/EEC 1992). In boreal, alpine and eastern countries of Europe, these habitats are considered to be in 'favourable' condition (European Commission 2009) and unwelcome invasions of *J. communis* into agricultural and other designated grassland habitats have even been reported in Scandinavia and Poland (Rosen 2005; Falinski 1998). However, within the Atlantic North and the Atlantic Central zones of Europe (EBONE 2009, www.ebone.wur.nl/UK, accessed 1 February 2012), both in the designated habitats and more widely, *J. communis* populations are declining and *J. communis* is of conservation concern. Factors impacting on natural regeneration of *J. communis* are noted as the main threats to the species (European Commission 2009; Joint Nature Conservation Committee 2010).

Success of natural regeneration is influenced by the availability of a seed source and microsites offering the correct conditions for germination and seedling survival (Eriksson & Ehrlén 1992). For a dioecious, sexually reproducing plant such as *J. communis*, all stages of the plant's life cycle have to be supported: pollination, viable seed production, seed dispersal and plant establishment, growth and development to reproductive maturity. As shown by studies of other long-lived (c. 200 years) conifer species, adult survival is likely to have a large influence on *J. communis* population dynamics with lesser importance placed on recruitment of individuals (indicated by successful germination or young seedling presence) for population survival (Thomas et al. 2007; Münzbergova et al. 2013; Kroiss & HilleRisLambers 2015). Nevertheless, recruitment appears to be a challenge for *J. communis* populations in the Atlantic North and the Atlantic Central zones of Europe.

Several studies have investigated reasons behind low seed production and viability. Many *J. communis* populations are aging and this is considered to reduce reproductive vigour (Ward 1982). Diffuse pollution has been shown to interrupt pollination, fertilisation and embryo development (Mugnaini et al. 2007), and nitrogen deposition, sulphur deposition, and increased temperatures can have a similar effect (García 2001; Verheyen et al. 2009; Ward 2010; Gruwez et al. 2014). A wide array of arthropods can act as pre-dispersal predators in *J. communis*, including mites (*Trisetacus quadrisetus*), and the chalcid wasp (*Megastigmus bipunctatus*) (Ward

1982; García 2001). Further, there may be decreased seed dispersal in areas where bird (*Turdus* spp.) numbers are lower (Eaton et al. 2009). Although it is thought that *J. communis* had historically high levels of pollen and seed-mediated gene flow, recent population fragmentation could be reducing effective gene flow with potential implications for the long-term fitness and survival of small populations even where viable seed production occurs (Van Der Merwe et al. 2000; Provan et al. 2008; Vanden-Broeck et al. 2011).

Timing the provision of suitable microsites is critical for successful regeneration of conifers as most have occasional mast years and the seed germinates when shed or following a short chilling period (e.g. Nixon & Worrell 1999). *Juniperus communis* has occasional years when seed production is abundant (Raatikainen & Tanska 1993; García et al. 1999; Bonner 2008; Ward 2010), but seed also displays a relatively deep dormancy which requires a longer period of exposure to natural winter conditions to break (Baskin & Baskin 2001; Bonner 2008). Seed is unlikely to germinate until the second spring following an autumn sowing and even then, germination can be sporadic (Broome 2003). Conditions suggested for successful germination and establishment of *J. communis* are associated with high light levels and unrestricted water availability is (Livingston 1972; Grubb et al. 1996; García et al. 1999). *Juniperus communis* is a community dominant in a range of open habitat types including upland acid grasslands, dry heathlands and lowland calcareous grasslands, and also occurs as a understorey species in pine woods and upland acid oak woodlands (Barkman 1985; Rodwell 1998a, b; Rodwell 1991; Thomas 2007). We therefore might expect the appearance of regeneration microsites and the processes by which they are created to vary with habitat type. Further, failure of *J. communis* to germinate and establish is thought to be due to a reduction in habitat suitability. Changes in site management leading to increased herbivore pressure are given as the primarily causes for reduced suitability (Thomas et al. 2007). Therefore, there may be an opportunity to enhance natural regeneration of *J. communis* if management appropriate for the habitat conditions can be identified. *Juniperus communis* is declining within the Atlantic North and the Atlantic Central zones of Europe and here efforts to conserve the species and address the declines are required by European and country level legislation. In order to develop better guidance for conservation practitioners we conducted a literature review and field trials to:

i. Synthesise information on conditions associated with *J. communis* regeneration and the efficacy of potential management interventions

ii. Test the most suitable candidate interventions identified from the synthesis in field trials, particularly those which appear most practical to implement on the type of sites where managers are keen to restore *J. communis* populations. The specific objectives of the trials were (1) to evaluate natural regeneration of *J. communis* in response to two interventions (scarification and summer grazing by cattle), (2) to identify plant cover and composition of microsites where regeneration occurred and (3) assess whether the interventions created three measures of microsite condition identified in (2) and in the literature review. Given the uncertainties of seed viability and dispersal for this species, a further objective (4) was to assess the germination of seed directly sown at the sites.

Methods

Methods are described in full in the online resource (Appendix S1); an outline of literature review and field trial methodologies is given here.

Literature review

We searched for information in two categories: i) surveys of *J. communis* (var. *communis* and var. *saxatilis*) sites where presence of regeneration was recorded, hereafter referred to as "regeneration surveys"; and ii) studies where management interventions had been applied in an attempt to enhance *J. communis* regeneration, referred to as "management studies". Information was sought from countries within Atlantic North and the Atlantic Central environmental zones of Europe (EBONE 2009). The scientific literature was searched (up to November 2015) using *Juniperus communis* as the key word. Further information was sourced from book chapters and from published and unpublished reports produced by conservation agencies and organisations.

Field trials

We implemented a six-year trial on upland acid grassland habitats to test whether *J. communis* regeneration could be enhanced by ground scarification and /or by summer grazing by cattle. Four study sites in Scotland were used (Table S1 in Appendix S1): 'Dorback', 'Pentland Hills', 'Fungarth' and 'Ballyoukan'. All sites had a population of *J. communis* var. *communis* containing reproductive female bushes growing within upland grassland and/or bracken (*Pteridium aquilinum*) communities. Scarification was applied at Dorback and Pentland Hills in the first year of the trial to produce a patchwork of bare areas with the matrix of unscarified vegetation acted as the control. The trial followed a blocked design (Figure S1 in Appendix S1). Grazing by cattle in the summer was applied annually at Fungarth and Ballyoukan to a target stocking intensity (Table S1 in

Appendix S1). A control area was provided at each site using stock proof fencing (Figure S1 in Appendix S1). Seeds collected from local *J. communis* bushes were sown at a rate of 1600 seeds per m^2 in both treatment and control areas. Seeds were extracted from berries prior to sowing and tested for viability. This was estimated as: 41% (Dorback), 29% (Pentland Hills), 49% (Ballyoukan) and 6% (Fungarth). Germination was assessed annually in all the sown plots. In addition, natural regeneration was assessed by searching a 10 m wide buffer around a sample of female bushes, annually. In the final year of monitoring, a systematic search of the site for *J. communis* seedlings was conducted at Ballyoukan and Fungarth only. Root collar diameter of seedlings was recorded, together with a description of the ground vegetation around each plant. Year of germination was estimated by dividing seedling root collar diameter by annual diameter stem increment figures. Vegetation monitoring was by annual measurements of vegetation height, vascular plant composition, and percentage cover of bare ground, litter and of all ground vegetation and moss species from permanent quadrats (0.25 m x0.25 m). Depending on the complexity of the vegetation, between 80 and 180 quadrats were located on each site, evenly distributed between treatment and control areas and between vegetation types (where within-site differences occurred) (Table S1 in Appendix S1).

Data analysis

We implemented all tests in the package R (version 2.13.1; The R Foundation for Statistical Computing www.R-project.org/). For example: effect of cattle grazing on *J. communis* seedling occurrence at the Fungarth site, was tested using a Welch Two Sample t-test; associations between plant composition and occurrence of *J. communis* seedlings was investigated in a Principal Component Analysis (PCA); the relationship of seedling age with plant composition was tested using general linear models. The PCA was the first stage of the investigation of vegetation characteristics of microsites where regeneration occurred and contained plant composition and cover data (untransformed prior to analysis) from quadrats containing recently regenerated (1 to 2 year old) *J. communis* seedlings and a random sample of the permanent vegetation quadrats of an equivalent area containing no *J. communis* seedlings. In the second stage, we examined the effect of the variables with the strongest loadings on PCA axis 1 and 2 in general linear models with root collar diameter (a proxy for seedling age) as the response variable, for all the quadrats containing regeneration (seedlings ≤1-10 years). We investigated whether the two interventions applied in our trial produced the site condition measures (vegetation height, occurrence of exposed bare ground, and the occurrence of exposed moss cover) associated with regeneration microsites. We used linear mixed effects models to test the effect of scarification treatment on vegetation height and exposed bare ground although due to failure of model convergence, results for the latter have been presented descriptively. Due to failure of model convergence, result for the grazing treatments are presented descriptively.

Results

Site conditions associated with *Juniperus communis* regeneration from the review of regeneration surveys and studies

Results from seventeen regeneration surveys (Appendix S2) and seven management studies (Appendix S3) have been considered in this review and summarised (Table 1). These surveys and studies represent *J. communis* populations occurring on the full range of habitat types species occupies in Britain and other countries in the Atlantic North and the Atlantic Central European environmental zones (lowland dry heathlands, calcareous grasslands, upland pine-birch woodlands, upland acid grasslands and montane/coastal heath).

Results from the from the review of regeneration surveys

The survey methods followed in sixteen of the regeneration surveys was consistent: there was an element of identifying sample units of *J. communis* (usually populations), recording evidence of recent regeneration and providing information about site conditions and the land use/ site management. Regeneration was defined by the presence of juniper individuals estimated to be around five years old or younger although detection of very young (1 to 2 years old) seedlings is noted as difficult (A. Appleyard 2014, Botanical Surveyor, Salisbury, Wiltshire, personal communication). Two regeneration surveys were repeat surveys separated by several decades, a further five were designed to resample historical records and the remainder were generally searches of particular areas of interest e.g. nature reserves (Appendix S2).

Frequency of regeneration was generally low. Reports on eight of the regeneration surveys provide figures for the number of *J. communis* samples containing regeneration out of the total surveyed. These show an occurrence of regeneration in between 5% and 33% (median = 23%) of the sample units, per regeneration survey, respectively (Appendix S2). One further survey provided a cumulative count of 160 seedlings per hectare appearing at one site over the course of three years (Appendix S2). For the remainder of the regeneration surveys, results are descriptive with only the terms ‘very little’, ‘several’ and ‘a few’ used to describe the occurrence of regeneration, or counts of seedlings reported but no area of survey given (Appendix S2). Regeneration appears to relate to parent population size for most habitat types (Table 1) with, for example, minimum populations size of c.50 bushes required for regeneration to occur in upland grassland habitats (Appendix S2). However, where repeat surveys were conducted, a decline in the frequency of regeneration or poor inter-annular seedling survival (P. Woodruffe, A. Appleyard & S. Fitzpatrick 2016, Botanical Surveyors, Salisbury, Wiltshire, personal communication) have been reported for *J. communis* in lowland calcareous grassland but not other habitat types (Appendix S2).

A short sward, and disturbed and bare ground/exposed mineral surface are associated with regeneration in the surveys of *J. communis* on upland grassland, lowland calcareous grassland and dry heathland sites (Table 1; Appendix S2). For *J. communis* populations on upland grassland in Scotland and heathland and grassland sites in Ireland, regeneration appeared to be associated with more nitrogen-limited sites (Appendix S2). On the very poor, dry heathland sites in the Netherlands, there are indications that regeneration is more prevalent on sites with higher base saturation of soil (e.g. 42% compared to 23%) or where there are pockets of higher pH (e.g. mean Hill-Ellenberg R value = 2.4) relative to the acidic surroundings (e.g. mean Hill-Ellenberg R value = 1.4) and also relatively more grass, fewer dwarf shrubs and more early successional mosses (Table 1; Appendix S2). Further, sites with little competition but shaded due to topographical position have been suggested as sites suitable for regeneration indicated by the presence of certain moss (*Hylocomium splendens*) and liverwort (e.g. *Lophozia ventricosa*) species characteristic of young *J. communis* stands (Appendix S3).

Reduced intensity of management (land use and site management) appeared to relate to presence of *J. communis* regeneration in several of the studies. For example reduced intensity of grazing by stock (usually sheep (*Ovis aries*) and cattle (*Bos taurus*) and other herbivores, e.g. rabbits (*Oryctolagus cuniculus*), is associated with regeneration in surveys of *J. communis* on upland grassland, lowland calcareous grassland and dry heathland sites (Table 1; Appendix S2; Appendix S3). Less intensive land management appeared to favour regeneration in open ground *J. communis* populations in Scotland, with regeneration being more frequent on land used for a combination of grazing and game interests rather than where management was for stock grazing only (Table 1; Appendix S2).

Management interventions used to encourage natural regeneration of *Juniperus communis* from the review of management studies

Reports on seven management studies were sourced; these investigated one or more of the following interventions: ground disturbance; reducing vegetation competition; reducing herbivore pressure; and changing soil pH (Table 1; Appendix S3). Three management studies were designed and monitored sufficiently to allow statistical analysis whilst the remaining management studies provided observational data only. Details on the type, extent and duration of interventions aimed at encouraging the regeneration of *J. communis* are given in Appendix S3. Low impact ground disturbance e.g. by turf stripping or scarifying ground by dragging cut *J. communis* bushes increased regeneration for all habitat types in nearly all the management studies (Appendix S3) with failure in one study attributed to the limited area over which interventions were applied and/or poor seed viability (Appendix S3). It has been suggested that greater ground disturbance caused by cultivation is detrimental to survival of regenerating and young *J. communis* bushes (Appendix S3). Reducing vegetation competition through grazing was successful in two management studies on a calcareous grassland site, as *J. communis* seedlings regenerated either in the presence of sheep grazing (Appendix S3) during the summer months or during breaks in the grazing regime (Appendix S3) although seedling height was reduced by grazing. In one study, however, vegetation control by mowing or by herbicide treatment did not enhance recruitment of *J. communis* (Appendix S3). Successful germination, in a trial where seeds were sown on a dry heathland site, was attributed to increasing soil pH by liming yet this intervention did not encourage natural regeneration when applied within the adjacent *J. communis* stand (Appendix S3). In two separate management studies on upland acid grassland sites, reducing herbivore pressure (e.g. by excluding rabbits) was reported to benefit *J. communis* regeneration although the significance of the treatment effects could not be tested (Appendix S3).

The interventions which appeared to promote regeneration most often (in 11 out of 12 surveys/studies) were those involving ground disturbance and reducing vegetation competition from the surrounding sward, particularly where they were applied in a less intensive way e.g. turf stripping rather than cultivation, sheep grazing rather than mowing. Lack of seed supply (or insufficient area over which treatment applied to successfully intercept available seed) was suspected as a cause of treatment failure in several of the management studies.

Germination of directly sown *Juniperus communis* seed in the field trials

Only two *J. communis* seedlings were recorded out of the 8000 (2500 of which were estimated as being viable) sown across all four sites, on both occasions in a scarified patch protected from stock grazing at the Pentland Hills site.

Response of *Juniperus communis* natural regeneration to intervention observed in the field trials

We wanted to evaluate the effect of two interventions (scarification and grazing) on *J.communis* regeneration. No regeneration was recorded from within the areas monitored around the *J. communis* bushes at any of the sites. However, more widely within the site Fungarth, four seedlings (maximum height of 33cm) were found in 2008 and seven more seedlings were found in 2009. This indicated regeneration was occurring so a more widespread, systematic search of the cattle grazing sites was instigated. By 2011, a total of 33 seedlings (approximately 10 seedlings/ha) had been recorded and all at Fungarth; 23 in the grazed and 10 in ungrazed area. The grazing intervention had been applied in 2006. The ten 'seedlings' germinating prior to 2006 are equally distributed between the treatment and control areas. However a comparison of the number of seedling germinating in each of the six years when cattle grazing was applied shows that more *J. communis* seedlings germinating in the treated area compared to the control ($t = 2.60$, $df = 7$, $P = 0.032$, $n = 12$).

Vegetation cover and composition characterising regeneration microsites at one cattle grazed field trial site (Fungarth)

Axis 1 of the PCA bi-plot (Figure 1) describes a continuum from quadrats with a high % cover of moss and herbs and low % cover of grass or *Pteridium aquilinum* to quadrats with a low % cover of moss and herbs and high % cover of grass or *Pteridium aquilinum*. Axis 2 describes quadrats with a vegetation community dominated by *Pteridium aquilinum* to those of the grass dominated community. Quadrats containing *J. communis* seedlings (1 to 2 years old) are associated with higher % cover of moss and form a cluster relatively separate from the samples containing no regeneration. Together axis 1 and 2 explain 46% of the variation. Loading values for the species groups used in the PCA are given in Appendix S4. Regeneration microsites therefore appear to be characterised by an exposed moss cover i.e. a cover of moss that is not overlaid by other ground vegetation. When percentages of plant cover (moss, herbs, grass, *Pteridium aquilinum* (the variables with the strongest loadings on PCA axis 1 and 2) occurring with *J. communis* 'seedlings' up to 10 years old are analysed using general linear models, % moss cover appears as the best explanatory variable of root collar diameter (model with moss having lowest AIC value); 'moss' cover was higher ($F_{1, 27}$ = 10.80, P = 0.003; R^2 = 0.29, n = 29) where the seedlings were younger, as indicated by smaller root collar diameters (Figure 2). 'Moss' cover was negatively correlated with 'grass' cover (correlation coefficient = -0.64). These relationships suggest that there was more than 80% moss cover and very little grass cover present at the regeneration microsites at time of germination. The main moss species were typical of upland acid grassland sites in Britain (e.g. *Rhytidiadelphus squarrosus*, *Pseudoscleropodium purum*, *Pleurozium schreberi* and *Hylocomium splendens*) (Rodwell 1998b).

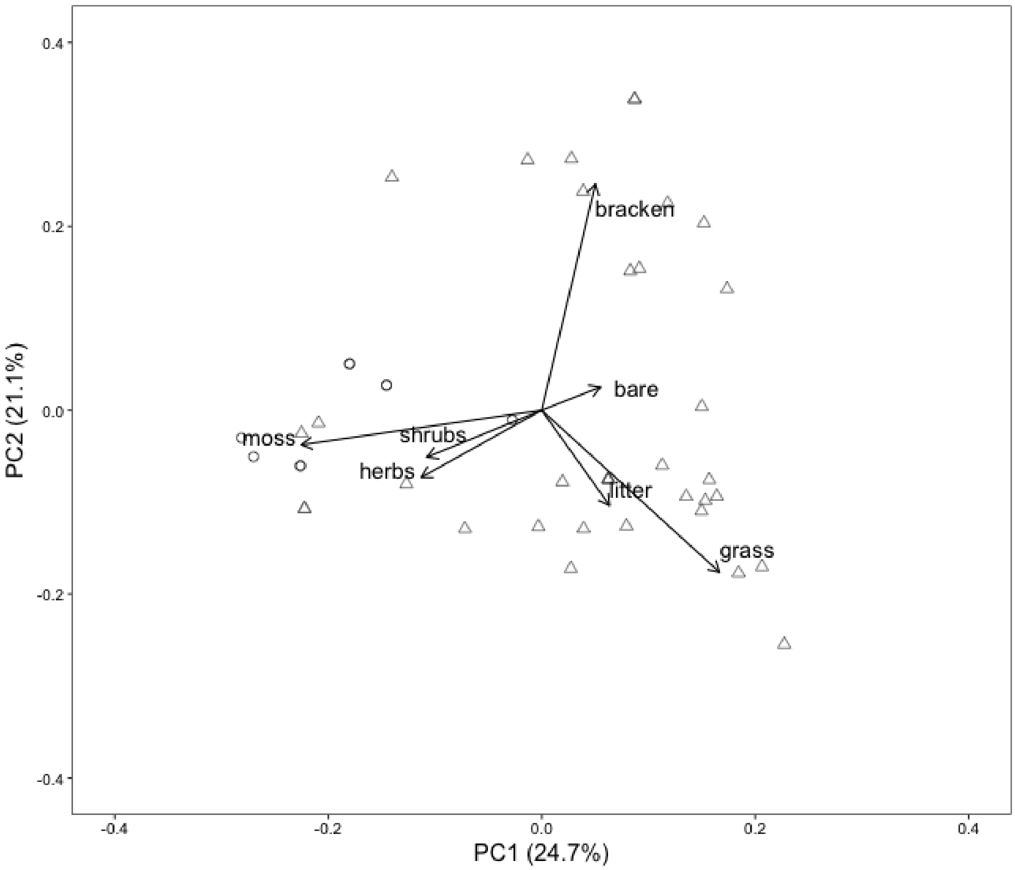

Figure 1: Principal component analysis bi-plot showing the distribution of ground vegetation cover variables at the field trial site, Fungarth (both grazed and ungrazed area), in samples (n = 45) with (○) and without (Δ) *Juniperus communis* natural regeneration; regeneration indicated by the presence of 1 to 2 year old seedlings.

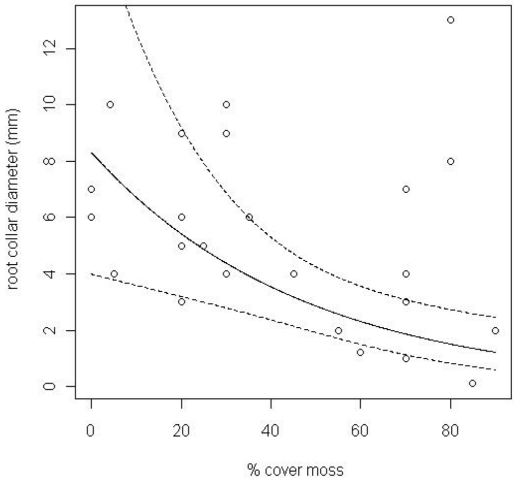

Figure 2: Vegetation composition of the *Juniperus communis* regeneration microsites and root collar diameter of seedlings at the field trial site, Fungarth (both grazed and ungrazed area) in 2011. Vegetation composition described as % cover of all moss species; relationships were analysed using general linear models (solid line indicates the lines of best fit with 95% confidence intervals shown as dashed lines).

Creation of regeneration microsites by scarification and grazing treatments used in the field trial

Scarification produced exposed bare ground microsites which reverted to a grass sward after two and three growing seasons at Pentland Hills and Dorback, respectively (Appendix S5). An exposed moss cover was observed in very few of the quadrats (c.10%) during the re-vegetation process indicating that scarification does not reliably result in a layer of moss covering the ground prior establishment of other ground flora species.

Differences in vegetation height between control and treatment plots were still detectable at Dorback and Pentland Hills after five growing seasons following scarification (ANOVA: $F_{1, 3} = 12.13$, $P = 0.040$, $n = 80$ for Dorback; $F_{1, 3} = 10.67$, $P = 0.047$, $n = 157$ for Pentland Hills). Scarified areas had a mean vegetation height of 6.10 ± 1.14 cm compared to 13.00 ± 1.65 cm in the control at Dorback, and 9.80 ± 2.49 cm in the scarified areas compared to 13.30 ± 2.90 cm in the control at Pentland Hills.

At the grazed sites, exposed bare ground and moss microsites were infrequent (Appendix S6) and although there is some evidence that frequency of exposed bare ground increased in the final year of the trial at Ballyoukan in the grazed area, there appears to be no effect of grazing treatment on frequency of bare ground at Fungarth or exposed moss at either site. Grazing appears to reduce sward height at Ballyoukan, and at Fungarth there is some evidence of grazing causing a reduction in sward height especially in comparison with pre-grazed conditions (Appendix S7).

Discussion

Unlike other parts of Europe (e.g. Alps and Scandinavia) where *J. communis* is in favourable condition (European Commission 2009), *J. communis* sites within Atlantic North and the Atlantic Central European environmental zones require action to perpetuate *J. communis* populations in the face of multiple threats. It is not clear why these regional differences exist but in an attempt to control for variations in wide scale possible influences (e.g. climatic) on *J. communis* regeneration, we examined the options for promoting *J. communis* natural regeneration in the Atlantic North and Atlantic Central zones only. The literature available for synthesis comprised seventeen regeneration surveys and seven management studies. Within these, data are often reported qualitatively or the quality of design and monitoring of the surveys and studies are insufficient to allow statistical analysis of data. As with any seedling survey where abundance is low, detection of infrequent and very young seedlings may be difficult and early stages of regeneration may be under estimated (McCarthy et al. 2013). However, an attempt to synthesise this range of information has not been undertaken before and this study provides insights in to the site conditions and management practices related to successful natural regeneration of *J. communis*. With an aim to strengthen the findings we tested the most suitable candidate interventions identified from the synthesis, in field trials.

Site and microsite conditions associated with *Juniperus communis* regeneration

The microsite conditions of the seed bed appears to be an important factor influencing regeneration of *J. communis* across the range of habitat types it occupies in the Atlantic North and the Atlantic Central zones of Europe. The regeneration surveys and management studies reviewed here indicate that reducing ground vegetation competition either by ground disturbance or lowering vegetation height, resulting in open/unshaded site conditions, are required for regeneration. However, regeneration microsites vary in the different habitat types. In calcareous grassland habitats, a bare surface appears to be the primary requirement for the regeneration of *J. communis* (Appendix S2; Wilkins & Duckworth 2011). Disturbed ground is also required within pine/birch woodland, acid grassland and dry heathland sites (Appendix S2). Microsites where we observed *J. communis* regeneration in the field trials conducted on acid grasslands were characterised by a cover of moss but an absence of taller vegetation. *J.communis* regeneration has been observed associated with a cover of unshaded moss on acid heathland sites and abandoned agricultural land (Falinski 1998; Appendix S2). Presence of a moss cover indicates that microsites must have high humidity at ground level - a requirement shown for *J. communis* regeneration in areas of Europe affected by summer drought (García et al. 1999). Mosses, along with lichens are often the first colonisers of nutrient poor-sites, where *J. communis* seedlings frequently occur (Wells et al. 1976). Moss cover has several positive effects on seed bed conditions, such as ameliorating temperature fluctuations, reducing frost heave as well as maintaining moist conditions (Parker et al. 1997; Groeneveld et al. 2007). The importance of preventing desiccation of seed of *Juniperus* species with extended stratification requirements such as *J. communis,* has long been recognised within the nursery trade (e.g. Heit, 1967). The surface of stones and rock fragments produced when calcareous soils are exposed may also maintain high humidity at the ground surface. Stones can act as mulch, reducing evapotranspiration of soil moisture (e.g. Perez 1998; Ma 2011) or provide a micro-watershed effect, creating suitable conditions for seedling establishment (Livingston 1972). In one survey, regeneration was associated with rock crevices which are assumed to have higher humidity (Appendix S2) and eroding chalk cliffs and limestone outcrops (often created by quarrying) have long been noted as suitable substrates for regeneration (Appendix S2; Grubb 1977; Ward 1981).

Soil fertility (usually reported in the reviewed literature as nitrogen availability and pH) also appears to be an important factor in determining appropriate site and microsite conditions. On acid habitat types, variations in soil fertility, even within a site, affected the occurrence of natural regeneration (Appendix S2). Vegetation studies on acid grassland sites reported that soil fertility affected vegetation succession on cleared ground, with an herbaceous sward as opposed to moss developing on sites with higher nutrient status (Miles 1973). On calcareous sites, the lack of soil in the regeneration microsite results in a relatively lower fertility of the surface material (Wells et al. 1976) and conservation practitioners have observed that on such sites, remaining topsoil acts as a growing medium and seed source for competitive native species, e.g. *Rubus fruticosus* (bramble), which rapidly colonise and shade areas prepared for *J. communis* regeneration (Wilkins & Duckworth 2011; F. Scully 2014, Community & Learning Ranger, National Trust, Guildford, Surrey, personal communication).

Management methods which create site and microsite conditions for *Juniperus communis* regeneration

The findings of this review suggest that management to create regeneration conditions for *J. communis* on all habitat types should aim to reduce competition from surrounding ground vegetation and provide protection from herbivores, primarily rabbits (Appendix S2). Reduced competition was most successfully achieved by manipulating herbivore management or mechanically removing ground vegetation. However, the outcome of applying similar management prescriptions is not always consistent between sites with differing soil fertility and highlights the difficulty of achieving both reduced vegetation competition and herbivore control (Appendix S3). Some evidence suggests that on acid dry heathland intensive disturbance (e.g. by cultivation) creates conditions less suitable for regeneration than the removal of surface litter and vegetation but there is limited evidence from the literature for the appropriate level of intervention on acid, upland grassland sites (Appendix S3). In our trials we tested scarification and cattle grazing in the summer but found they did not reliably enhance the natural regeneration of *J. communis*. Of the two interventions, summer cattle grazing appeared to have more potential for stimulating natural regeneration but confidence in predicting the results of this treatment at other sites is low. Scarification is clearly an inappropriate treatment on upland acid grassland sites. Evidence of creating regeneration microsite conditions by the two management treatments used in the field trials is also lacking. Unlike other studies (Ozols & Ozol 2007; Takala et al. 2012), we failed to show that a prolonged period of cattle grazing in the summer months increased the area of the site dominated by a moss cover. This was despite the partial removal of the bracken canopy by the cattle at our trial site (Fungarth), the effect of which has been linked with moss colonisation in other studies (Novak 2007). We found scarification was ineffective in creating an exposed moss cover that persisted for several years, instead a grass sward rapidly developed. Perhaps failure to develop a moss cover at our trial site was due to soil fertility being too high as a result of increasing nitrogen mineralisation from the soil disturbance (Russell 1961). On calcareous sites the success of management in promoting *J. communis* regeneration appears to be influenced by the depth of soil overlying the calcareous rock (and therefore the fertility of the site), and structure of the surface. Regeneration was reported to occur in a short sward resulting from stock grazing on thin soils in two of the management studies (Appendix S3). These types of sites also appear from the regeneration surveys to be the most suited to producing bare ground microsites by appropriate levels of stock grazing (Appendix S2). However, the experience of conservation practitioners suggests that scarification is a more reliable method of producing microsites which support *J. communis* regeneration particularly when the surface is composed of large chalk fragments (Wilkins & Duckworth 2011; F. Scully 2014, Community & Learning Ranger, National Trust, Guildford, Surrey, personal communication; J.

Carey 2014, Countryside Officer, Bucks County Council, Aylesbury, Buckinghamshire, personal communication). These subtleties of interactions between disturbance type/ intensity, habitat type and site fertility, and development of the correct microsite may help explain the apparent contradictions over management regimes (type, duration and periodicity) which give rise to *J. communis* regeneration.

Wider constraints on *Juniperus communis* regeneration

Land use and site management changes, particularly changes in herbivore management and pressure, are viewed as strong drivers for changes in site suitability (Thomas et al. 2007; Fajhon 2013b). Over the last few centuries changing economic pressures has led to marginal land (often steeper slopes or nutrient poor grassland and heathland which is often associated with *J. communis* regeneration) has been over or under grazed by sheep/cattle, abandoned or ploughed (e.g. Wells et al. 1976; Appendix S3; Ward 1981). There is potential to reinstate grazing or increase protection of sites from herbivores and these types of manipulations have been identified as useful in our synthesis and further tested in the field trials. There have also been wide scale changes in soil fertility over last few decades. These changes have been associated with increased soil nitrogen levels and acidification as a result of atmospheric deposition of ammonia and nitrogen oxides and by sulphur dioxide, respectively, and, although atmospheric deposition levels across Europe are lower than they were 20 years ago, there are still exceedances of critical loads for nitrogen (RoTAP 2012). Where site conditions have changed it may be possible to apply habitat manipulation to develop a seedbed but the causal factors for site change may have wider impacts. Failure to produce viable seed has been linked to high temperatures and nitrogen and sulphur deposition interrupting embryo development (Gruwez et al. 2014). It is possible that at many sites the unsuitability of microsites due to site fertility may indicate more fundamental failures in *J. communis* regeneration.

The importance of an adequate seed supply for successful natural regeneration is supported by the review; all the regeneration surveys which considered population size indicated a positive relationship between population size and regeneration (Appendix S2). All the *J. communis* populations studied in our trial produced berries and viability of sown seed (per population) ranged from 6% to 49%. This would seem adequate for natural regeneration, as Gruwez et al. (2013) reports recruitment at sites with 13% seed viability but no recruitment with 3% seed viability. However, the germination rate was low, with only two of the estimated 2500 viable seeds sown germinating. The absence of germination in our trial may be due to post-dispersal seed predation for example by mice (*Apodemus sylvaticus*) (García et al. 2001). Seedlings may have also been removed by small herbivores (rodents and slugs) before we recorded them; losses reported from other studies can be large, e.g. 6 seedlings out of 10,000 seeds survived the first year (García 2001). In hindsight, it may have been prudent to have provided protection to the patches of sown seed in our trial.

Conclusions

Natural regeneration is a fundamental process in the conservation of plant populations, and for *J. communis*, may be the only conservation option where risk of spread of pathogens e.g. *Phytopthera austracedrae* (Green et al. 2014) from planting stock is high. The focus of this work is on relationships between site conditions and habitat management aimed at the restoration, through natural regeneration, of *J. communis* populations in the parts of NW Europe where the species is declining. By drawing together and adding to the existing body of information, we have further highlighted the difficulty in promoting the natural regeneration of *J. communis*. These findings, however, should be considered in the context of the wider constraints to natural regeneration recognised for *J. communis*: population fragmentation influencing gene flow, senescing/aging parent population and pre-dispersal seed predation causing poor and infrequent seed production, reduced dispersal success and low seed viability.

Site conditions tolerated by the parent bushes of *J. communis* can differ from the microsites required for germination therefore habitat manipulation is required to develop a seedbed. Regeneration microsites need to be open (unshaded by ground vegetation) and provide moist conditions but may vary in appearance in different habitats. In calcareous grasslands, regeneration microsites are stony/bare or vegetation is short or sparse; in upland acid grasslands and dry heathlands microsites are disturbed areas sometimes with a moss cover. Grazing and ground disturbance are two commonly used techniques to create regeneration conditions. However, we found neither treatment to be a reliable intervention for enhancing natural regeneration of *J. communis* in upland acid grassland habitats. Similarly, many regeneration trials reviewed produced inconclusive findings and this synthesis showed mixed results for similar management interventions. No single type and intensity of management intervention appears best in all situations although grazing a site continuously appears inappropriate. Greater knowledge could be gained if more consist and quantifiable methods are used in future management studies and regeneration surveys.

We suggest that where interventions are attempted, the soil fertility as well as the moisture availability and vegetation competition should be considered. For example, on acid grasslands focusing on sites where soil nutrient regime is poor, so that the intervention produces an extended successional stage of moss cover prior to development of a grass sward. Further, protection measures should be included as browsing by herbivores particularly rabbits is associated with failure of *J. communis* to regenerate, and post-dispersal seed predation may also reduce regeneration success. Managers should assess the potential of the site to support regeneration microsites, apply management measures for a minimum of five years, and be prepared to wait longer for results, as regeneration times are long.

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Table 1: Support for the effects of site variables on promoting (Δ) or restricting (▼) regeneration of *Juniperus communis* by habitat type. Number of regeneration surveys (S) or management studies (T) reporting effect are indicated beside triangle. With the exception of Lowland Heathland, soil pH values are drawn from Pyatt et al. 2001 and soil moisture regime (SMR) and soil nutrient regime (SNR) from Pyatt unpubl. 2000 (SNR classes: Very Poor (VP), Poor (P), Medium (M), Very Rich (VR); SMR classes: Moist (M), Fresh (F), slightly Dry (SD)).

Habitat Upland/Lowland		Bare ground/ disturbance	Reduced sward height	Herbivore pressure	Soil nutrient levels	Soil moisture	Parent population size
Lowland calcareous grassland/ scrub (NVC types CG3, CG4 & W21); soil pH = 4.5 -7.5, SMR = F, SNR = VR.	S	Δ^{2}	Δ^{2}	$\blacktriangledown^{2}$ -if no break in stock grazing $\blacktriangledown^{3}$ -if browsing by rabbits Δ^{3} -if grazing intermittent	$\blacktriangledown^{1}$ - better if soil fertility is low Δ^{1} - better if soil pH is higher	Δ^{1} -negative effect of summer drought	Δ^{2} - particularly young bushes and bushes bearing berries
	T	Δ^{1}	Δ^{1}	Δ^{1} -if summer sheep grazing used Δ^{1} -if grazing intermittent			
Lowland heathland (NL/Belgium/ Denmark); soil pH = 3.8-4.8[7,10.]	S	Δ^{2}	Δ^{3}	Δ^{2} -if grazing is managed $\blacktriangledown^{1}$ -if browsing by rabbits	Δ^{2} -with base enrichment of soil		
	T	$\blacktriangledown^{1}$ Δ^{1}			Δ^{1} -with base enrichment of soil.		
Upland acid & mesotrophic grassland/scrub and heathland (UK-NVC type W19 & H15); soil pH = 3-5, SMR = M-F, SNR = VP-M.	S	Δ^{2}	Δ^{1}	Δ^{2} -if fluctuating or in pulses $\blacktriangledown^{4}$ -if exposed to grazing/more extensive landuse	$\blacktriangledown^{2}$ -better on more acidic and nitrogen limited sites	Δ^{2} -layering promoted (bushes propagate by stems touching ground)	Δ^{5}
	T	Δ^{1}		$\blacktriangledown^{2}$ -if stock and rabbits are not excluded			
Pine/birch woodland (UK –NVC type W17/18); soil pH = 3-4, SMR = SD-F, SNR = VP-P.	S				$\blacktriangledown^{1}$ -better on more nitrogen limited sites	Δ^{1}	Δ^{1}
	T	Δ^{1}	Δ^{1}	$\blacktriangledown^{1}$ -small rodents and slugs			

Appendix S1. Methods

Appendix S2. *Juniperus communis* regeneration surveys conducted within the Atlantic North and the Atlantic Central environmental zones of Europe.

Appendix S3. *Juniperus communis* management studies conducted within the Atlantic North and the Atlantic Central environmental zones of Europe.

Appendix S4. Loading values for species groups used in the Principal Component Analysis (Figure 1).

Appendix S5. Change in exposed bare ground over six years at the two trial sites subject to initial scarification treatment.

Appendix S6. Change in occurrence of exposed bare ground and exposed moss cover over six years at the two cattle grazed trial sites.

Appendix S7. Change in vegetation height at the two cattle grazed trial sites.