The future of the Teesdale rarities in a changing climate: How will environmental alterations interact to dictate the persistence of species at their range margins?

HOBBS, JETHRO,FREDERICK,KAY

The future of the Teesdale rarities in a changing climate: How will environmental alterations interact to dictate the persistence of species at their range margins?

By

Jethro Frederick Kay Hobbs

Department of Biosciences,

Durham University,

2020

Submitted for the degree of

Master of Science (by research)

Declaration

Acknowledgements

I would like to extend my sincere gratitude to my supervisor, Dr Bob Baxter, for continual support and advice throughout the course of the project. Thanks are also due to Martin Furnace of Natural England, for help and cooperation with fieldwork.



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1. Background to the study

1.1 Upper Teesdale environment

Within the Upper Teesdale National Nature Reserve, Widdybank Fell (G. R. NY820290), the research location of chapters 1 and 2 in the present study, covers an area of approximately 5.5Km^2 from around 400 to 526.5m asl (Jones, 1973). Along with the adjacent Cronkley fell, the area is renowned for its unique flora assemblage, discussed in the following section. These well documented fells consist of two approximately flat hill tops, within the Northern Pennines Area of Outstanding Natural Beauty (AONB), supporting regularly grazed upland and arctic alpine vegetation.

Being approximately equidistant between the Atlantic Ocean and North Sea, Upper Teesdale experiences a relatively stable, persistently wet climate, with a range of only around 10^{o}C between the average temperatures of the coldest and warmest months (Lewthwaite, 1999). Nevertheless, the area receives prolonged winter snow cover and has been classified as a sub-arctic environment (Bellamy *et al,* 1969).

Such upland habitats across the UK are thought to be some of the most susceptible to climate change (Berry *et al*, 2002). Arctic-alpine vegetation assemblages have thus been predicted to experience range reductions in the UK (Trivedi *et al,* 2008). Persistence of many upland plant species is related to a number of changes to the abiotic environment, such as increased soil erosion and fire risk (House *et al,* 2010), loss of soil carbon and increased flood risk (Orr *et al,* 2008). In addition to the impacts of geophysical and hydrological processes, alterations to weather patterns are also predicted to affect upland species in the UK. Predictions for reduced summer rainfall have raised concerns regarding the longevity of areas of moist blanket peat (Clark *et al,* 2010) and it is suggested that UK upland areas will experience an increase in graminoid vegetation (House *et al,* 2010). In conjunction with the detrimental impacts of anthropogenic processes, such as grazing and frequent change of land use, on native plant species (Stevenson and Thompson, 1993), the effects of future climate change are also predicted to have negative knock-on effects on higher trophic levels (Renwick *et al,* 2012).

Upland areas of the Pennines across northern England, including Widdybank Fell, are largely lacking any tree cover (Cambers, 1974; Lewthwaite, 1999), a state which is maintained by a harsh climate and regular grazing (Squires, 1970; Chambers, 1974; Lewthwaite, 1999). The major resulting habitats types on Widdybank fell are heath, marsh, ombrogenous bog and calcareous grassland (Jones, 1973; Lewthwaite, 1999).

1.2 Teesdale flora

Three species of nationally rare plants were chosen for the present study, *Gentiana verna, Primula farinosa* and *Viola rupestris,* to represent species at the edge of their geographical distributions. *G. verna* is a prostrate, herbaceous evergreen found widely in alpine environments across Europe (Elkington, 1963). *P. farinosa* and *V. rupestris* are perennial rosette-forming herbs, with a primarily boreal and sub-arctic European distributions *V. rupestris* is less low- growing than *P. farinosa* and considerably more branched (Doody, 1975; Hampe and Petit, 2003). They belong to a group of species collectively known as the Teesdale rarities.

The Teesdale flora has been well studied due to the presence of numerous nationally rare plant species. Originally thought to have persisted throughout the last glacial in ice-free regions (Wilmott, 1930 [as cited by Pigott, 1956]), it is now generally accepted that arctic-alpine species recolonised from southern refugia, remaining in cooler areas such as the Teesdale, Craven Pennines, Cwm Idwal, Ben Lawers and the Burren (Pigott, 1956; Gibbons, 1978; Lewthwaite, 1999).

Several species display unique physiologies in Teesdale, and some such as *Dryas octopetala* and *Polygala amorella* resemble alpine and Scandinavian ecotypes respectively with the small leaves associated with cold climates (Pigott, 1956; Gibbons, 1978). *Gentiana verna* reproduces entirely vegetatively in Teesdale (Gibbons, 1978), a feature common at range edges (Beatty et al, 2008). According to it's uniqueness within the UK, the area, under the management of Natural England is a Site of Special Scientific Interest (S.S.S.I). Of particular importance for many of the rare plant species is the Saccharoidal limestone, partially metamorphosed by the Whin Sill igneous intrusion (Fearn, 1973; Lewthwaite, 1999). Low phosphorous availability has also been proposed as a mechanism for maintaining the vegetation species composition of the region (Lewthwaite, 1999; Turner *et al,* 2003). The geology of the area gives rise to a variety of soils within a small area, including the prominent peats, gleyed podsols and calcareous brown earths (Gibbons, 1978). The floral diversity has previously been linked to this heterogenous geomorphology (Johnson *et al,* 1971).

Topographically, the study site on Widdybank fell is unremarkable, consisting of a gently sloping plateau draining in all directions, barring to the north, into the River Tees and its tributaries.

1.3 Introduction to research topics

1.3.1 Cow Green Reservoir

The Cow Green reservoir was constructed on the lower slopes of Widdybank fell during the late 1960s and early 1970s (Vaughn *et al,* 2009). This flooded a portion of the S.S.S.I. classified site (Lewthwaite, 1999), leading to considerable opposition from botanists of the time (Pigott, 1957; Bellamy, 1965 [as cited in Lewthwaite, 1999]).

Due to the thermal inertia of water, lakes can alter local air temperature (Hostetler *et al,* 1994), in the same manner as oceans do (Piccoloroaz *et al,* 2015).

1.3.2 Experimental warming and grazing

In the face of a changing climate, organisms are faced with three main options: track suitable habitat either spatially (Davies & Shaw, 2001; Kelly & Goulden, 2008) or temporally (Badeck *et al,* 2004; Chmielewski & Rötzer, 2001; Richardson *et al,* 2013), adapt to their new environment (Jump & Penuelas, 2005; Aitken *et al,* 2008) or suffer reduced reproductive success (Inouye, 2008; Kudo *et al,* 2004), leading to population decline and ultimately extinction (Thomas *et al,* 2004; Thuiller *et al,* 2005).

Following the methodology adopted by the international tundra experiment (ITEX), the use of open-top passive warming chambers is now common practise for simulating the effect of predicted future increases in air temperature (e.g. Bay, 1996; Welker *et al,* 1997; Sullivan and Welker, 2005). A modification of this methodology was employed in the present study to the same effect.

Grazing is a common feature of Upper Teesdale fells and, consequently, its exclusion has previously been shown to alter the local vegetation dynamics and was observed to effect growth and abundance of less common species (Elkington, 1981; Smith *et al,* 1996).

The interaction between grazing and rising air temperatures is little studied, however, some evidence suggests grazing can reduce negative impact of warming on sward quality and species richness in Tibetan plateau pastures (Klein *et al,* 2004; Klein *et al,* 2007).

Climate change has been linked to the decoupling of trophic interactions (Winder and Schindler, 2004) and the breakdown of mutualistic interactions (Memmott *et al,* 2007). It has also been noted that competitive interactions should be factored into predictions of the ecological impacts of climate change (Brooker, 2006; Clark *et al,* 2011).

Despite this, no study has yet, to my knowledge, attempted to empirically test the effect of increased temperatures on the intensity of interspecific interactions. In the Upper Teesdale assemblages, this is a particularly pertinent line of questioning as low levels of competition are thought to be important for the existence of many of the nationally rare species found here (Marshall, 1971).

1.3.3 Species climate change tracking

While some exceptions have been observed (e.g. Meiszkowska *et al,* 2006; Crimmins *et al,* 2011), it is well established that, as the global climate has warmed, species have tended to shift their ranges higher altitudes and latitudes and to experience advances in spring phenology (Parmesan and Yohe, 2003; Lesica and McCune, 2004; Lenoir *et al,* 2008; Holzinger *et al,* 2008). It has also been observed that the same rates of movement are not experienced across the entire range of a species, leading to net expansions and contractions of species ranges (Anderson *et al,* 2009).

1.3.4 Species distribution modelling

Advances in the capabilities of geographical information systems (GIS) have led to the increasing popularity of species distribution modelling (SDM) for predicting the biogeographical impact of projected climate change (Peterson, 2001). With the application of machine learning algorithms, niche modelling became yet more accessible and moved away from the classical mechanistic model construction towards a correlative approach (Wiley *et al,* 2003). The widespread use of "black-box" computing methods such as the MaxEnt software package (Phillips, 2005) has caused concern that many researchers do not fully understand the assumptions of the models they are creating (Yackulic *et al,* 2013). Nevertheless, the current availability of climate and species distribution data present a wealth of opportunities for predicting ecological responses to projected climate change.

The climate data available is considered by some to be of too coarse a resolution for SDMs (Franklin *et al,* 2013), and the resolution of widely used data sets is often attained by interpolation, rather than direct measurement (e.g. Hijmans *et al,* 2005). In addition to this, microclimate and topography can play a more important role in determining species distributions at the regional scale (Bennie *et al,* 2008). As no fine scale climate data is yet available for Upper Teesdale, it is not possible to predict the future local distribution of the rarities, but inferences can be made about the potential UK distribution from the Europe-wide occurrence data.

1.3.5 Aims of the present study

In order to better inform future conservation efforts, the present study aims to address the following broad research questions regarding the nationally rare relic species:

1. How will a warmer climate affect growth of the study species, and how will this interact with grazing and interspecific competition?
2. How does the Cow green reservoir modify the local climate of Widdybank Fell?
3. How have these species responded to post-industrial increases in temperatures across their European ranges?
4. What dictates distribution of these species, do they exhibit regional adaptation and how will their distribution change in the future?

2. The effects of experimental warming and grazing on Upper Teesdale plant species

2.1 Introduction

2.1.1 Ecological impacts of temperature

Upland and sub-arctic habitats are some of the most susceptible to climate change in the UK (Berry *et al*, 2002). At 54.66˚N, and being above 400m altitude, Widdybank fell is one such area.

The persistence of a species can be determined by: maximum (Richter & Kolmes, 2005), minimum (Woodward, 1988), and variation in (Vasseur, 2014) temperature. Additionally, heat sum of the growing season can be an important factor (Woodward, 1988) as can the duration of the growing season (Galen & Stanton, 1995). Similarly, altered patterns of precipitation caused by a warming climate will affect plant growth, but changes in precipitation are not uniform across the globe so the overall impacts are harder to predict (Trenberth, 2011).

The effects of temperature on photosynthetic rate (Bernacchi *et al,* 2001; Sage and Kubien, 2007; Smith and Dukes, 2013) and biomass accumulation (Criddle *et al,* 1997; Wang and Camp, 2000; Anderson *et al,* 2006) are well established. Although this often depends on the environment a plant is acclimated to (Hikosaka *et al,* 2005; Yamori *et al,* 2014), it was hypothesised that experimental warming would induce greater biomass accumulation, compared to control conditions.

2.1.2 Ecological impacts of grazing

Following anthropogenic forest clearance across prehistoric Britain, grazing pressure, primarily from sheep, has maintained a plagioclimax with few trees in Upper Teesdale (Squires, 1970; Chambers, 1974; Lewthwaite, 1999). Although there is evidence the area was historically home to large herbivores such as elk (Blackburn, 1952), exclusion of grazing on Cronkley fell (adjacent to the location of the present study) has been shown to benefit the nationally rare species *Dryas octopetella* and *Helianthemum canum* by reducing *Festuca sp* and bryophyte cover (Elkington, 1981). In the present study, it was thus hypothesised that the reduced graminoid cover, and resulting decrease in competitive interactions, in simulated grazing plots would lead to greater biomass of the study species. However, conversely, removal of grazing in another working meadow in Upper Teesdale resulted in significantly lower species richness after only 4 years (Smith *et al,* 1996).

The factor most limiting the growth of the Teesdale rarity species is thought to be competition, rather than climatic conditions (Marshall, 1971). For this reason, it was also hypothesised that, in conjunction, experimental warming and grazing simulation will work synergistically to increase biomass accumulation, by both increasing metabolic rate and reducing competition intensity for the study species.

2.1.3 Effects of temperature on competitive interactions

Alteration of ecological interactions by climate change are often overlooked in predictions (Post & Pedersen, 2008), and Suttle et al (2007) argued that the autecological responses commonly investigated are of little significance in the absence of holistic studies. Differential spatial and temporal, i.e. distributional and phenological, responses of species to increasing temperatures often lead to disruption of ecological interactions (Schweiger et al, 2008; Gustine et al, 2017), known as trophic mismatches (Cushing, 1969). A study of over 100 species predicted that serious mismatches will occur, for instance, between plants and pollinators, reducing the duration of co-occurrence (Memmott et al, 2007).

Tansley (1917) famously demonstrated that plants grown in their native environment will outcompete those species which are less well adapted. However, greater investment in seeds from plants grown in more favourable conditions can also convey a greater advantage than local adaptation (Santon and Galen, 1997). As the species studied here are at the less extreme edge of their arctic-alpine distribution, competitor species closer to the centre of their ranges will likely be better suited to the local environment.

There is growing evidence that future climate change will result in increased frequencies of temperature (Bita and Gerats, 2013), water (Porporato *et al*, 2004) and even mineral (Lynch and Clair, 2004) stresses. The stress gradient hypothesis suggests that as abiotic stress increases in a giver environment, the proportion of interspecific interactions that are facilitative will also increase (Maestre *et al,* 2009; He *et al,* 2013). While this hypothesis assumes that all species in a system experience greater abiotic stress, it has been noted that species are more exposed to environmental stressors at their range margins (Vergeer and Kunin, 2013). If species which are not at their range margins, e.g. one of the dominant species on Widdybank Fell, *Sesleria caerulea,* do not experience such high levels of stress as those at their range margins, e.g. the study species, then it follows that these species will become more prosperous and thus offer more competition than facilitation.

It has been noted that some of the alpine plant species found in Upper Teesdale grow well in warmer, lower elevation gardens across the UK. It is suggested that this is the case only because competitor plant species, weeds, are removed (Marshall, 1971). Marshall (1971) also reported that the dominant graminoid species in Upper Teesdale increase biomass accumulation under experimental warming. It was, therefor, hypothesised that experimental warming would increase success of grasses, thus increasing the intensity of competition experienced by the study species in the present study.

2.2 Methodology

2.2.1 Experimental design

Plants of the study species were grown *in-situ*, in either (a) control, (b) simulated grazing or (c) competition removal conditions, with experimentally passively warmed and un-warmed variants of each. Three replicates of each treatment were established as the species emerged, starting on 28/01/2019 for *Gentiana verna* and 16/02/2019 for *Primula farinosa* and *Viola rupestris* and ending on 20/06/2019 for *G. verna* and *P. farinosa* and 26/06/2019 for *V. rupestris*, giving study durations of 140, 121 and 127 days for *G, verna, P farinosa* and *V rupestris* respectively.

Plots for the three species were situated within 200m of each other, all having the same aspect. Soil pH values were 6, 5.7 and 6.3 for the *P. farinosa, V. rupestris* and *G. verna* plots respectively.

2.2.2 Warming procedure

Warming conditions were imposed by the use of conical, open-top passive warming chambers. These were constructed from 1 mm thickness polyethylene tetraphthalate (Wootton Industries Ltd, Rotherham, UK). Chambers had a base diameter of 28 cm, top diameter of 12 cm and a height of 18 cm, to accommodate the small, low-growing study species (Fig 1.1.).

2.2.3 Simulated grazing procedure

Simulation of grazing was achieved by clipping the surrounding graminoid vegetation to a uniform height, as low as possible to the ground surface, without disturbing the target experimental plants. Clipping was repeated approximately twice each month to maintain a constant simulated grazing pressure. Isolation treatments of the target experimental plants were achieved by removing all plant growth at ground level to a radius of 10cm around each individual study plant (one per plot) (Fig 1.2.).

2.2.4 Growth metrics

Plant leaf area, which correlates strongly with biomass (Jonasson, 1988), was used as a non-destructive, repeatable measure of growth of each individual study plant over the course of the experiment. Photographs were taken of target plants against a contrasting white background base plate, using a single-reflex camera (Canon DS126091; Tokyo, Japan) with a 24 – 105mm lens (Cannon; Tokyo, Japan). Base plates were marked with quadrats of a known area, to which extent photographs were cropped (Fig 1.3.a). The camera was supported by a tripod (Manfrotto 055cl; Cassola, Italy), maintaining a position parallel to the baseplate. Using the software package ImageJ (National Institute of Health, Maryland, USA; University of Wisconsin, USA), pixels occupied by the plant were distinguished from those of the baseplate (Fig. 1.3.b), using the Otsu threshold method (see Vala and Baxi, 2013). Results were imported into Excel and the total plant area calculated ([plant pixel number / total pixel number] × quadrat area).

2.2.5 Competition metrics

Competition intensity was determined using the formula:

$$\text{Relative competition intensity} = \frac{(\text{Control plant growth} - \text{Isolated plant growth})}{(\text{Control plant growth} + \text{Isolated plant growth})}$$

This was based on work by Armas *et al* (2004) in which plant mass, a strong correlate of area (Jonasson *et al,* 1988), used in the present study, was originally used. The formula generates positive or negative values, representing facilitative and competitive interactions respectively.

One-way analysis of variance (ANOVA) and Fisher's least significance *post-hoc* analyses were used to test for significant differences between treatment mean values, using SPSS 24 (Armonk, New York, USA).

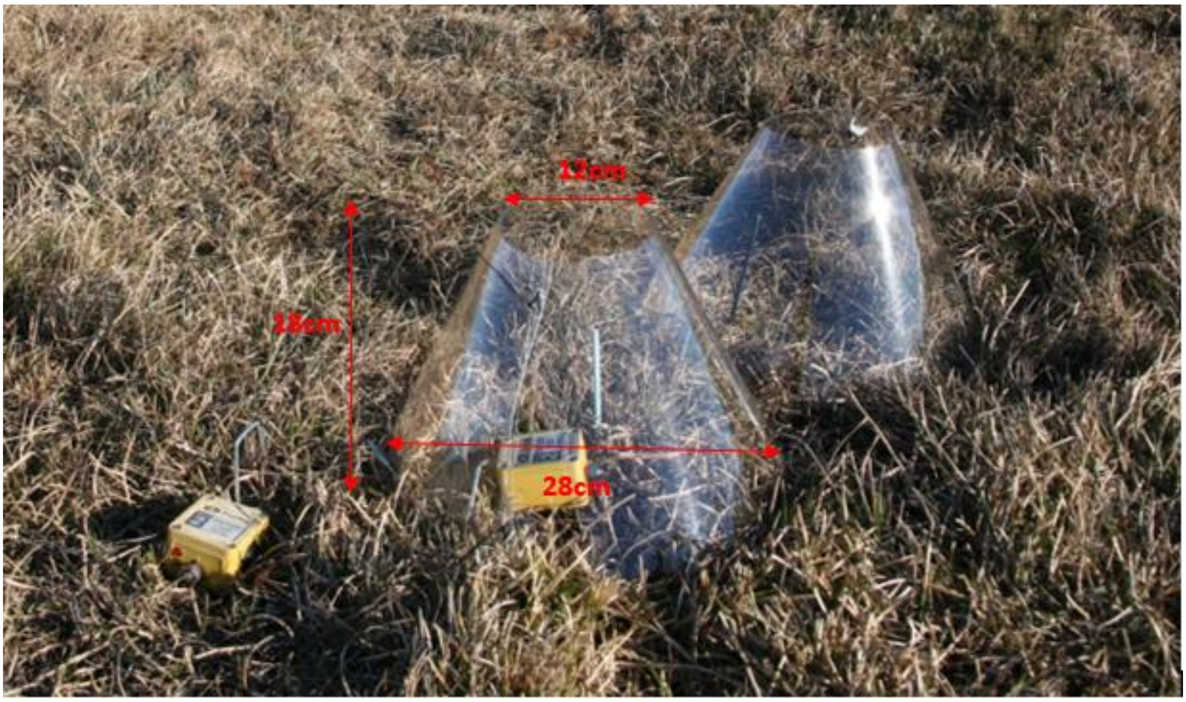

Figure 1.1. Two conical passive open-top warming chambers used on Widdybank fell during the spring of 2019, with dimensions indicated in red.

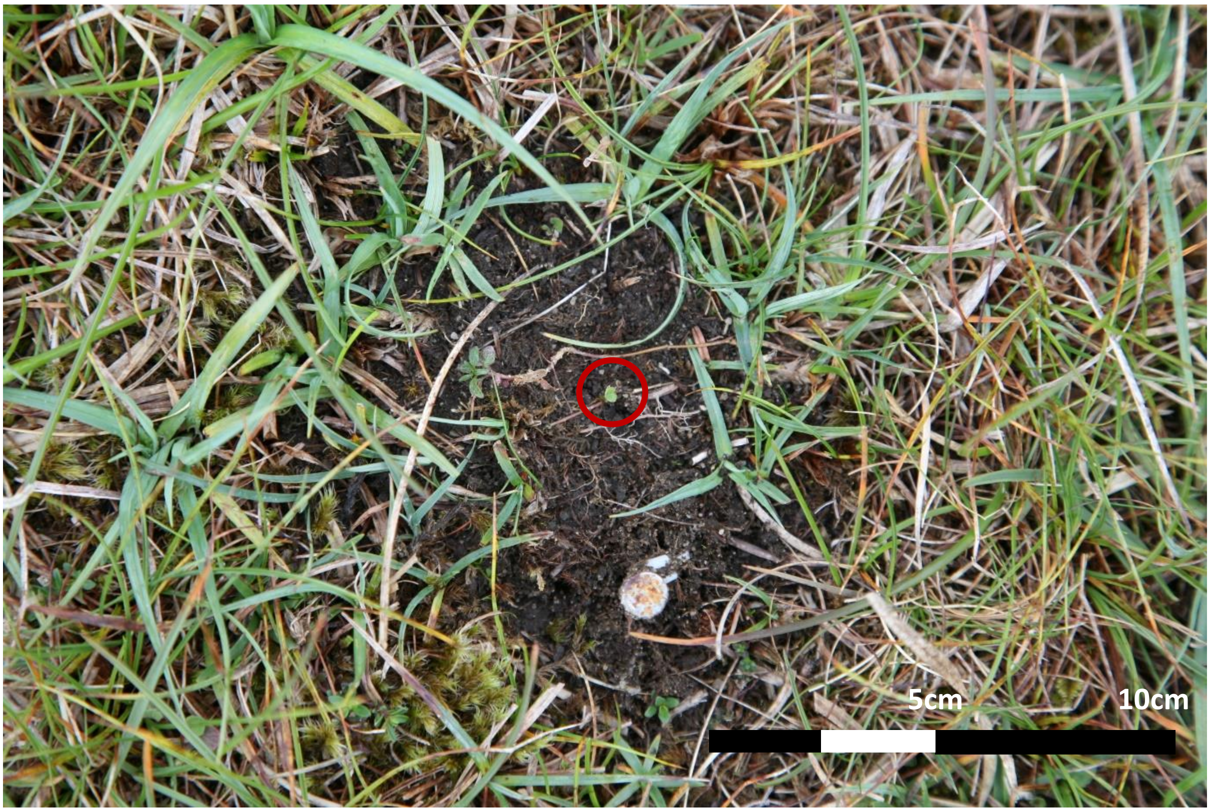

Figure 1.2. An example of a plot with all competitor vegetation removed around *Viola rupestris*, circled, after one month, showing marked graminoid encroachment.

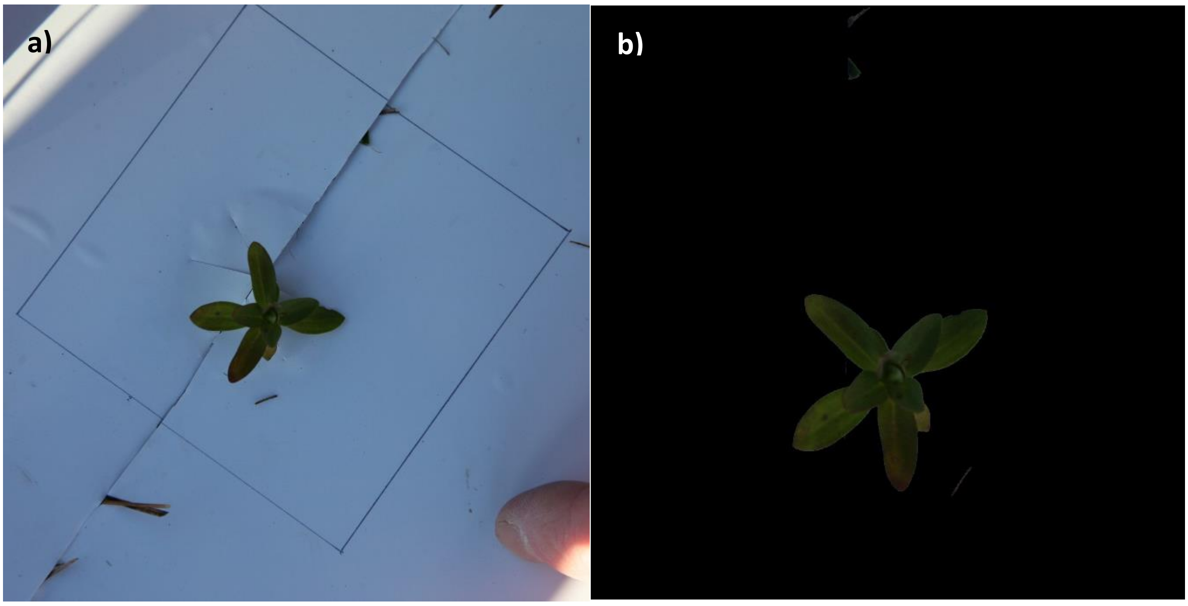

Figure 1.3. a) Unedited image showing a *Gentiana verna* plant against a base plate marked with 100cm^2 quadrat and b) the same image clipped to the extent of the quadrat outline and edited in ImageJ, using the Otsu threshold method, to contrast the plant with the base plate.

2.3 Results

2.3.1 Leaf area responses

No significant difference was found in mean leaf area growth between treatments in *G. verna* ($F_{(3,11)}$ – 1.31, ***P*** > 0.05 [Fig 1.4.c]) or *V. rupestris* ($F_{(3,11)} = 1.23$, ***P*** > 0.05 [Fig 1.4.b]). Warmed *P. farinosa* plants did, however, exhibit mean leaf area growth greater than that of the clipped, un-warmed treatment, but not significantly different from the true control or warmed, clipped treatments ($F_{(3,11)} = 4.02$, ***P*** < 0.05 [Fig 1.4.a]).

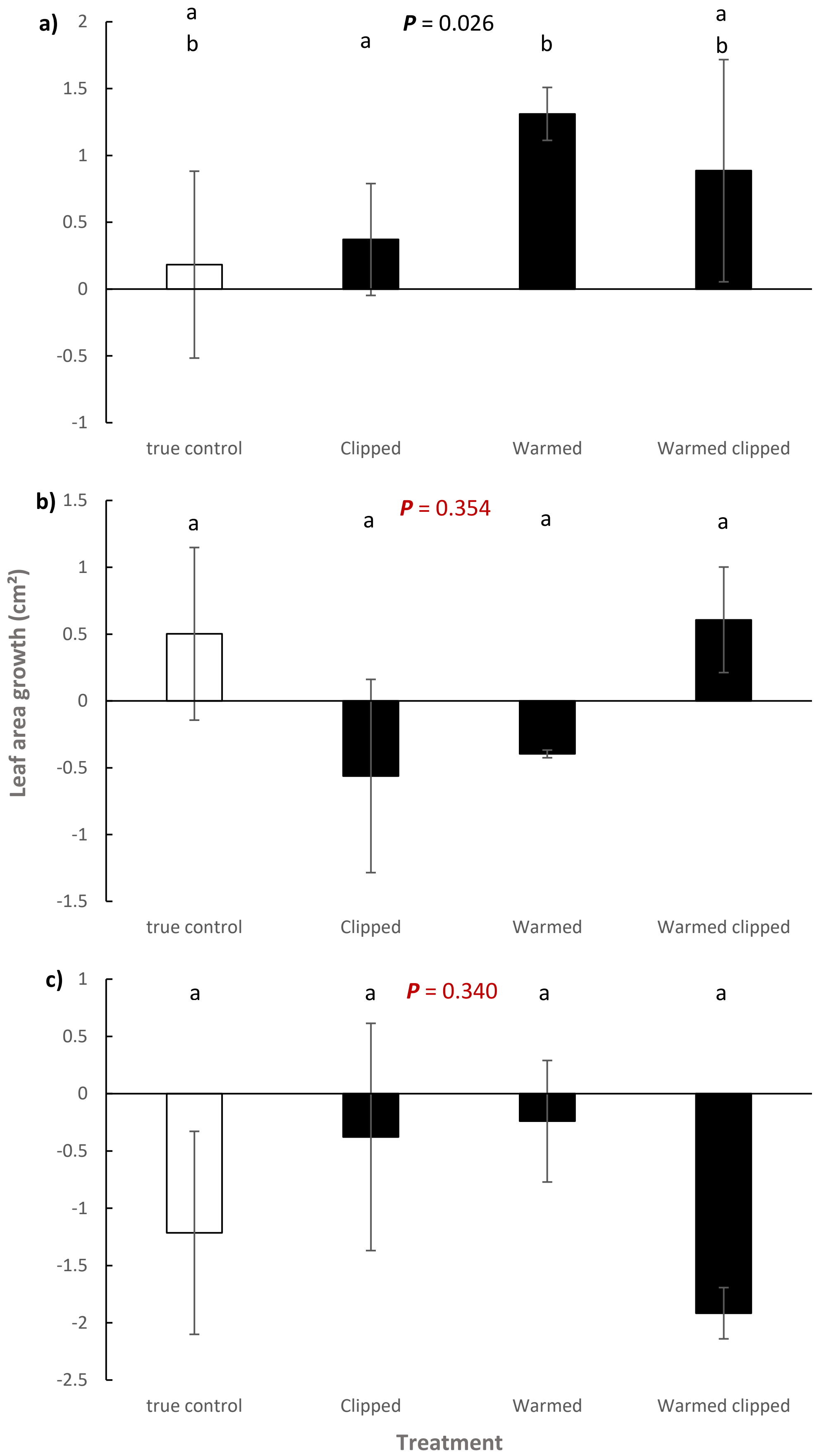
a)
P = 0.026
a
b
a
b
a
b
2
1.5
1
0.5
0
-0.5
-1
true control
Clipped
Warmed
Warmed clipped
b)
P = 0.354
a
a
a
a
1.5
1
0.5
0
-0.5
-1
-1.5
true control
Clipped
Warmed
Warmed clipped
Leaf area growth (cm²)
c)
P = 0.340
a
a
a
a
1
0.5
0
-0.5
-1
-1.5
-2
-2.5
true control
Clipped
Warmed
Warmed clipped
Treatment

Figure 1.4. Mean a) *Primula farinosa,* b) *Viola rupestris* and c) *Gentiana verna* leaf area growth (cm^2) after 79, 83 and 142 days treatment respectively (n = 3 in each treatment). Standard error is indicated by error bars, ***P*** values represent the results of One-way ANOVA. Letters indicate significant differences between treatment means (Fisher's Least significant difference, ***P*** < 0.05).

2.3.2 *Primula* dry biomass accumulation

Mean dry mass of *P. farinosa* was found to be significantly higher after 83 days treatment in all warmed treatments, compared to un-warmed treatments (F (5,17) = 5.74, ***P*** < 0.01 [Fig 1.5.]). No significant differences were found between means of warmed treatments or un-warmed treatments. This demonstrates that the only factor *P. farinosa* responded to was experimental warming.

Relative growth rate (RGR) was not significantly affected by the treatments in the present study for any of the species investigated.

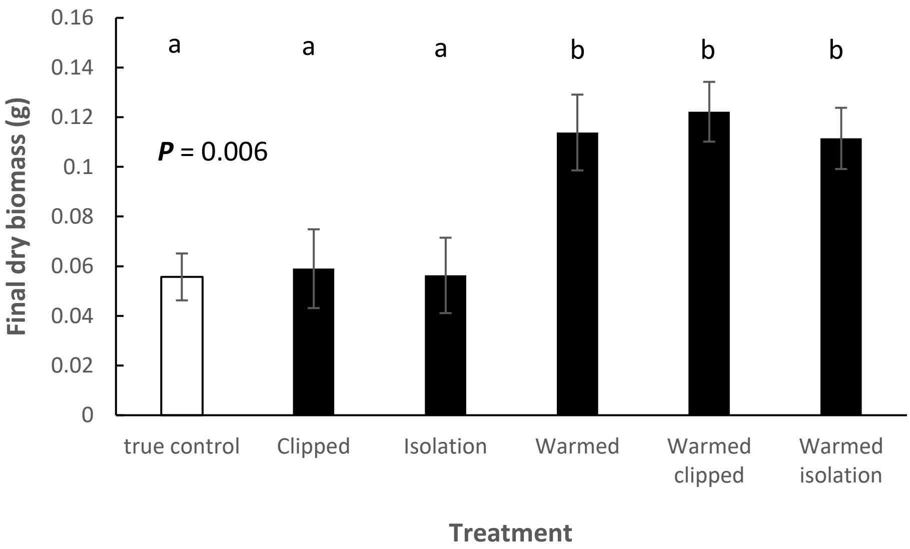

Figure 1.5 Mean dry mass of *P. farinosa* after 83 days treatment (n = 3 in each treatment). Standard error is indicated by error bars and ***P*** value represents the results of one-way ANOVA. Letters indicate statistically significant differences between treatment mean values (Fisher's Least significant difference, ***P*** < 0.05).

2.3.3 Competition intensity

Mean (±SEM) un-warmed interaction intensities in *G. verna* (-0.05 ± 0.41), *P. farinosa* (0.42 ± 0.71) and *V. rupestris* (0.32 ± 0.39) were not significantly different to mean intensities under experimental warming ((0.71 ± 0.69, -0.36 ± 0.14 and 0.80 ± 1.37 respectively) t (4) = - 1.2, ***P*** > 0.05; t (4) = 0.43, ***P*** > 0.05; t (4) = - 0.34, ***P*** > 0.05 [Fig 1.6.]).

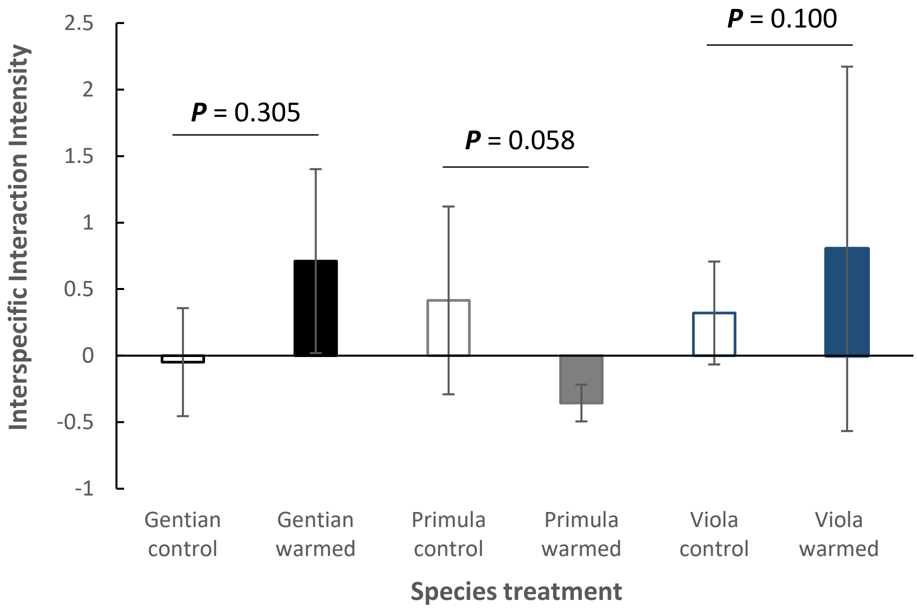

Figure 1.6. Mean relative interaction intensity experienced by *Gentiana verna, Primula farinosa* and *Viola rupestris* under control and experimentally warmed conditions, after 142, 83 and 79 days treatment respectively (N = 3 in each treatment). Standard error is indicated by error bars, ***P*** values represent the results of independent samples t-test.

2.4 Discussion

2.4.1 Effects of warming and grazing simulation

Neither *G. verna* nor *V. rupestris* leaf area showed any significant differences between any of the short-term treatments imposed, indicating that, in the locality, these species are unaffected by warming or grazing simulation or the two in conjunction. *P. farinosa* exhibited significantly higher leaf area in the warmed treatment compared to the un-warmed, clipped treatment. Whilst no differences were found between the un-warmed treatments or the warmed treatments. The absence of any impacts from the grazing simulation in the present study could likely be due to grazed areas becoming more resistant to grazing pressure (Adler *et al,* 2004), whereby the effects of grazing are inversely proportional to historic grazing levels (Cingolani *et al,* 2005).

Leaf area production per plant was chosen as a plant growth parameter as it may be more pertinent to the competitive success of a plant than simple biomass measurements i.e. it reflects the area of land in which a plant has successfully outcompeted the surrounding vegetation. This assumption was based upon the phenomenon of plants that take up a larger amount of space tending to be competitively dominant (Schwinning and Weiner, 1998) and leaf area strongly predicting competition, for example, from weed plants amongst crops (Kropff and Spitters, 1991). It is, however, likely that the final leaf area measurements of the present study were taken too late in the season, as late growing season leaf senescence resulted in negative growth values in some instances.

It is important to note that whilst the chambers raised the mean air temperature, a plants persistence can be determined by the temperature extremes (Woodward, 1988; Richter and Kolmes, 2005) or the duration of the growing season (Galen and Stanton, 1995).

Whilst total leaf area is not a true measure of a plant’s productivity, point intercept data correlate strongly with plant biomass (Jonasson 1988). As pixel-based analysis is effectively a very high-resolution variation of the point quadrat methodology, this was opted for as a non-destructive sampling method. Whilst some criticisms have been made of pixel analysis methods, for instance, regarding uneven reflectance and shadow casting (Rich, 1990), the major variable with the potential to affect image capture in the field, illumination intensity, has been shown to have little effect on analysis results (Leister *et al,* 1999).

For *P. farinosa,* all warmed treatments had significantly higher end of growing season mean dry masses than the un-warmed treatments, whilst no significant differences were found within either the warmed or un-warmed treatments. This indicates that *P. farinosa* biomass accumulation benefits from experimental warming, whilst grazing has no observable effects. The positive effects on *P. farinosa* dry matter production observed, could be due to little alteration in competition due to its sparsely vegetated surroundings (Fig. 1.7).

Figure 1.7 An example of the sparse vegetation ground cover typical of the areas in which *Primula farinosa,* circled, is found on Widdybank fell.

2.4.2 Effects of experimental warming on competition intensity

No significant differences were found in competition intensity under warmed and un-warmed conditions in any of the species investigated. This is perhaps surprising, as a fundamental prediction of the Lotka-Volterra competition models is that ecological perturbations will lead to changes in species interactions (Khasminskii and Klebaner 2001; Lui and Chen, 2003). It has previously been noted that both the intensity and importance of competition increases with system productivity (Sammul *et al,* 2000), which may explain the lack of any response in the relatively unproductive uplands of Teesdale. It should be noted, however, that the difference between mean interaction intensity for warmed and unwarmed *P. farinosa* was only marginally non-significant and a clear negative effect of competition was observed under experimental warming. This suggests that, with further replication, detrimental impacts of warming may be established, as would be anticipated for a species as the lower, colder, extreme of its range.

The non-significant changes in competition intensity recorded are due to removal of competitors having no positive or negative detectable impact on growth. This suggests that the plants are limited by an environmental factor other than competitive interactions. In the case of *P. farinosa* this may well be temperature as chambers had a clear positive effect on their growth, however *G. verna* and *V. rupestris* are apparently limited by some other factor. Whilst warming did not affect growth of these latter species, it is important to note that they are already at the lower limit, in terms of latitude or altitude, of their respective ranges. These are the regions predicted to be lost from species ranges

under climatic warming (Thuiller *et al,* 2008; Levin, 2011), so the species are likely not to benefit from increased temperatures here, where the environment is becoming potentially more favourable for species from lower latitudes and elevations (Van Grunsven *et al,* 2011; Telwala *et al,* 2013).
The theoretical increase in abiotic stress generated by a warmed climate (Porporato *et al*, 2004; Lynch and Clair, 2004; Bita and Gerats, 2013) appears to have had no impact on facilitative interactions either, as would be predicted by the stress-gradient hypothesis (Maestre *et al,* 2009; He *et al,* 2013). It is, however, worth noting that, while the chambers effectively increased temperatures, they have no impact on the surrounding area. This may lead to an influx of natural water or nutrient levels from the surrounding, un-warmed, areas which may have otherwise been altered by natural climate change.

The fact that the species studied here are at their range margins could also impact the findings in terms of local adaptation, which is thought to confer greater resistance to climate change and competition to individuals at the edge of their ranges (Sagarin and Gaines, 2006).

Relative interaction intensity (RII), a measure of the strength of competitive or facilitative interactions, is thought to be the most suitable metric for plants (Aramas *et al,* 2004). This measure was opted for in the present study, as competition intensity values can be derived easily from simple removal experiments.

On average, humidity was 1.92 % lower in the chamber warmed, removal plot than in the chamber warmed control plot and 5.64 % lower in the un-warmed removal plot compared to the un-warmed control plot. Most probably due to the removal of bryophyte ground cover, this may have negatively impacted the plants in the removal plots, working antagonistically with the intended effects of competitive release. The RII metric used measures both the strength of competitive and facilitative interactions, however no statistically significant negative effects of bryophyte removal were observed.

2.4.3 Warming chamber efficacy

Chambers raised the mean ground-level air temperature by 1.3 °C and reduced relative humidity by 1.5 %, whilst soil temperature and air temperature variance were not affected. The confounding decrease in humidity, associated primarily with shelter from precipitation, is an established phenomenon for any open-top chamber (OTC) design (Wookey *et al*, 1993).

Aside from the effects on mean temperature, OTCs have been shown to cause around a 25 % decrease in freeze-thaw events (Bokhorst *et al,* 2011) and can increase snow cover duration (Wipf and Rixen, 2010).

OTCs are also known to decrease photosynthetically active radiation (PAR) wavelengths reaching plants, through light attenuation of the clear plastic materials used in chamber construction (Debevec and MacLean, 1993). However, Day *et al* (1999) found Polyethylene tetraphthalate (PET) to cause only an 11-12 % reduction, and conical chambers, as used here, tend to have a smaller effect than more common hexagonal designs (Slade and Roslin, 2016). Nevertheless, this still introduces an inherently confounding variable into all chambered treatments, which will receive only around 90 % of the PAR received by unwarmed treatments.

OTCs minimise environmental confounding variables (Marion *et al,* 1997), and are believed to be a more realistic representation of climate warming than closed top chambers (Bokhorst *et al,* 2011). Additionally, they create more natural concentrations of atmospheric carbon dioxide and humidity within the vegetation layer due to the opportunity to continually exchange air with the open lower atmosphere above (Slade and Roslin, 2016).

2.4.4 Implications of the study

Overall, warming and grazing did not appear to have any observable effects on the growth of the study species and not impact of warming was found on competition intensity. Future controlled grazing experiments, both in winter and spring-autumn, could benefit the overall study of the potential future of the Teesdale flora. Further work would also benefit from investigating the effects of vegetation warming on overall reproductive output as well as the allocation of resources to growth *versus* reproduction, to better understand the effects of grazing and warming on future population longevity. It is also clear that the results generated herein had low statistical power and more replicates would be needed to truly establish the ecological effects of *in-situ* experimental manipulations.

3. The effects of reservoir proximity on the temperature environment pf Widdybank Fell

3.1 Introduction

3.1.1 The Cow Green reservoir

Filled during the autumn of 1971 (Lewthwaite, 1999), the Cow green reservoir in upper Teesdale was constructed to fulfil the growing water demand of industrial towns in the Teesside area (Kennard and Reader, 1975). The reservoir has a maximum depth of only around 25m (Kennard and Reader, 1975), but a comparatively high capacity of 40.9Mm^3 (McCulloch, 2004).

Although the construction was sanctioned by parliament, the reservoir was subject to considerable opposition due to the planned partial flooding of the site of special scientific interest (S.S.S.I.) at Widdybank fell (Lewthwaite, 1999). It was also suggested that the reservoir could alter the local climate, threatening the nationally rare plant species present on the remaining portion of the fell (Bellamy, 1965 [as cited in Lewthwaite, 1999]; Bradshaw, 1966 [as cited in Lewthwaite, 1999]).

3.1.2 The effect of waterbodies on their surrounding environment

Lakes interact with their surrounding environment in several ways, including atmospheric gas exchange (Potes *et al,* 2017), alteration of local wind and precipitation patterns (Hjelmfelt and Braham, 1983) and by acting as dispersal barriers to terrestrial organisms (Houle, 1998).

One of the most important land-water interactions if the net import of nutrients by lakes from the surrounding land (Duchesne *et al,* 2001). However, seasonally, soils may receive a net nitrogen input from water bodies as is the case during spawning events of anadromous salmonids (Helfield and Naiman, 2001). The link between dam construction and inhibition of anadromous migration is intuitive and well established (Larinier, 2000).

Natural lakes differ from reservoirs in terms of surface versus sub-surface water discharge (Kennedy and Walker, 1990), it is suggested that reservoirs will thus disperse nutrients and store heat to a greater extent (Wright, 1967 [as cited in Kennedy and Walker, 1990).

Much like the ocean, lakes are known to moderate the temperature of surrounding land (Hostetler et al, 1994), by means of their high thermal inertia (Piccolroaz et al, 2015). Lakes are thus net heat exporters during the winter months (Haginoya et al, 2009) as are regions containing many lakes (Jeffries et al, 1999). This phenomenon has long been known to be correlated with both lake area and depth (Gorham, 1964). Similarly, coastal areas have been shown to exhibit smaller fluctuations in air temperature diurnally, as well as seasonally (Scheitlin, 2013). Due to their thermal inertia, lake temperatures tend to lag behind air temperatures of the surrounding area, causing the effect on seasonality mentioned above (Lenters *et al,* 2005)

The Cow green reservoir has been shown to have increased invertebrate biomass due to nutrient enrichment (Armitage, 1976), increased fish size and reduced fecundity due to alterations to phenology (Crisp et al, 1983) and facilitated upstream expansion of submerged angiosperms due to slower, less variable flow rates (Holmes and Whitton, 1977). Approximately 35 years after its construction, faunal changes were still more pronounced in the dammed river Tees than in the adjacent, unaltered, Maize beck (Armitage, 2006).

As the land surrounding the Cow green reservoir is composed largely of organic peat soils (Turnar *et al,* 1973), the area leaches humic acids into the reservoir water (Turner *et al,* 2003). In humic lakes with low levels of light transmission, the portion of the lake exchanging heat energy with the atmosphere, the epilimnion, is smaler than in clear water lakes, leading to a lesser effect on the local climate (Heiskanen *et al,* 2015). However, the Cow green reservoir rarely develops such thermal stratification (Crisp *et al,* 1977).

3.1.3 Ecological effects of lakes on their surrounding environment

While the ecological effects of the reservoir on the aquatic biota is well studied, little is known of the effect on the terrestrial vegetation. In a paper by Huntley et al (1998), winter heat export was observed from the Cow Green reservoir in the upper Teesdale, and a 0.25˚C moderation of maximum and minimum temperatures was recorded in the 27 years since its construction. Crucially for the local vegetation, grass temperature minima were significantly moderated and snow cover significantly reduced, but no effect was observed on daily temperature ranges. Huntly et al (1998) concluded that the reservoir construction was the only cause to which shifts in vegetation could be attributed since the earlier work by Jones (1973). It is hypothesised that mean daily temperature will be higher, and variation in temperature will be smaller, closer to the edge of the Cow Green reservoir.

Growing degree days (herein, GDDs) are a measure of heat accumulation during the growing season (McMaster and Wilhelm, 1997) commonly used to predict the timing of growth and reproductive events in crop plants (Worthington and Hutchinson, 2005).

Based on the above literature, the following hypotheses were developed regarding the Cow Green reservoir.

1. Mean winter temperature will be higher closer to the reservoir.
2. Temperature range will be smaller closer to the reservoir.
3. Minimum temperature nearer to the reservoir will lag behind minimum temperatures experienced further from the reservoir.
4. Minimum temperatures experienced will be less severe closer to the reservoir.

3.2 Methodology

3.2.1 Temperature data collection

To assess the impact of lake proximity on the winter and early spring temperature environment at grass canopy height, a transect of Tinytag temperature loggers (Gemini data loggers, Chichester, UK) was setup (Fig 1). Spanning a distance of approximately 1.4Km east of the high-water mark of the Cow green reservoir, the loggers ran for the period November 7th to April 15th, 2018 to 2019. This gave a continuous dataset for the winter and transition into the growing season. Loggers were placed in patches of uniform vegetation type (calcareous lowland grassland of the Festuco-Brometea nodum, (see Jones 1973)), which did not exhibit any topographical discontinuities such as depressions or severe slope angles i.e. in a uniform orientation over an altitude range of 495 to 520m.a.s.l. Efforts were made to deploy loggers at regular intervals, within these constraints. The distance between loggers was reduced within 0.5Km of the reservoir high-water mark, in order to increase data resolution for this region, where the impact of the reservoir was expected to be more pronounced. Loggers were set to record the maximum, minimum and hourly temperatures, from which mean temperature, mean daily temperature range, growing degree day (GDD) sum, mean temperature at 11p.m. and number of frost days were calculated.

3.2.2 Data analysis

The data set was divided into early winter, 7th November to 31st December, 2018, and spring, 1th March to 15th May, 2019, in order to test if the lakes effects were seasonal.

A frost day was defined as any day during which the temperature dropped below 0˚C at least once. This represents air frost, but at ground level, rather than at the standard height of a meteorological station, 1.25m (https://www.metoffice.gov.uk/weather/guides/observations/how-we-measure-temperature).

The following formula was used to calculate growing degree days:

$$\text{GDD} = \left[\frac{\text{Maximum daily temperature + Minimum daily temperature}}{2}\right] - \text{Base temperature}$$

The sum of these daily values is then calculated for the period in question, usually the full growing season, to ascertain the total heat units experienced by a plant (McMaster and Wilhelm, 1997). The base temperature represents the temperature value below which the plant in question is unable to grow (Miller *et al,* 2001). In this study, a GDD base temperature of 2˚C was used, based on reports of minimum temperature requirements of 0 – 4.5 ˚C for floristically similar environments in Italian mountain pastures at 600-1600m asl (Romano *et al,* 2014).

The mean time of day at which the minimum daily temperature was recorded for each logger was determined and temperature measured daily at 11p.m. was used to represent the coldest period of each day.

Data from one, potentially faulty, logger was judged to be outlying, reporting 13 fewer frost days than the mean (s.d. 4.15), and 15 days fewer than predicted by linear regression for its distance from the reservoir. The logger data were thus subsequently removed from all analyses.

Linear regression analyses were used to test for relationships between distance from the reservoir and the temperature variables described using SPSS 24 (Armonk, New York, USA).

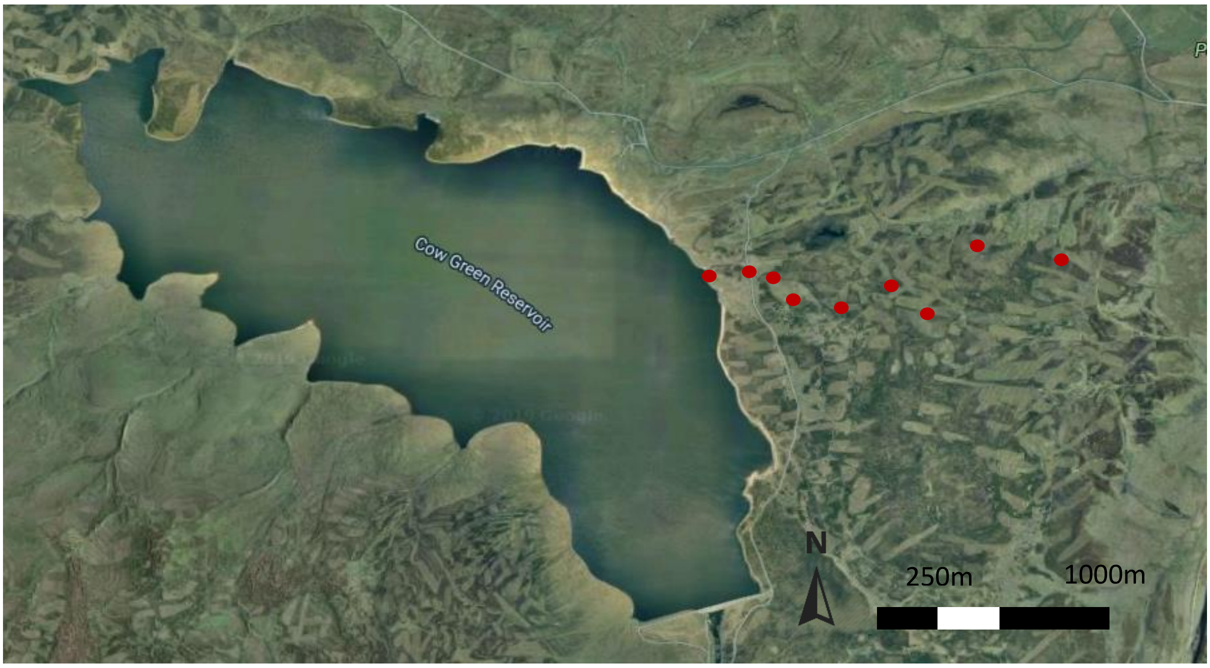

Figure 2.1. Points indicate the locations of data loggers, note some points represent multiple loggers in close proximity. Satellite imagery sourced from Google maps (https://www.google.com/maps), accessed 29/08/2019.

3.3 Results

3.3.1 Mean temperature

No significant relationship was found between distance from the reservoir edge and mean winter to spring temperature ($F(1,13) = 0.13$, $\boldsymbol{P} > 0.05$, $R^2 = 0.01$ [Fig 2.2.]), mean winter to spring daily temperature range ($F(1,13) < 0.01$, $\boldsymbol{P} > 0.05$, $R^2 = 0.01$ [(Fig 2.3.]) or winter to spring growing degree day sum ($F(1,13) = 0.25$, $\boldsymbol{P} > 0.05$, $R^2 = 0.14$ [Fig 2.4.]).

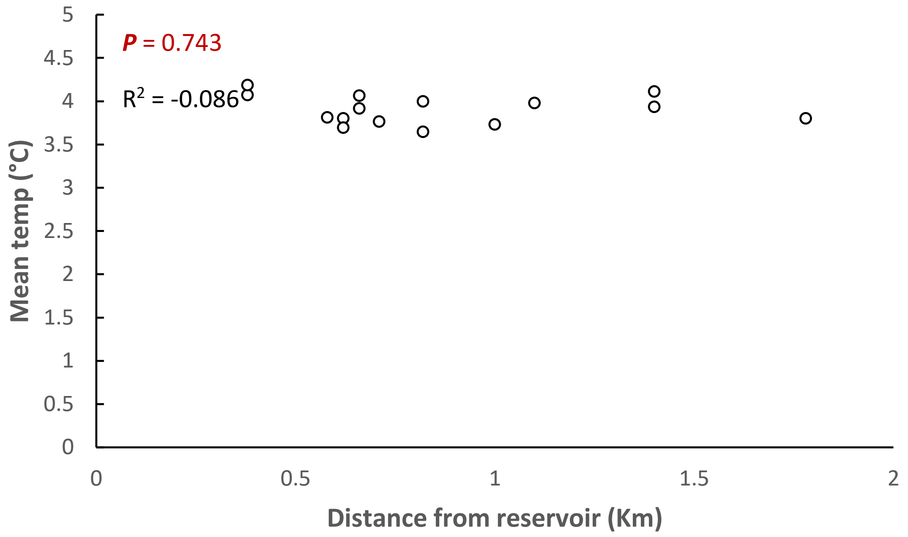

Figure 2.2. Relationship between distance from reservoir edge and mean winter to spring temperature, recorded over the period 07/11/18 to 14/05/19 (n = 15). ***P*** and R^2 values indicate the results of linear regression

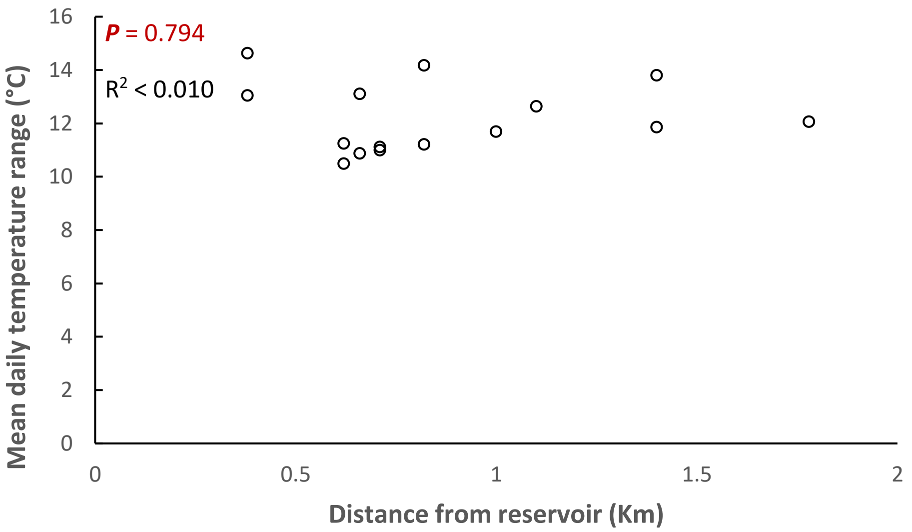

Figure 2.3. Relationship between distance from reservoir edge and winter to spring mean daily temperature range, recorded over the period 07/11/18 to 14/05/19 (n = 15). ***P*** and R^2 values indicate the results of linear regression.

3.3.2 Growing degree days (GDDs)

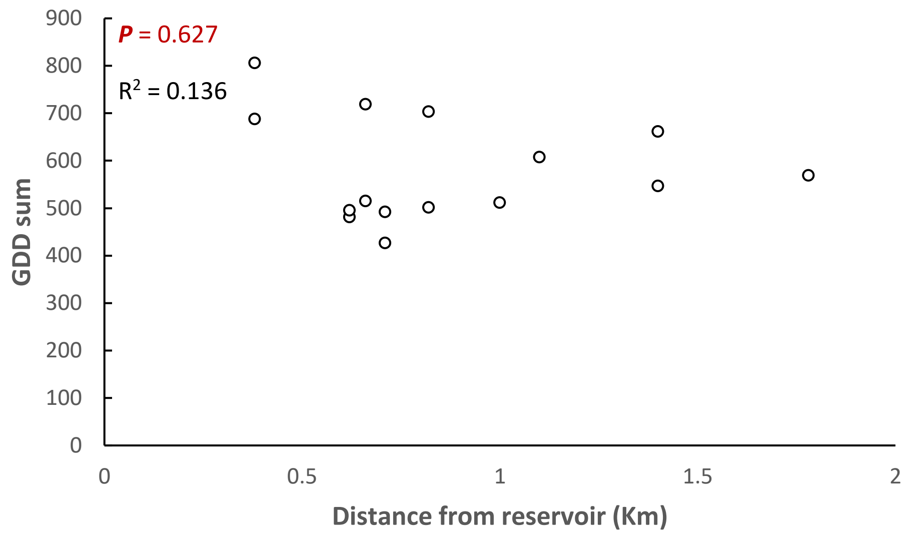

Figure 2.4. Relationship between distance from reservoir edge and winter to spring growing degree day sum, recorded over the period 07/11/18 to 14/05/19 (n = 15). P and R^2 values indicate the results of linear regression.

3.3.3 Temperature minima

Mean 11 pm temperature (taken to represent the coldest time of each day (see Fig. 2.7.)), of the 2018 to 2019 winter to spring transition, showed a significant linear relationship with distance from the reservoir ($F(1,13)$ 11.20, $P \leq 0.005$, $R^2 = 0.46$ [Fig. 2.5.]). This illustrates that sites further from the reservoir tended to experience colder temperatures during this period of the night, equating to a moderation of 11 pm temperatures of around 0.4°C at the reservoir edge, compared to 1.4 Km from its edge.

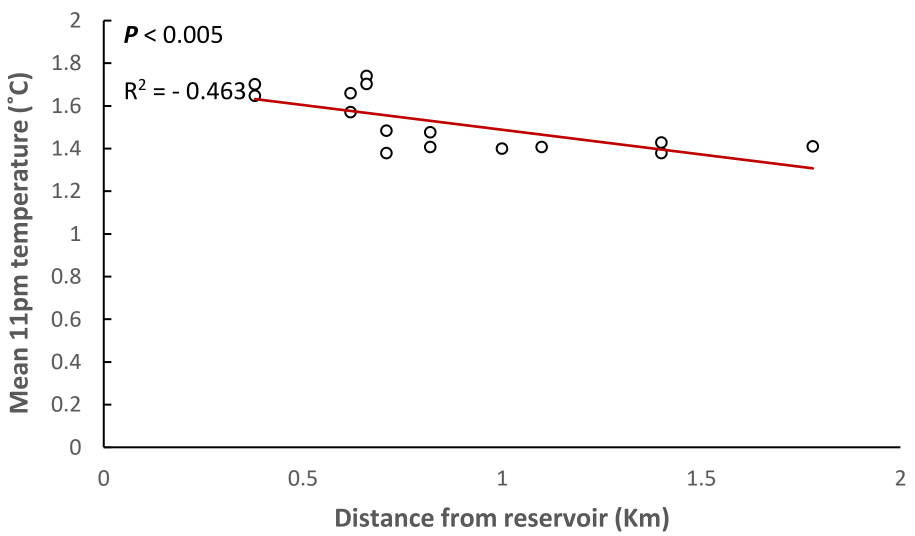

Figure 2.5. Relationship between distance from reservoir edge and winter to spring mean 11 pm temperature, recorded over the period 07/11/18 to 14/05/19 (n = 15). P and R^2 values indicate the results of linear regression and trend line is calculated using least squares method.

Total number of frost days recorded on Widdybank fell (Fig 2.6.) was significantly related to distance from the reservoir (F(1,13) = 8.10, ***P*** < 0.05, R^2 = 0.38). Sites further from the reservoir thus tended to experience more days (approximately 5 days more at 1.4 Km from the reservoir compared to its edge) with frost at ground level.

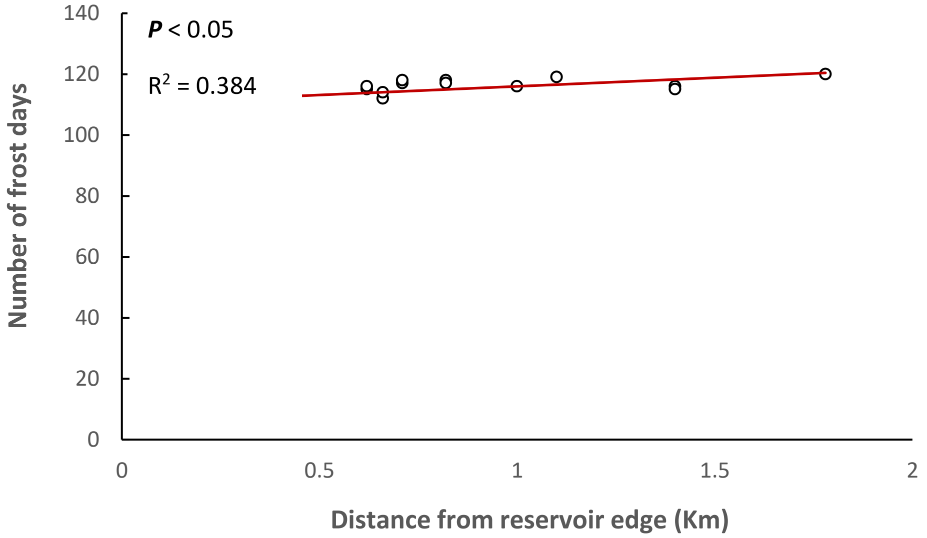

Figure 2.6. Relationship between distance from reservoir edge and winter to spring number of frost days recorded, recorded over the period 07/11/18 to 14/05/19 (n = 15). ***P*** and R^2 values indicate the results of linear regression and trend line is calculated using least squares method.

3.3.4 Temperature lag and seasonality

No significant relationship was found between distance from the reservoir and the time of day at which the minimum daily temperature was recorded (F (1,13) < 0.01, ***P*** > 0.05, R^2 < 0.001 [Fig 2.7.]).

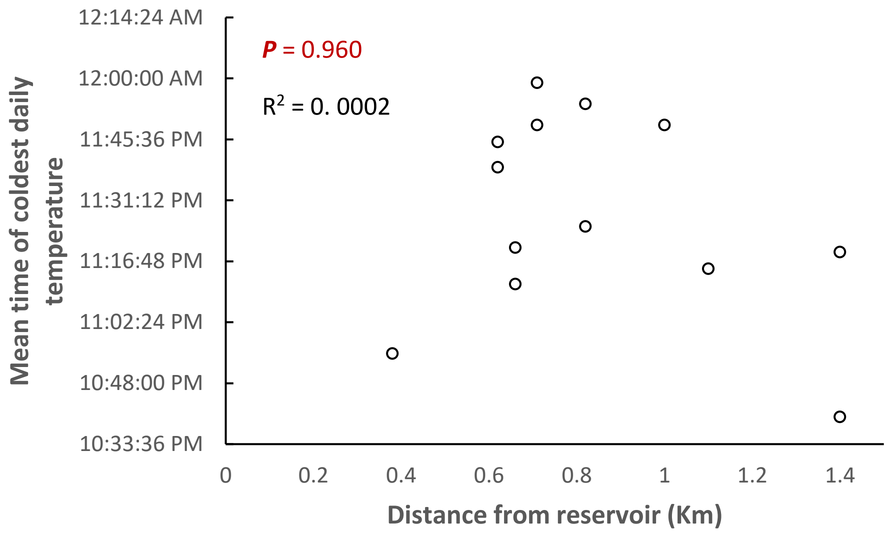

Figure 2.7. Relationship between distance from reservoir edge and mean time of day at which minimum temperature was recorded, recorded over the period 07/11/18 to 14/05/19 (n = 15). ***P*** and R^2 values represent the results of linear regression.

A significant relationship was found between mean winter temperature and distance from the reservoir (F (1,13) = 7.70, ***P*** < 0.05, R^2 = 0.37 [Fig 2.8.a]), but no such relationship was found for mean spring temperature (F (1,13) = 0.67, ***P*** = 0.43, R^2 = 0.05 [Fig 2.8.b]). This indicates that the lake exerts a warming effect of around 1.5°C, over the distance of 1.4Km, during the winter months, but no effect during the spring.

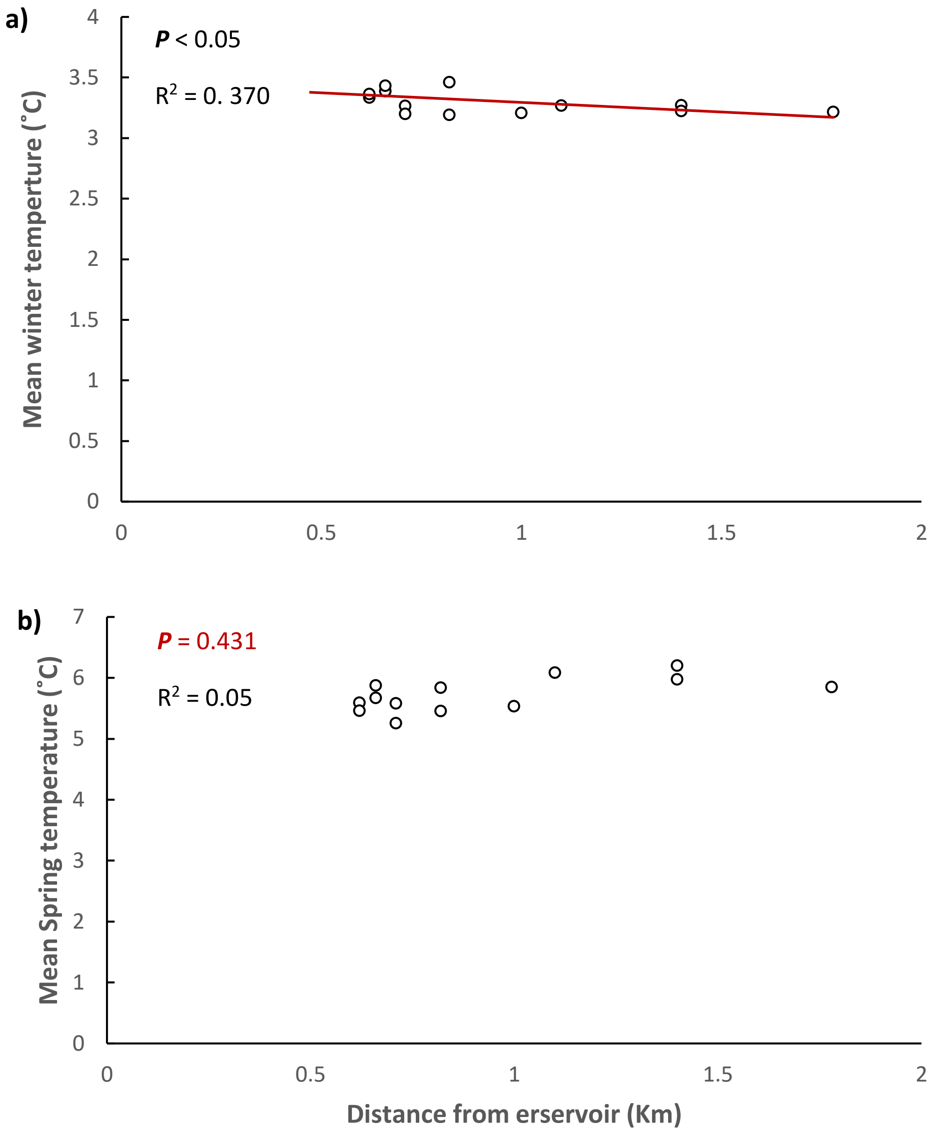

Figure 2.8. Relationship between distance from reservoir edge and mean a) winter and b) Spring temperature, recorded 0ver the periods 07/11/18 to 31/12/18 and 01/03/19 to 15/05/19 respectively (n = 15). ***P*** and R^2 values indicate the results of linear regression and trend line is calculated using least squares method.

3.4 Discussion

Prevailing winds in the area are south westerly (Huntley *et al,* 1998), approximately parallel to the transect, drawing air from the lake towards the temperature loggers. This means that the effects of lake proximity should be most easily observed where the transect was sited.

The water temperature in a lake is the function of both its depth and area (Gorham, 1964) and the high heat capacity of water (Faizal and Rafiuddin, 2011). At 3km long and under 1km wide, with a maximum depth only 25m (Kennard and Reader, 1975), the Cow Green reservoir is relatively small. Despite this, Huntley *et al* (1998) concluded that changes in vegetation of the area observed since a previous survey pre-reservoir filling (Jones, 1973) can, for the most part, be attributed to its construction. The lag between lake and adjacent lower atmosphere air temperatures, characteristic of water bodies (Lenters *et al,* 2005), was also observed for Cow Green (Huntley *et al,* 1998).

3.4.1 Mean air temperature at vegetation height

No significant relationship was found between distance from the reservoir and mean temperature for the study period 07/11/18 – 14/05/19. As this study period encompassed two seasons, and the thermal energy budget of lakes is highly seasonal (Katz *et al,* 2011), it is possible that Winter and Spring may have opposing effects on local air temperature. To test this, the data set was split into early Winter (07/11/18 – 31/12/18) and Spring (01/03/19 – 15/05/18). A significant, negative linear relationship was found between distance from the reservoir and mean Winter temperature. This follows the patterns of Winter heat export by lakes reported worldwide (Jeffries *et al,* 1999; Büyükalaca *et al,* 2003; Haginoya *et al,* 2009). No such relationship was found for mean Spring temperatures. The inverse of the relationship observed in Winter was expected, given the typical lag of lake temperatures, and common phenomenon of summer heat import by lakes (Büyükalaca *et al,* 2003; Haginoya *et al,* 2009). It would appear that, for the Cow Green reservoir, Spring is a thermally transitional stage, during which no net effect is exerted on local air temperatures.

3.4.2 Temperature range

No significant relationship was found between distance from the reservoir and the mean daily temperature range. This conflicts with evidence that water bodies reduce air temperature variation of the surrounding area (Scheitlin, 2013). Huntley *et al* (1998), however, reported the same results for this reservoir 20 years previously. It was also reported that maximum and minimum temperatures (at standard height of 1.5m (Met office Stevenson screen)) were both moderated by the construction of Cow Green (Huntley *et al,* 1998). These findings indicate that the lake exerts no observable effect on the temperature range experienced in the vegetation boundary layer by low-growing plants during the Winter and Spring. The temporal resolution of these measurements could have been too fine to observe any measurable signal due to lake proximity, i.e. only measuring daily temperature ranges. Future work would thus benefit from testing the effect of lake proximity on yearly temperature range, another important dictator of species persistence (Hijmans *et al,* 2005).

3.4.3 Growing degree days

Growing degree days (GDDs) are an important predictor of plant growth stages (Miller *et al,* 2001), including those of grassland forbs (Hutchinson *et al,* 2000). Using a 2°C base temperature, based on results from floristically similar Italian montane pastures (Romano *et al,* 2014), no significant relationship was found between distance from the reservoir and GDD sum. This appears counterintuitive given the colder winter temperature experienced further from the reservoir, but more extreme maximum temperatures are also more likely further from the water, which could lead to analogous sum values.

3.4.4 Temperature minima at vegetation height

The mean time at which the minimum daily temperatures recorded were not significantly related to distance from the reservoir. Again, this is possibly due to the temporal resolution of the data being too high to be affected by the reservoir's temperature lag i.e. it may take a longer time period for a lag effect to be established between reservoir and adjacent atmospheric temperatures. To the closest hour, 11 pm exhibited the coldest daily temperatures on average. The mean 11 pm temperature was found to be significantly negatively related to distance from the lake, supporting the earlier findings that Cow Green moderated minimum temperatures (Huntley *et al,* 1998).

A significant positive relationship was found between distance from the reservoir and total number of frost days during the study period, further indicating that the lake exerts winter warming effects, reducing temperature extremes. This is particularly relevant to the local vegetation as even single short freezing events can be lethal to many plants (Pearce, 2001). Frost exposure is also important for the timing of key lifecycle events (Wheeler *et al,* 2015) and is even used to define the growing season in some cases (Suckling, 1989). As frost days were defined as any day during which the temperature dropped below 0 °C, this did not take into account the duration of freezing events, thus 1 minute or 12 hours bellow 0 °C were classified the same, which may have affected data analysis and interpretation. Future work would, therefor, certainly benefit from also investigating the length of freezing events at different distances from the reservoir.

While the Teesdale rarity species are not actively growing during the winter months, It is important to note that winter temperatures can also affect plant growth during the growing season, for instance, by altering the timing of germination (Yu et al 2010) or summer nutrient uptake ability (Weih and Karlsson, 2002).

3.4.5 Implications and limitations of the study

It should be noted that the relationships between some of the variables investigated and distance from the reservoir could, in fact, have been curvilinear. While building a large number of non-linear regression models was beyond the scope of this study, there are two possible effects of the present approach to data analysis which should be considered. Firstly, assuming all relationship were linear may lead to incorrect rejection of relationships as non-significant, based on linear regression output values. This is unlikely to be the case given the limited ability to precisely discern the most accurate regression line with the small sample sizes used. Secondly, linear regression analyses ignore the possibility that the relationship between the variables is stronger at one end of the transect. This is likely the case as some of the scatter plots appear to become asymptotic further from the reservoir's edge. In order to accurately determine the nature of these relationships, a higher resolution of data loggers would need to be deployed.

While changes in mean temperature can be the ultimate dictator of a species distribution (Parmesan and Yohe, 2003; Lesica and McCune, 2004; Holzinger et al, 2008), the persistence of a species is often dictated by the maximum (Richter and Kolmes, 2005), minimum (Woodward, 1988) or variation in temperature (Vasseur, 2014). The Cow Green reservoir thus has the potential to affect the local vegetation by protecting it from extreme cold temperatures. Aside from preventing damage as a direct result of freezing, this may also impact the timing of emergence of some species, although, in the present study, no temperature lag was observed due to the reservoir. The recorded spring temperatures indicate that the reservoir will have no effect on the early growing season for the arctic-alpine flora growing adjacent to it. Future work would benefit from also investigating the effects on soil temperature, which has important influences on plant growth, particularly nutrient uptake (Dong *et al,* 2001; Pregitzer and King, 2005). Finally, It is important to note that the data collected were for a single year, so generalisations should be avoided, and conclusions should not be drawn from these data in isolation.

4. Responses of the study species to post-industrial climate change across their European ranges

4.1 Introduction

4.1.1 Species distributions

Tracking environmental change is more restricted in the largely two-dimensional terrestrial environment, compared to the three-dimensional aquatic environment, and is harder still for those organisms which are sessile

The fundamental determinants of a species' distribution are soil characteristics, species interactions, population dynamics, dispersal barriers and, predominantly, temperature and water availability (Blach-Overgaard *et al,* 2010).

4.1.2 Upper Teesdale environment

Within Upper Teesdale National Nature Reserve, Widdybank fell (G. R. NY820290) covers an area of approximately 5.5Km^2 from around 400 to 526.5m asl (Jones, 1973). The major habitat types of the area are heath, marsh, ombrogenous bog and calcareous grassland (Lewthwaite, 1999). These upland and sub-arctic habitats are some of the most susceptible to climate change in the UK (Berry *et al*, 2002). Being only 80km from the coast to the east and west, Teesdale does not experience particularly wide fluctuations in temperature, having monthly means of 2.2^{o}C and 12.3^oC in February and July respectively (Lewthwaite, 1999). The oceanic climate also leads to regular precipitation, 250 days a year, with around 60 days of annual snow cover (Lewthwaite, 1999).

Of the three species studied, *P. farinosa* and *V. rupestris* are classified as northern-montane and *G. verna* as alpine (Marshall, 1971), all of which are far from their core ranges in the UK.

4.1.3 Upper Teesdale vegetation

The Teesdale flora has been well studied due to the presence of numerous nationally rare plant species. Originally thought to have persisted throughout the last glacial in ice-free regions (Wilmott, 1930: as cited in Pigott, 1956), it is now generally accepted that arctic-alpine species recolonised from southern refugia, remaining in cooler areas such as the Teesdale, Craven Pennines, Cwm Idwal, Ben Lawers and the Burren (Pigott, 1956; Gibbons, 1978; Lewthwaite, 1999). Such microclimatic areas, even those which are transient can allow species to persist in an otherwise unsuitable environment (Pardini *et al,* 2015).

4.1.4 Ecological responses to climate change

Changes in latitude (Van Grunsven *et al,* 2010; Chen *et al,* 2011), altitude (Kelly and Goulden, 2008; Lenoir *et al,* 2008; Chen *et al,* 2011) and phenology (Claland *et al,* 2007; Gordo and Sanz, 2010) of plants associated with climate change are well documented. In their renowned 2003 meta-analysis of species responses to increased global air temperatures, Parmesan and Yohe found strong patterns of movement towards higher altitudes and latitudes and advancement of spring phenology.

In the current chapter some simple exploratory analyses were conducted to identify any trends in the spatial and temporal distributions of *G. verna, P. farinosa* and *V. rupestris* and their major competitor *S. caerulea* as they pertain to their temperature environment. It was hypothesised that, across their respective European ranges, the study species would have shifted towards higher altitudes and latitudes and would now have a significantly earlier growing season during the post-industrial era. The remaining data available on the species' distribution, longitude, has no direct uniform effect on climate. It was thus hypothesized that no change would have occurred in the longitude of occurrences of the study species during the same time period.

4.2 Methodology

4.2.1 Species occurrence data

Data records of species occurrences were downloaded for the three study species, *Gentian verna, Primula farinosa* and *Viola rupestris* from the open source database the Global Biodiversity Information Facility (GBIF.org, Copenhagen, Denmark; accessed 17/05.2019). In addition, the dominant graminoid competitor of these species on Widdybank fell, *Sessleria caerulea,* was investigated. Linear regression analyses were used to determine trends over time, for the 200 year period between the years 1800 and 2000, in the latitude, longitude, elevation and day of year that the species were recorded.

Records for P. farinosa in Japan and Russia were removed from the analyses undertaken here as they skewed regression results, particularly those related to longitude. This was due to the fact that occurrences only appear in records since 1935 and 1948 for Japan and Russia respectively.

4.2.2 Phenological shifts

From the regression models of trends in the timing of recorded occurrences of the species studied, the change in the most probably day of the year for an occurrence to be recorded was calculated. For the dates determined in this way, for the years the 1900 and 2000, an approximation of the mean temperature across the species ranges, during the 20th century, was calculated using data from weather stations in Stockholm, Munich, Durham and Geneva. By subtracting the mean temperature of the most probable occurrence day in 1900 from that of the most probable occurrence day in 2000, the effect of the observed changes in phenology of the species studied on the temperatures they experience was estimated. Daily temperature data for European weather stations were obtained from Tank *et al* (2002, http://www.ecad.eu).

4.2.3 Range shifts

To estimate how latitude affects temperature, 10,000 random points were generated, in QGIS 3.6.2. (Open source geospatial foundation; Chicago, USA) to extract mean annual terrestrial air temperature data from the Worldclim.org raster data set bio_1 (Hijmans *et al,* 2005). Linear regression analysis was used to determine the mean change in annual temperature per degree of latitude, which was found to be 0.62˚C for the period between the years 1960 and 1990. Using the linear regression models of latitudinal changes in the recorded occurrences of the species studied, the effects of these latitudinal shifts on the mean annual temperatures experienced by the species studied, across their respective European ranges, were calculated for the period between the years 1900 and 2000.

The rate of temperature decrease with increasing altitude is termed the dry adiabatic lapse rate (Blandford *et al,* 2008). A dry adiabatic lapse rate of 0.55˚C per 100m elevation is regarded as approximately usual (Körner, 2007), and this is confirmed for montane environments in northern Italy where the three study species grow (Rolland, 2003). Linear regression models constructed for the study species' observed elevations, between the years 1900 and 2000, were used to approximate the distance, in meters, that the species ranges have shifted altitudinally. An adiabatic lapse rate of 0.55˚C was therefore used to calculate the extent to which altitudinal shifts of the species have counteracted, or amplified, concurrent global surface air temperature increase (˚C).

4.2.3 Net effect of distributional and phenological shifts on the temperature environments of the study species

By calculating the sum of the above mentioned effects of the altitudinal, latitudinal and phenological shifts of the study species on the mean temperatures experienced by them for the 20th century, a net temperature change figure, induced by the species' niche tracking, was obtained.

Distributions of the study species are predominantly European, and thus lower longitude generally equates to more oceanic environments across their ranges. As longitude *per se* has no uniform linear relationship with temperature, it was excluded from calculations. However, mean temperature and temperature variance data for seven locations, representing an east to west transect across Europe, were included to indicate the effect longitude may have across the species ranges (Table 3.2.).

All statistical analyses were carried out using simple linear regression in SPSS 24 (Armonk, New York, USA).

4.2 Results

4.2.4 Phenology

G. verna and *P. farinosa* both showed small, but highly significant trends in records towards occurrence later in the year (F (1, 180) = 16.04, ***P*** < 0.001, R = 0.15 [Fig 3.1.]; F (1, 401) = 680.80, ***P*** < 0.001, R = 0.12 [Fig 3.1.a, b]), as did their major competitor species *S. caerulea* (F (1, 791) = 1187.05, ***P*** < 0.001, R = 0.14 [Fig 3.1.d]). No significant trend was found in *V. rupestris.*

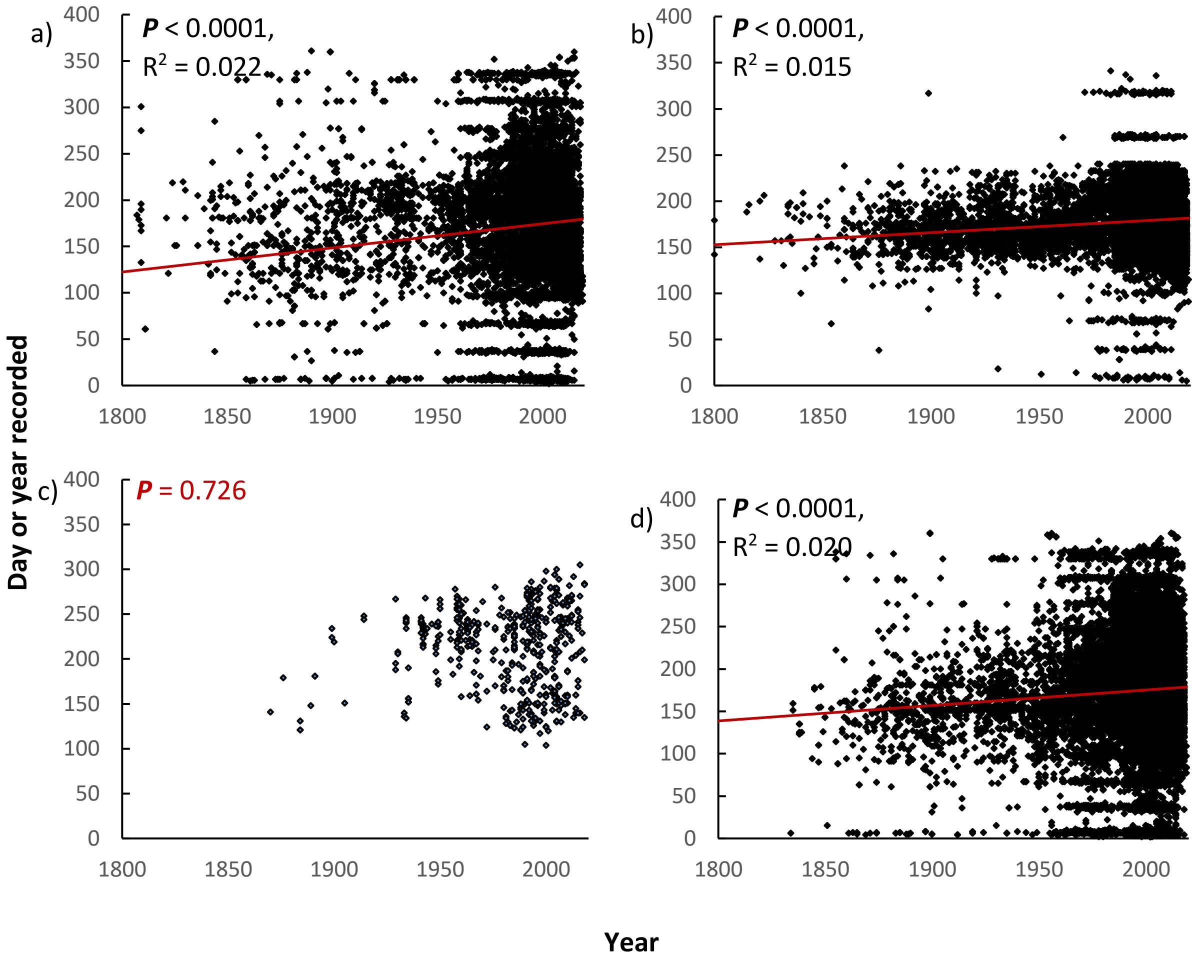

Figure 3.1. Trends in day of the year on which occurrences were recorded 1800 to 2000 for a) *G. verna,* b) *P. farinosa,* c) *V. rupestris* and d) *S. caerulea* (n = 181, 402, 674 and 792 respectively). ***P*** and R^2 values represent the results of simple linear regression and trend lines were calculated using the least squares method.

4.2.5 Latitude

Small, but significant trends were found towards lower latitudes of recorded occurrences of *G. verna* (F (1, 187) = 5.76, ***P*** < 0.05, R = 0.11 [Fig 3.2.a]), *P. farinosa* (F (1, 408) = 217.90, ***P*** <0.0001, R = - 0.10 [Fig 3.2.b]), *V. rupestris* (F (1, 708) = 170. 80, ***P*** < 0.0001, R = - 0.10 [Fig 3.2.c]) and *S. caerulea* (F (1, 752) = 641.22, ***P*** < 0.0001, R = - 0.11 [fig 3.2.d]). Although the relationship not strong, it is uniform across all four species.

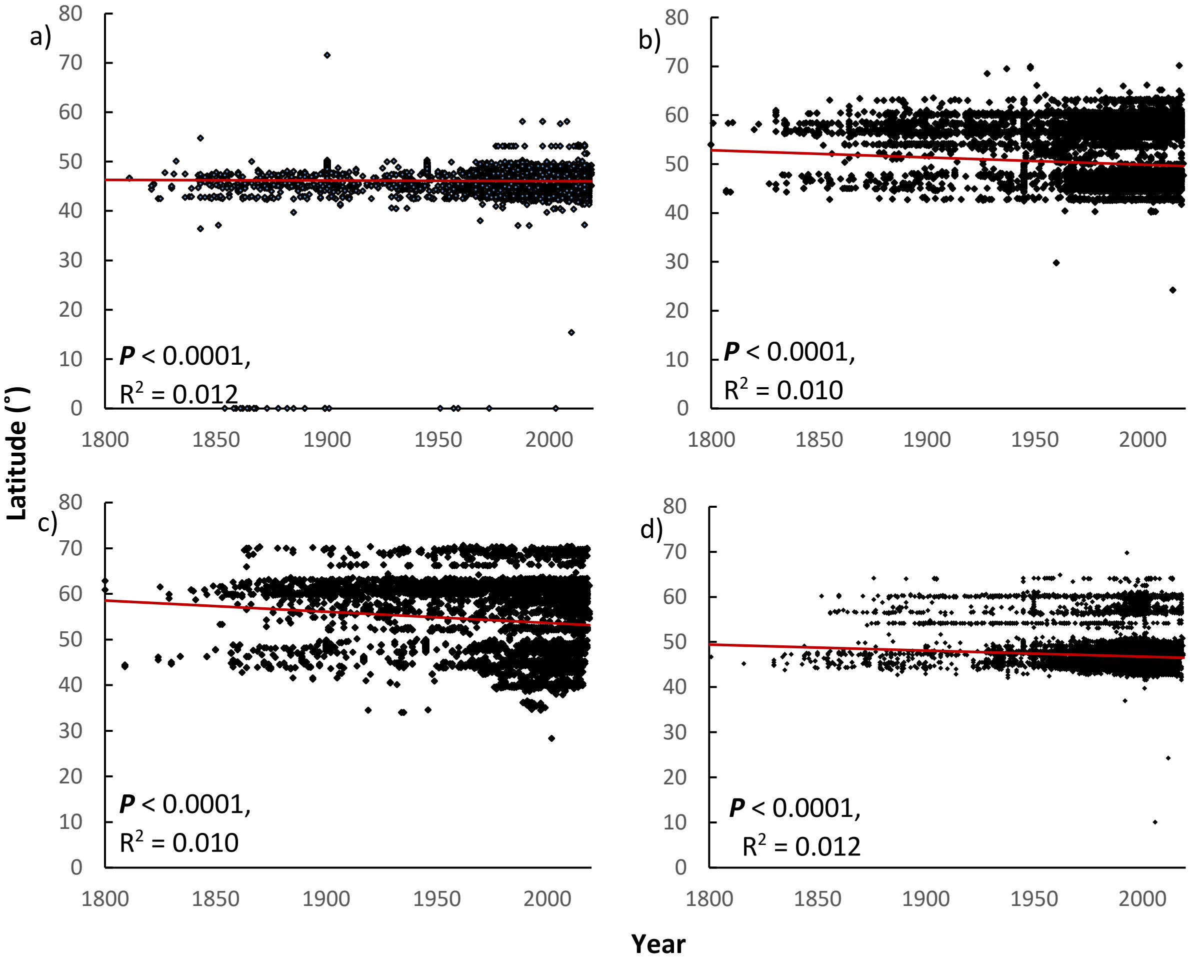

Figure 3.2. Trends in latitude at which occurrences were recorded 1800 to 2000 for a) *G. verna,* b) *P. farinosa,* c) *V. rupestris* and d) *S. caerulea* (n = 188, 409, 709 and 753 respectively). ***P*** and R^2 values represent the results of simple linear regression and trend lines were calculated using the least squares method.

4.2.6 Longitude

Significant trends were found showing a shift towards lower longitudes of recorded occurrences of *G. verna* (F (1, 188) = 13.17, ***P*** < 0.0001, R = -0.256 [Fig 3.3.a]), *P. farinosa* (F (1, 409) = 27.75, ***P*** <0.05, R = 0.02 [Fig 3.3.b]), *V. rupestris* (F (1, 706) = 107.90, ***P*** < 0.0001, R = -0.118 [Fig 3.3.c]) and *S. caerulea* (F (1, 789) = 78.01, ***P*** < 0.0001, R = 0.037 [Fig 3.3.d]). For species distributed across Europe, a decrease in longitude of recorded occurrences indicates a move toward more maritime environments.

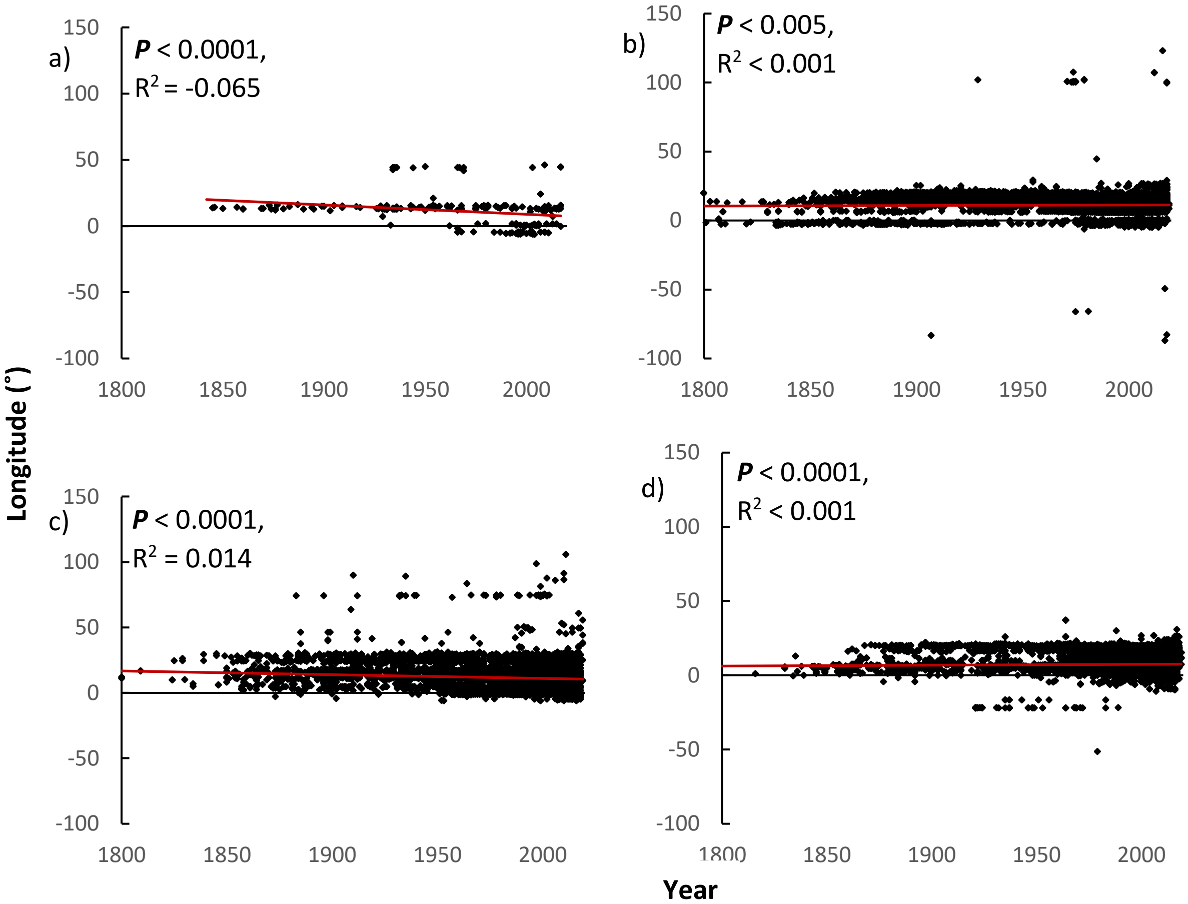

Figure 3.3. Trends in longitude at which occurrences were recorded 1800 to 2000 for a) *G. verna,* b) *P. farinosa,* c) *V. rupestris* and d) *S. caerulea* (n = 189, 410, 707 and 790 respectively). ***P*** and R^2 values represent the results of simple linear regression and trend lines were calculated using the least squares method.

4.2.7 Elevation

Significant upward trends in the altitude of recorded occurrences were found in *P. farinosa* (F (1, 409) = 8.29, ***P*** <0.005, R = 0.14 [Fig 3.4.b]), *V. rupestris* (F (1, 709) = 30.23, ***P*** < 0.001, R = 0.21 [Fig 3.4.c]) and *S. caerulea* (F (1, 772) = 11.00, ***P*** < 0.001, R = 0.12 [Fig 3.4.d]), while no significant trend was found in *G. verna* (F (1, 189) = 2.03, ***P*** > 0.05, R = 0.01 [Fig 3.4.a])

0.037

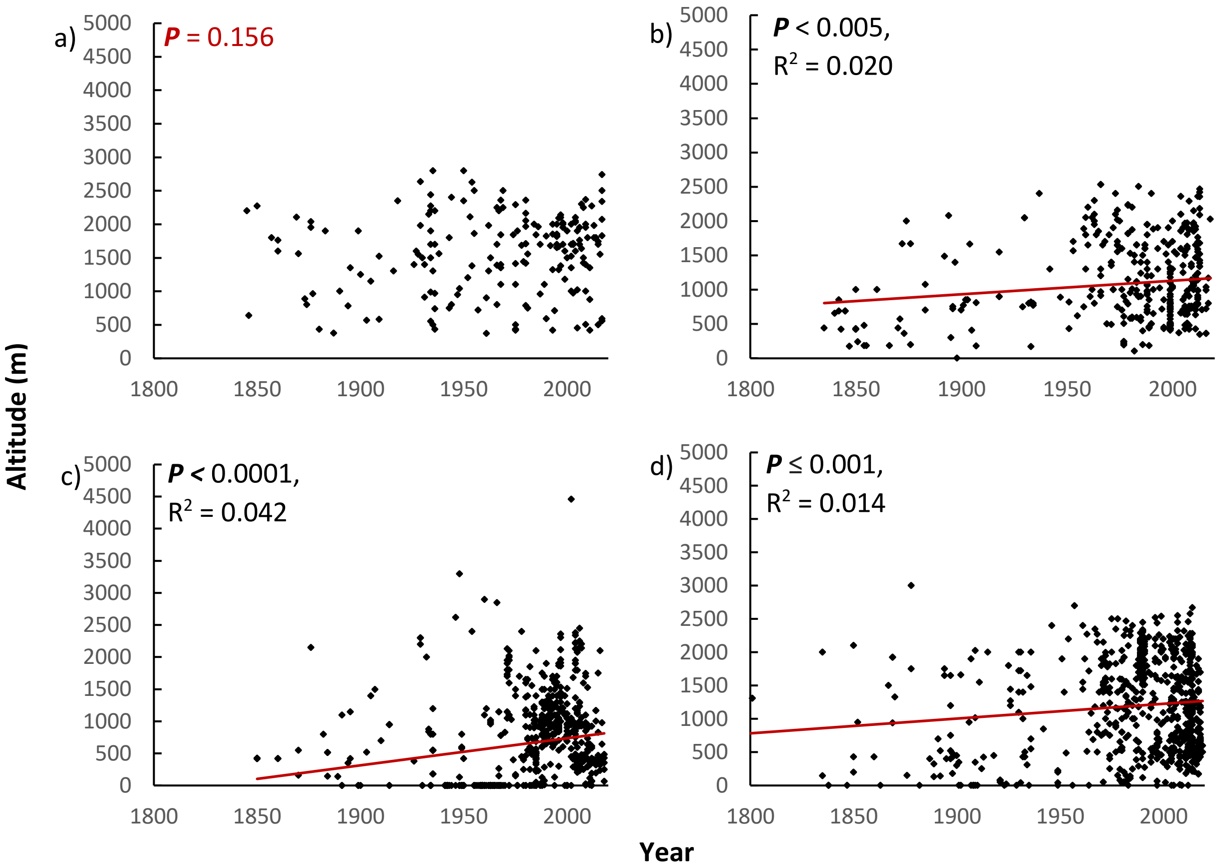

Figure 3.4. Trends in elevation at which occurrences were recorded 1800 to 2000 for a) *G. verna,* b) *P. farinosa,* c) *V. rupestris* and d) *S. caerulea* (n = 190, 410, 710 and 773 respectively). ***P*** and R^2 values represent the results of simple linear regression and trend lines were calculated using the least squares method.

4.2.8 Net temperature changes

Using the regression equations herein, the overall effects of the phenological and distributional shifts, outlined above, on the temperature environment the plants inhabit were calculated, as outlined in the relevant methodology section.

V. rupestris showed the largest net change in temperature of occurrence locations, - 2.01˚C, with *G. verna* and *P. farinosa* showing only 0.13˚C and -0.26˚C changes respectively (Table 3.1.). The larger net temperature change experienced by *V. rupestris* was driven predominantly by an upward shift in elevation of recorded occurrences. While *P. farinosa* recorded occurrences also increased in elevation, a large enough increase to exert around a 1°C decrease in ambient temperature, this was largely ameliorated by the confounding effects of later phenology and lower latitudes.

G. verna experienced the smallest net temperature change, and the only positive net change, resulting from a slight decrease in latitude of recorded occurrences and slight advancement of phenology.

Table 3.1. Change in temperature resulting from shifts in elevation, latitude and phenology of *G, verna, P. farinosa* and *V. rupestris,* 1900 to 2000, as calculated by linear regression. Net changes represent the sum of all other column values. N/A represents non-significant change in variable over time.

	Elevation ˚C change	Latitude ˚C change	Phenology ˚C change	Net ˚C change
Gentiana verna	N/A	+ 0.06	+ 0.07	+ 0.13
Primula farinosa	-1.09	+ 0.31	+ 0.52	- 0.26
Viola rupestris	-2.32	+ 0.31	N/A	-2.01

Table 3.2. Shows temperature data for seven weather stations chosen to represent an east to west, and thus continental to maritime transect across Europe, with approximately uniform latitudes (Fig 3.5.). Longitudinal data was not included in the above net temperature change calculations as it has no uniform effect on temperature. These data are included only to illustrate potential effects across the study species' core ranges. Mean temperature is not significantly related to longitude ($F (1, 5) = 0.77$, $\boldsymbol{P} > 0.05$, $R^2 = 0.13$) but is strongly related to temperature variance ($F (1, 5) = 361.14$, $\boldsymbol{P} < 0.0001$, $R^2 = 0.98$).

Table 3.2. Mean yearly temperature and temperature variance for seven weather stations, forming an east to west transect across Europe. Geographical coordinates of each weather station are indicated by longitudinal and latitudinal values (2.d.p).

	Longitude (˚)	Latitude (˚)	2000 – 2010 Mean temperature	2000 – 2010 Temperature variance
Galway	-9.1	53.3	9.84	19.34
Dublin	-6.2	53.3	9.79	14.18
Oxford	-1.2	51.8	11.11	30.93
Cologne	7	50.9	10.84	46.78
Prague	14.4	50.1	11.26	67.05
Krakow	19.9	50.1	8.85	74.13
Kiev	30.5	50.5	9.11	97.58

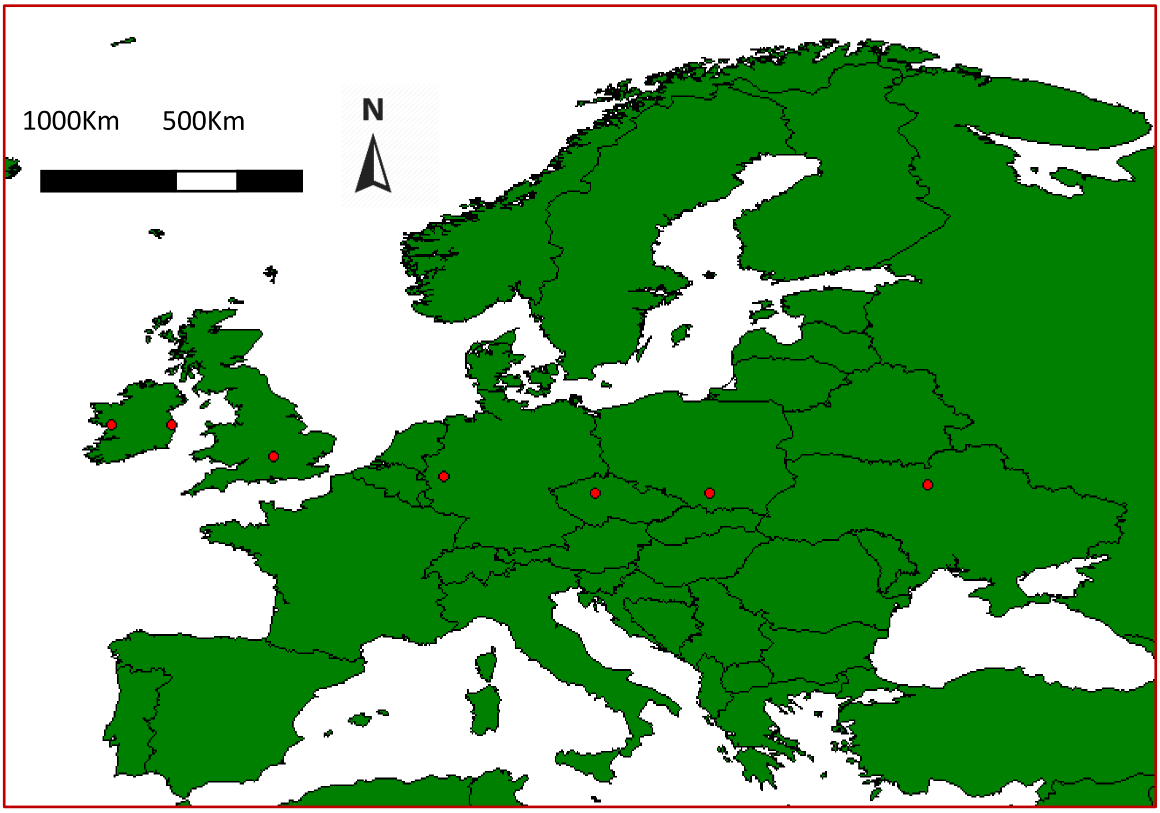

Figure 3.5.Locations of the weather stations used to calculate the temperature data shown in Table 3.2, chosen to represent a longitudinal transect across Europe.

4.3 Discussion

4.4.1 Shifts in post-industrial phenology

With the exception of *V. rupestris,* a trend towards occurrences being recorded later in the year was found across all species. For *G. verna* and *P. farinosa*, this equated to a delay of phenology by 0.13 and 0.12 days per year respectively i.e. the species are now observed later in the year. For the spring growing species *G. verna* and *P. farinosa* (Elkington, 1963; Hambler and Dixon, 2003), this represents a shift towards warmer summer weather. While this appears counterintuitive for arctic-alpine species given global temperature increases during the post-industrial era (IPCC AR5 WG1 Summary for policy makers, 2013), it may be explained, in part, by alterations to the seed stratification process during warmer winters. Yu *et al* (2010), for example, reported delays to spring phenology in vegetation of the Tibetan plateau due to winter warming preventing seed chilling requirements from being met, leading to delays in germination. Given the perennial nature of the study species (Elkington, 1963; Doody 1975; Hambler and Dixon, 2003), however, later germination is unlikely to have a major impact on overall occurrence timings. These results do appear to conflict with delays in phenology reported for arctic (Henry and Molau, 1997) and alpine (Rammig *et al,* 2010) plant species. Meta-analyses which have also found phenology advances of 0.23 to 0.63 days per year to be a common phenomenon across taxa (Parmesan and Yohe, 2003; Root *et al,* 2003).

4.4.2 Shifts in post-industrial latitude

Each of the study species showed a minor decrease in latitude over the period 1900 to 2000, 0.1° (*G. verna*), 0.5° (*P. farinosa*) and 0.5° (*V.* rupestris). As these species are restricted to the northern hemisphere, this conflicts with the established phenomenon in the existing literature, suggesting that increasing global temperatures are causing many species to shift their ranges towards the poles (e.g. Parmesan and Yohe, 2003; Hicklng *et al,* 2006; Chen *et al*, 2011). The three study species are predominantly found in Europe, where the major mountain ranges, the Alps, Pyrenees and Caucasus, are towards the south of the continent. These cooler, high-altitude areas may explain the decreases in latitude found during the last 200 years. To test this, the number of recorded occurrences of each species, 1900 to 2000, in the latitudinally adjacent countries, Germany and Austria, were plotted. Germany was chosen to represent a higher latitude, lower altitude region, relative to Austria. Based on this hypothesis, an increase in occurrences in Austria, relative to those in Germany would be expected. This pattern was found in *P. farinosa,* while almost identical relationships were found for *G. verna* in both countries and no significant relationship was found for *V. rupestris* in either country (Fig 3.6). This implies that the southward range shift of *P. farinosa* may be related to a shift towards higher altitudes, but this is likely not the case for *G. verna* or *V. rupestris.*

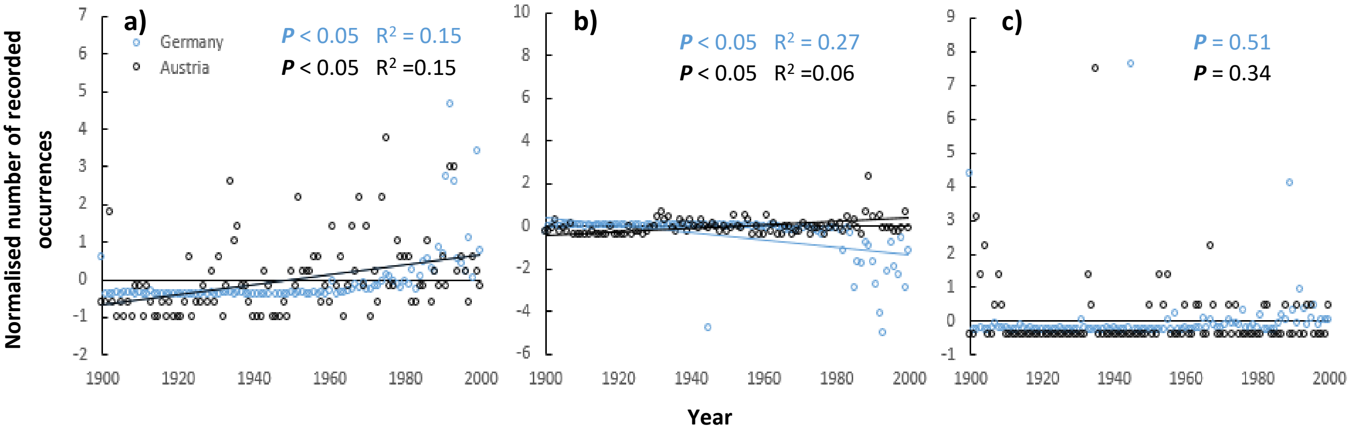

Figure 3.6. Normalised number of recorded occurrences of a) *G.verna,* b) *P.farinosa* and c) *V.rupestris* each year in Germany and Austria, 1900 to 2000, as shown by GBIF datasets. Trend lines were calculated using the least squares method, ***P*** and R^2 values indicate the results of simple linear regression.

4.4.3 Shifts in post-industrial longitudes

A uniform decrease in mean longitude was found across the three study species and their major competitor in Upper Teesdale, *Sesleria caerulea.* Longitude has no direct linear relationship with temperature as latitude and altitude do. However, in Europe, lower longitudes tend to represent a more maritime environment (Fig. 3.7). Areas closer to the coast exhibit smaller seasonal and diurnal temperature fluctuations (Scheitlin, 2013), due to the high heat capacity of the oceans (Faizal and Rafiuddin, 2011). This is reflected by the positive relationship between longitude and annual temperature variance shown in Table 2. In Europe, the release of thermal energy from the Atlantic Ocean during winter, and its transport by prevailing south westerly winds make the Maritime-Continental climate gradient particularly pronounced (Seager *et al,* 2002). This suggests that the species studied may have shifted towards environments with less temperature variation in the post-industrial era. This is possibly a response to the increases in global atmospheric temperature variation, which have occurred due to anthropogenic climate forcing, associated with a greater atmospheric heat budget (Schär *et al,* 2004; Meehl and Tebaldi, 2004).

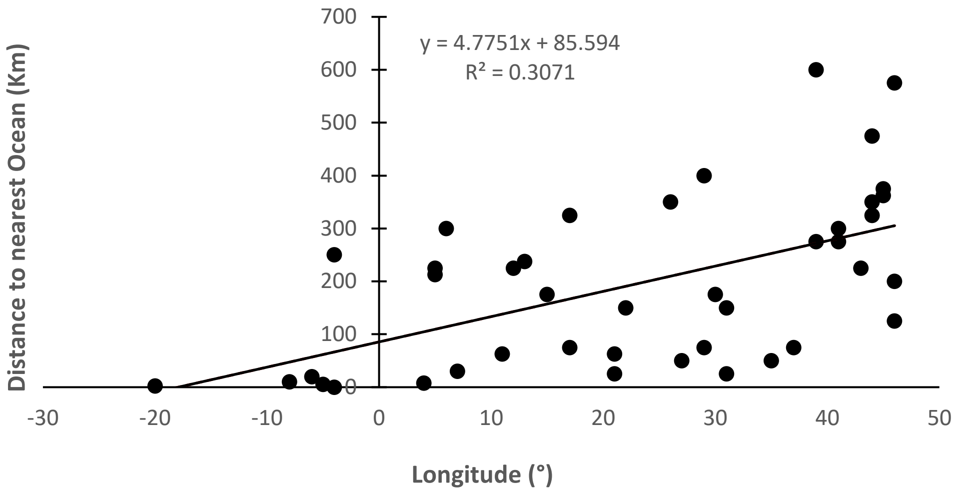

Figure 3.7. Relationship between longitude and distance from nearest ocean at 50 random points within Europe, defined by the coordinates -25 to 47˚E, 32 to 74˚N. Trend line was calculated using the least squares method, ***P*** and R^2 values indicate the results of simple linear regression.

Records for *P. farinosa* in Japan and Russia were removed from analyses as they skewed regression results, particularly longitude i.e. the highest longitudes were only recorded recently, increasing the probability of a positive relationship between longitude and time. Occurrences only appear in records since 1935 and 1948 for Japan and Russia respectively, however, there is no reason to assume that *P. farinosa* was not present in either country before this point.

4.4.4 Shifts in post-industrial altitudes

P. farinosa and *V. rupestris* exhibited respective increases of 4.2 m and 2.0 m altitude per year over the period 1900 to 2000, whilst no significant relationship was found for *G. verna*. The increase of 4.2 m per year for *V. rupestris* is relatively large compared to an average of 2.8 m per year found cross alpine plants (Walther *et al,* 2005) and 0.85m per year found for boreal-montane vegetation (Savage and Vellend, 2015).

4.4.5 Net effect of distributional and phenological shifts on temperature environment

The net temperature changes calculated for the study species for the period 1800 to 2000, based on their shifts in phenology, latitude and altitude, indicate little change for *G. verna* and *P. farinosa*, but a large decrease for *V. rupestris* (refer to Table 3. 1.). Altitudinal shifts were the largest single contributors to the net temperature changes calculated for *P. farinosa* and *V. rupestris,* accounting for estimated -1.09°C and -2.32°C changes respectively.

It is important to note that net temperature changes calculated here are relative to a concurrent increase in global mean surface temperature of *ca* 0.85°C from 1880 to 2012 (IPCC AR5 WG1 Summary for policy makers, 2013). This equates to a *ca* 0.64°C increase for the period 1900 to 2000, assuming a constant rate of temperature change. Accounting for this, *G. verna, P. farinosa* and *V. rupestris* are estimated to have experienced net changes in mean temperature of occurrence locations of +0.77°C, +0.38°C and -1.37°C respectively. These reflect concerns that many plant species will not be capable of shifting their ranges fast enough to trach their thermal niches under future climate change scenarios (Neilson *et al,* 2005).

These calculations, while for the period 1900 to 2000, used the regression models built for the period 1800 to present. This results in a larger dataset to extrapolate trends from; however, as the regression models are linear, this may not truly reflect the variable changes that occurred post 1900 due to the irregular rate of climate change (Watanabe *et al,* 2014; Smith *et al,* 2015). It is also important to note that the impacts of latitude and altitude on temperature are, by no means, uniform, so approximations of the mean effects per unit distance were used in the present study. In addition to the net temperature changes experienced by the study species, they will also likely experience smaller annual temperature variations across Europe in the future due to their shifts towards lower longitudes.

The positive net temperature changes calculated for *G. verna* and *P. farinosa* indicate that these species have not shifted their ranges or phenologies sufficiently to fully track the spatial and temporal movement of their fundamental niches. The positive net temperature change value calculated for *V. rupestris* shows that the species has altered its distribution and phenology more than enough to counteract the effects of a warming climate, effectively "out-running" climate change. One possible explanation for this is a potential lag effect between the effects of the "little ice age" which occurred in Europe from around a thousand years ago until the mid-nineteenth century (Grove, 2001; Nesje and Dahl, 2003). This may have caused *V. rupestris* to inhabit warmer regions e.g. at lower elevations prior to the 1800 date used for the regression models herein. Such lags in the ecological effects of climate change have been recorded before (e.g. Bertrand *et al,* 2011), but this affect was not observed in the other two study species in the present study.

The strong role played by increasing altitude of recorded occurrences, for both *P. farinosa* and *V. rupestris,* in the net temperature changes calculated suggests this may be the primary response induced to ameliorate the impacts of increased temperatures. This is most probably due to the smaller distance required for a species' range to shift in order to track it's thermal niche, as has been reported before (Bush and Hooghiemstra, 2005 [as cited in Colwell *et al,* 2008]). This does pose a potential threat to the species for the future, as uphill range expansion is fundamentally limited by peak altitude (Dirnböck *et al,* 2011; Bertrand *et al,* 2011) and can lead to isolation of high-altitude populations (Peterson 1995; Finn *et al,* 2016).

4.4.6 Ecological impact of phenological and distributional shifts

Whilst only the major competitor species within the Teesdale vegetation matrix, *S. caerulea,* was investigated, it did exhibit the same predominant responses observed in the other study species. This suggests that the existing competitor species in the Teesdale assemblage would be affected by a warming climate in a similar manner to the study species. Further work would benefit from testing this with experimental warming of *S. caerulea* in Upper Teesdale.

Spatial and temporal changes in species' ranges lead to novel species interactions (e.g. Stralberg *et al,* 2009; Herstoff and Urban, 2014; Alexander *et al,* 2015) and potential trophic mismatches (Edwards and Richardson, 2004; Durant *et al,* 2007; Doiron *et al,* 2015). Research usually focuses on the bottom-up effects of these ecological disruptions; for example, the effects of food plant phenology on herbivores (e.g. Post *et al,* 2007; Post *et al,* 2008). However, mutualistic plant-pollinator interactions are also predicted to be negatively affected by phenological mismatches (Memmot *et al,* 2007). Between plant species, extended leaf phenology has been shown to lead to competitive dominance (Smith and Hall, 2016) and un-equal phenological alterations could likely cause new competitive dominances to arise through spatial pre-emption in the future (Brewer, 2003). Conversely, competitive release of less affected species may potentially arise. Range expansion into novel environments may disrupt ecological interactions due to a lack of mutualistic interactions (Hampe and Petit, 2005) or enemy release, the phenomenon of invasion due to lack of predation (Keane and

Crawley, 2002). Contrasting effects may be observed where novel species begin to infringe on the range of species in question.

The trends observed in the present study are for all occurrence data worldwide and future work may benefit from dividing data into geographically distinct ranges, as ecotypes may exhibit local adaptation to their environment (e.g Joshi *et al,* 2001; Becker *et al,* 2006; Liancourt *et al,* 2013). All trends analysed herein were based on changes in the mean values. However, investigating changes in extremes of altitude, latitude, longitude and phenology may offer insights into the future persistence of the study species. The three nationally rare species studied here were insufficient to establish general trends in range and phenology for the Teesdale rarities and further research is needed to illuminate climatic responses for the assemblage as a whole.

4.4.7 Limitations of the study method

The variables investigated herein may not be the only contributors to a species' thermal environment, for instance, vegetation can modify their own microclimate by reducing heat convection (Körner, 2007).

It is also important to note that focusing on unidimensional, unidirectional responses to climate change, such as directional range shifts, has been shown to cause underestimates of the scale of species responses (VanDerWal, *et al,* 2013).

All data sourced from GBIF are subject to a number of issues; these include inaccurate recordings from unverified collaborative editing and no knowledge of the sampling intensity. The number of occurrences of each species studied, per year, has increased rapidly, especially since 1950 (Fig 3.8.), however it is not possible to distinguish between the effects of increased sampling intensity and increased abundance. Uneven increases in sampling intensity in different countries due to non-uniform socio-economic development could also likely skew analyses of linear relationships over time. Additionally, distinguishing the effects of temperature increase from its covariates, such as habitat fragmentation and degradation is not possible.

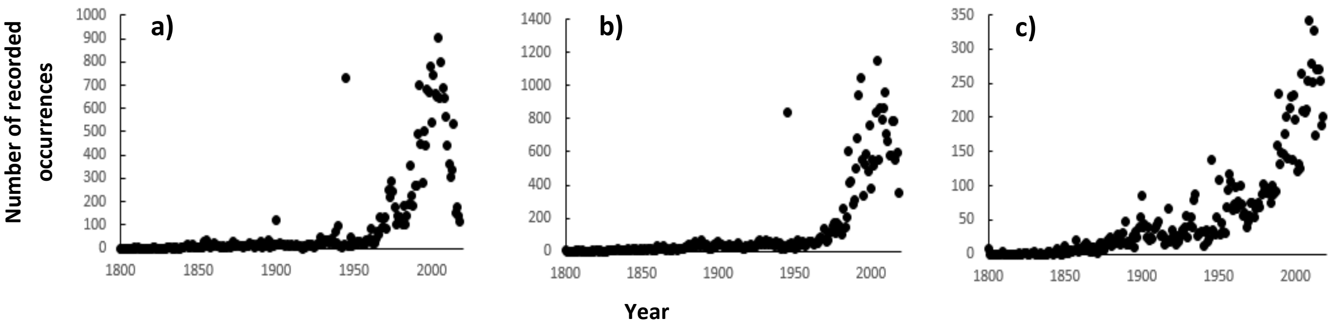

Figure 3.8 Number of recorded occurrences of a) *G.verna,* b) *P.farinosa* and c) *V.rupestris* each year, 1800 to 2018, as shown by GBIF datasets.

The scatter plots for *G. verna, P. farinosa* and *S. caerulrea* show that a large number of occurrences are recorded on the first of each month, most likely an artefact of the GBIF database often assigning records which specify a month, but not an exact date, to the first of that monthd. Without removing all records for the first day of any month, or converting these to the 15th, the middle of the month, it is not possible to remove this bias. This latter approach was avoided as it would necessitate removing all genuine records from these dates. This does, however, mean that these dates may be inaccurate by up to -30 days, however, this phenomenon is present in records from all years so introduces no inherent bias in itself.

Analysis of all trends in species distribution were carried out using simple regression, assuming all relationships studied are linear and monotonic. As the rate of climate warming is not constant (Watanabe *et al,* 2014; Smith *et al,* 2015), this is not a realistic representation of species responses, i.e. a species must alter the severity of its response to match the rate of climatic change. However, as the responses observed here are small, this method was deemed most appropriate to identify the basic underlying trends in distribution and phenology of the study species.

5. Predicted 2050 distribution of the study species

5.1 Introduction

5.1.1 Species climate tracking

The distributional shifts of species in response to recent changes in climate are well established (e.g. Parmesan and Yohe, 2003). It is also common for leading and trailing edges to move at different rates (e.g. Anderson *et al,* 2009), leading to either range expansion or contraction, but no common trends have been established across taxa. As established in the previous chapter, the species in question have experienced shifts in latitude, longitude, altitude and phenology of occurrences in the post-industrial era.

5.1.2 Species distribution models

Predicting the distribution of a species can be approached using mechanistic or correlative techniques. Mechanistic models involve defining and quantifying the physiological constraints which limit the species' persistence or abundance (Kearney *et al,* 2010). Defining the temperature range suitable for a species and mapping this in space is a common example of such a model (Buckley *et al,* 2010). This method is more applicable to predicting the distribution of plants as their presence can be directly linked to environmental variables like temperature through its effects on their metabolic processes (Criddle *et al,* 1994). For consumer species at higher trophic levels, distribution and abundance are determined by the distribution of their food source, rather than directly by their physical environment, a phenomenon known as the ideal free distribution (Bernstein *et al,* 1999). Establishing the exact limits of a species' tolerances can be time-consuming, so such methods are increasingly being avoided.

In contrast, correlative models reverse engineer the process of quantifying limiting factors by instead illuminating the statistical relationships between known occurrences of a species and environmental data (Kearney *et al,* 2010). Such models are often regression-based, with generalised linear models being one of the most popular techniques (Buckley *et al,* 2010).

Correlative models can be advantageous as they allow the use of very large data sets with which to establish causal relationships but are subject to a number of limitations which will be outlined in the subsequent discussion section.

Broadly referred to as ecological niche models, these techniques aim to define the environmental conditions in which a species can survive (Warren, 2012), defined by Hutchinson (1957) as the niche or n-dimensional hypervolume. When the areas of earth which meet the appropriate environmental criteria are mapped geographically, this forms the basis of the species distribution model (SDM) (Kearney and Porter, 2004). Once the species' niche has been defined, it can be projected onto past (Martínez-Meyer *et al,* 2004) or predicted future (Peterson *et al,* 2002) climate scenarios to compare where a species could live under different environmental conditions.

5.1.3 Maximum entropy modelling (MaxEnt)

Most correlative modelling approaches, in addition to spatial environmental data, require data on presences and absences of the species in question for part of their known range. MaxEnt is has the added advantage of using only known occurrence data to perform the same task (Phillips, 2005). MaxEnt is a machine learning algorithm-based software package (Elith *et al,* 2010) and is widely used for predicting species distributional responses to predicted future climate scenarios (e.g. Bradley *et al,* 2010; Milanovich *et al,* 2010; Khanum *et al,* 2013).

It was hypothesised that, under projected climate warming scenarios for 2050, no net changes in the area of habitat suitable for the species studied would be predicted by maxent models. It was also hypothesised that, under future climate change scenarios, predicted areas of suitable climate would be at higher latitudes.

In addition to its use generating distribution models, MaxEnt also allows the user to see which environmental variables were the strongest predictors of a species' occurrence, from which inferences about environmental requirements can cautiously be made (Young *et al,* 2011).

5.1.4 Regional adaptation of plant ecotypes

The phenomenon of plants preforming better, in terms of growth and reproduction, in their home environment, relative to non-local plants of the same species is well established (e.g. Joshi *et al,* 2001; Leimu and Fischer, 2008). It has also been shown that many plant species do not inhabit exactly the same niche across the entirety of their range (Wasof *et al,* 2013).

In their UK populations, the study species *G. verna* (Elkington, 1963) *P. farinosa* (Hambler and Dixon, 2003) and *V. rupestris* (Jonsell *et al,* 2000) are geographically isolated from their respective core ranges in Eurasia. They also live in a less variable maritime environment than their counterparts in alpine, arctic and boreal regions (Lewthwaite, 1999).

It was thus hypothesised that the species studied would inhabit a significantly different set of environmental conditions in its UK range, compared to its continental range, representing regional environmental adaptation.

5.2 Methodology

5.2.1 Species occurrence data

Geographical coordinates of species occurrences were downloaded via the open source database, the Global Biodiversity Information Facility (GBIF.org, Copenhagen, Denmark; accessed 17/05/2019). These data were collated from field survey, herbarium and museum collection data.

5.2.2 Climatic variable data

Raster data for 19 bioclimatic variables were downloaded from WorldClim (Hijmans *et al,* 2005; http://www.worldclim.org/). These data are interpolated from precipitation and temperature data from meteorological stations worldwide, for 1960 to 1990 (current). The data sets used were designed to represent biologically meaningful predictors of habitat suitability (Hijmans *et al,* 2005) and are well used in studies (e.g Wang *et al,* 2010; Yang *et al*, 2013; Remya *et al,* 2015). Data for the same bioclimatic variables for 2050, based on the IPCC's representative concentration pathway 6 (RCP 6) were also downloaded from WorldClim. The most severe of the IPCC's four future climate scenarios, RCP 8.5, is more extreme than the projections generated by most other models (Riahi *et al,* 2011). RPC 6 was thus chosen for use in the present study because it represents the most severe scenario likely to occur. For a general overview of the differences between the IPCC's RCP projections, see Fig 4.1. The Beijing climate centre climate system model 1.1 (BCC-CSM1-1) global circulation model was used in the construction of current and future distribution predictions. All climate data were at a spatial resolution of approximately 1Km^2 (Khanum *et al*, 2013).

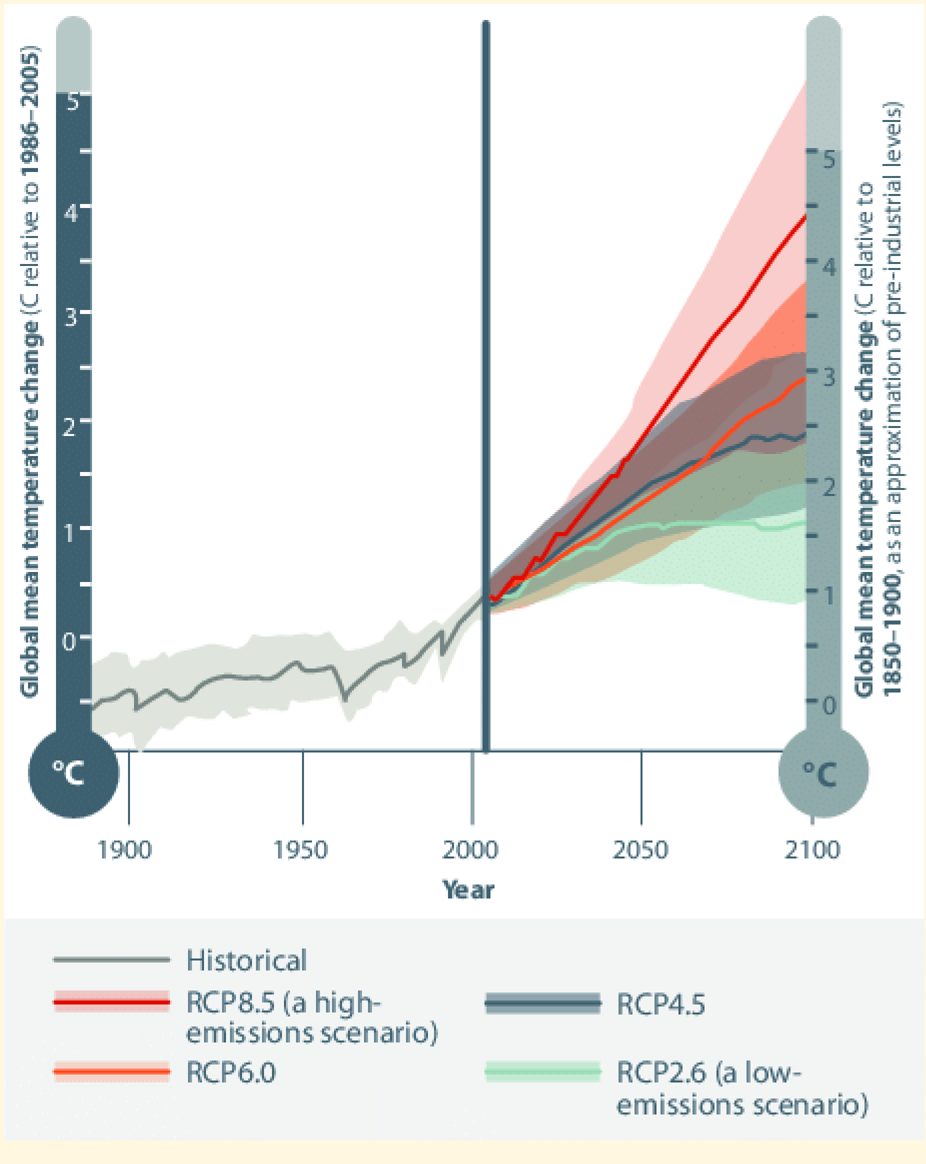

Figure 4.1. This figure illustrates the projected effects of the IPCC's relative concentration pathway (RCP) scenarios on future mean global air temperature (reproduced from Ansuategi *et al,* 2015).

Soil water pH in H_2O at 5cm depth and soil water capacity at depths of 5cm and 30cm were downloaded via the International Soil Reference and Information Centre (Hengl *et al,* 2017). The resolution of these data were altered to $1km^2$ to match that of the bioclimatic layers, allowing for model outputs to be created in regular $1km^2$ pixels.

5.2.3 Model application

The maximum entropy approach (MaxEnt 3.4.1; Phillips *et al,* 2006) was used to model current and future habitat suitability for the study species using the above-mentioned climate data.

This is a user-friendly software package which requires only that the modeller inputs the relevant climate and concurrent species distribution data. The model output generated is that with maximal entropy i.e. the closest to spatially uniform, within the constraints of the environmental requirements of the species (Phillips *et al,* 2017). The model also ensures that the mean values of each environmental variable used in its construction are equal in the predicted and known distributions of the species (Phillips *et al,* 2017). This method has been shown to be mathematically equivalent to models generated using Poisson regression (Renner and Warton, 2013), but does not require the collection of confirmed absence data.

Here models were constructed using only the occurrence records for the same period as the climatic data were recorded, 1960 to 1990. This is important for predictive performance as models are created by inferring the environmental requirements of species based on the environmental conditions they have been observed to live in. Thus, in order to establish a causal relationship between climatic conditions and species occurrence, the occurrence data and climate data must be concurrent.

As true, verified absence data are not available for the study species, certain assumptions were made regarding the data available. A pseudo absence dataset was created, using the MaxEnt default settings, whereby 10,000 random grid cells, not known to contain the species in question, are drawn from the area studied to represent absences (Hertzog *et al,* 2014).

The logistic output format is simply a log transform of the raw MaxEnt output values calculated for each map cell (Merow *et al,* 2013). This output format was chosen as it equates to the probability of a species' presence under the environmental conditions at a given location (Phillips and Dudik, 2008). This thus creates a model output suitable for converting to a binary form i.e. classifying cells as either suitable or unsuitable. For this purpose, the equal training sensitivity and specificity threshold was used to categorise environmental suitability of cells as it has been shown to have a high prediction accuracy (Cao *et al,* 2013). Models were then trained, using only 10% of the data, as the occurrence data sets used were very large.

Environmental variables were tested for collinearity using Pearson's correlation in SPSS 24 (IBM, Armonk, New York, USA). Variables with a correlation coefficient above 0.8 were regarded as highly collinear, as in Khanum *et al* (2013). Stepwise removal of the highly correlated variables with the lowest predictive power, as shown by jackknife analysis, was carried out. Once no two variables with a highly collinear relationship remained, all remaining variables contributing less than 1% to the model's predictive ability were removed, provided this did not decrease the receiver operating character (ROC) area under curve (AUC). Ten cross validation replicates of each model were run, following the procedure in Elith *et al* (2011) and Khanum *et al* (2013). The resulting mean ROC AUC value was then used to indicate model performance. Permutation importance values calculated by MaxEnt were reported to indicate the predictive power of each variable used.

Models for the four major European ecotypes of *P. farinosa* were created with occurrence data from the UK, Austria, Spain and Sweden, to represent each of the regions of Europe inhabited by *P. farinosa.* Ecotype-specific models could only be generated for *P. farinosa* due to small sample sizes for *G. verna* and *V. rupestris* in the UK. 10,000 random pointes were extracted from the predicted distributions, using QGIS 3.6.2, to calculate mean longitude and latitude suitable for each ecotype.

Permutation importance values from MaxEnt's variable contribution analyses were used to make inferences regarding the environmental determinants of the study species' distributions. These values represent the extent to which the final model's accuracy decreases when each environmental variable is removed from the model in turn (Philips, 2005). Maxent calculates these values by default, normalising them to percentages for ease of interpretation (Philips, 2005).

For the variables which best predicted *P. farinosa* distribution in the UK, values were extracted from the Bioclim raster layers at the occurrence locations recorded in the four ecotype regions stated above. For *P. farinosa,* the variables annual temperature range, and isothernality, the magnitude of day/night temperature variation relative to winter/summer variation (O'Donnell and Ignizio, 2012), were extracted. These data were used to compare differences in the most important climatic conditions experiences by plants of each ecotype. Significant differences in geographical coordinates and variable values for the different ecotypes were tested for using One-way ANOVA and Games-Howell *post-hoc* analysis in SPSS 24 (IBM, Armonk, New York, USA).

5.3 Results

5.3.1 European distributions

MaxEnt distribution models for the three study species gave area under curve (AUC) of the receiver operating characteristic (ROC) values higher than would be predicted using random models, 0.5, in all cases. For each species, the most effective climatic predictors of occurrence pertained to their temperature, rather than precipitation conditions (Table 1).

Once highly correlated variables were removed, the models generated ROC AUCs of 0.952 (± 0.002) for *G. verna,* 0.929 (± 0.004) for *P. farinosa* and 0.925 (± 0.006) for *V. rupestris.* Models predicted 11.6 %, 1.4 % and -19.7 % net changes in European range areas for *G. verna, V. rupestris* and *P. farinosa* respectively by 2050, based on the IPCC's RCP 6 (Fig 4.2.). No significant differences were found between current and future mean latitude or longitude of predicted ranges for any of the study species.

a)


Retained range
Gained range
Lost range
N
250 500 1000 Kilometres

b)


Retained range
Gained range
Lost range
N
250 500 1000 Kilometres

c)


Retained range
Gained range
Lost range
N
250 500 1000 Kilometres

Figure 4.2. Current predicted ranges and predicted range expansion and reduction by 2050 for a) *G. verna,* b) *P. farinosa* and c) *V. rupestris,* as shown by Maximum entropy modelling, using the equal training sensitivity and specificity threshold (n = 10 for each species). Models are based on the IPCC's representative concentration pathway 6. Satellite imagery obtained from ArcGIS (accessed 07/08/2019).

5.3.2 Environmental predictors of study species distribution

G. verna and *V. rupestris* were both best predicted by temperature seasonality, while *P. farinosa* was best predicted by mean temperature of the warmest quarter of the year (Table 4.1.). *P. farinosa* and *V. rupestris* showed a similar division of model contribution between the variables used, while the model for *G. verna* relied heavily on temperature seasonality, which alone accounted for 67.5% of the predictive power of the model (Table 4.1.). The soil variables pH and water capacity, at 5 and 30 cm depth, all contributed less than 1% to the overall models and were subsequently removed, leaving only climatic variables.

Table 4.1. Contribution of climatic variables to the final MaxEnt models generated for a) *G. verna* b) *P. farinosa* and c) *V. rupestris* (n = 10 for each species). Values indicate the permutation importance, as calculated by the MaxEnt software package.

a)

G. verna	Mean variable importance (%)
Temperature seasonality	67.5
Precipitation of driest month	12.0
Max temperature of warmest month	8.9
Precipitation of wettest quarter	4.2
Mean temperature of coldest quarter	3.8
Mean diurnal range	2.2
Precipitation of coldest quarter	1.4

b)

P. farinosa	Mean variable importance (%)
Temperature seasonality	37.2
Mean temperature of warmest quarter	26.4
Precipitation of warmest quarter	16.0
Mean temperature of coldest quarter	11.4
Precipitation of coldest quarter	4.1
Precipitation of driest quarter	3.8
Mean diurnal range	1.1

c)

V. rupestris	Mean variable importance (%)
Min temperature of coldest month	34.7
Temperature seasonality	27.1
Mean diurnal range	16.7
Mean temperature of warmest quarter	10.9
Mean temperature of wettest quarter	4.3
Precipitation of wettest month	3.3
Precipitation of driest quarter	1.9

				Precipitation of coldest quarter	1.1

5.3.3 *Primula farinosa* ecotypic variation

The European *P. farinosa* range is divided into four major regions, Scandinavian, British, Pyrenean and Alpine (see Fig 4.3.), represented by Sweden, the UK, Spain and Austria, respectively. Lacking suitable upland, sub-arctic or alpine areas, there are few recorded occurrences outside of these areas; exceptions include the Caucasus, Carpathians and Baltic regions.

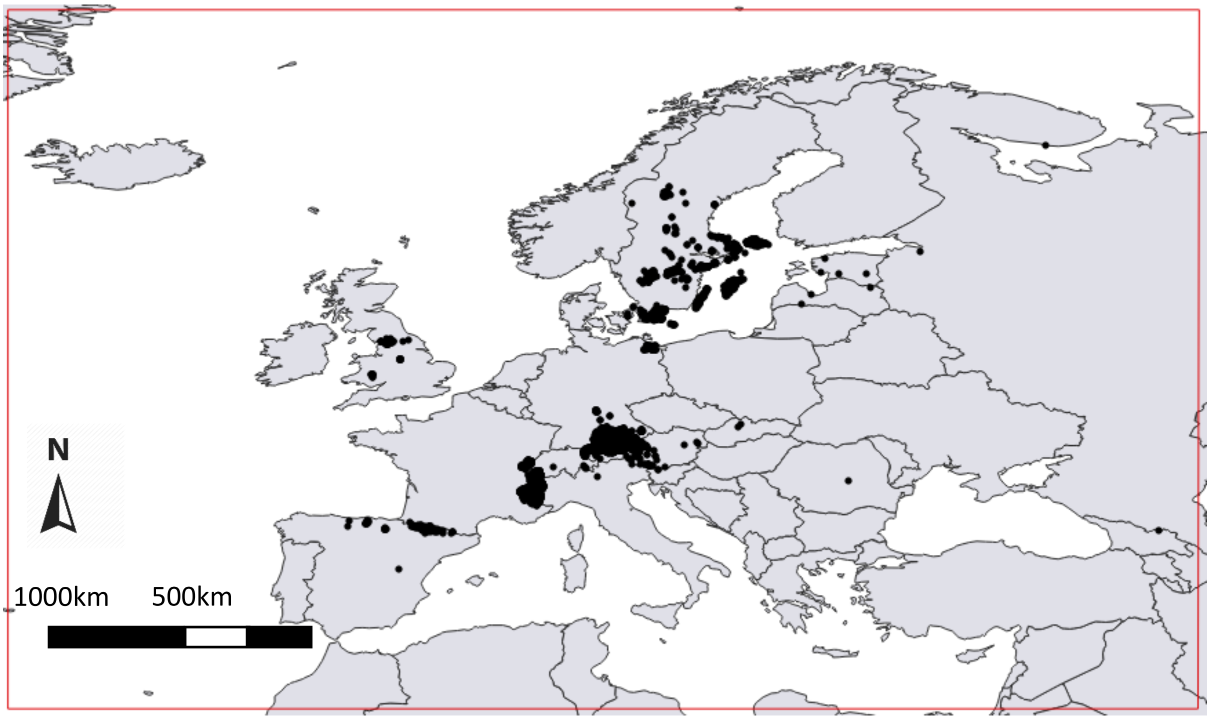

Figure 4.3. Recorded occurrences of *P. farinosa* across Europe, 1970 to 2000, as shown by the Global Biodiversity Information Facility database (GBIF.org).

Models created using the strongest environmental correlates of plants in each individual region generated markedly different predicted potential distributions (Fig 4.4.). Mean longitude and latitude of the predicted potential distributions were significantly different between all ecotypes investigated (Fig 4.5.). All ecotypes showed mean longitudes and latitudes significantly different from the overall model for the species, with the exception of UK latitude (Fig 4.5.a). Models indicate that the only other region containing plants with environmental tolerances suitable for the UK climate was the Pyrenees (Fig 4.4.c).

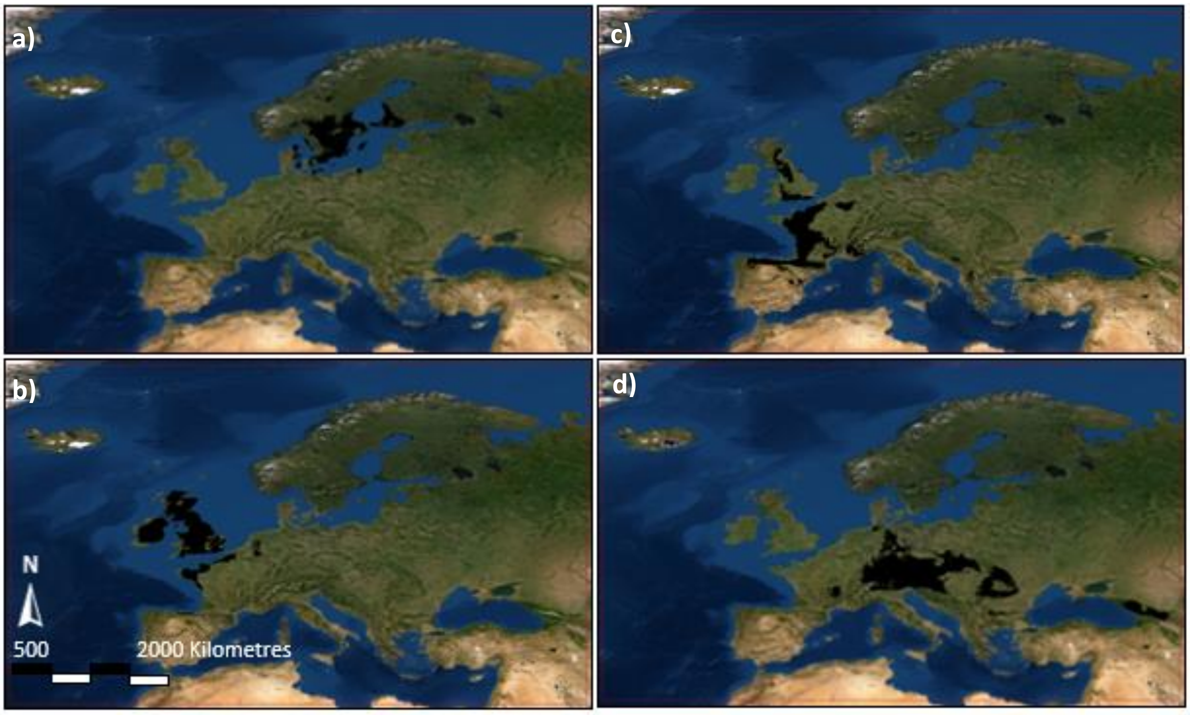

Figure 4.4. Current predicted ranges for *P. farinosa* based on occurrence data for a) Sweden, b) UK, c) Spain and d) Austria, as shown by Maximum entropy modelling, using the equal training sensitivity and specificity threshold (n = 10 for each species). Models are based on the IPCC's representative concentration pathway 6.

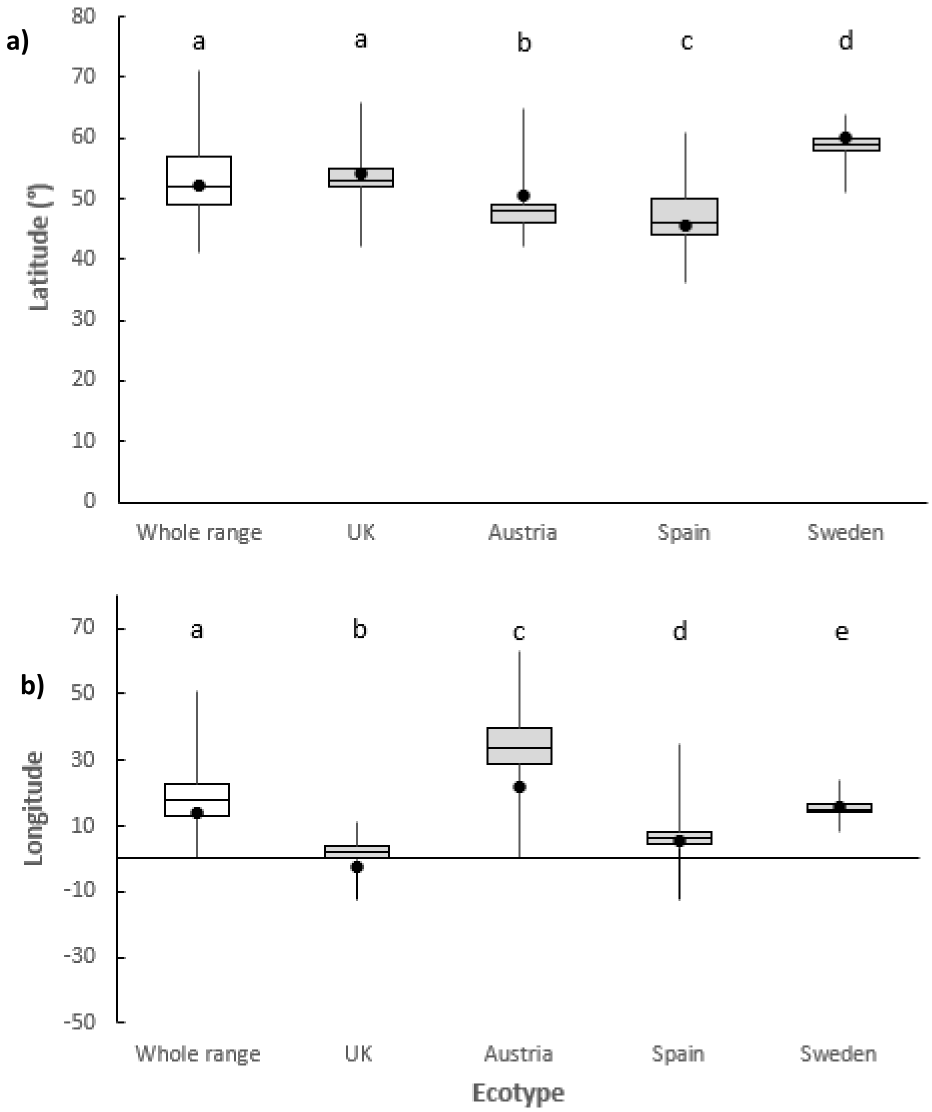

Figure 4.5. Median a) latitude and b) longitude of random points in current predicted ranges of *P. farinosa* ecotypes (n = 1000 in each ecotype). The top and bottom of boxes represent the 75th and 25th percentiles respectively, whiskers represent maximum and minimum values within groups. Dots show mean values and letters indicate significant differences between group means, as shown by One-way ANOVA and Games-Howell *post-hoc* analysis ($P < 0.05$).

In contrast to the seven climatic variables used to build the model for the full European distribution, the model created for UK occurrence records relied on only two variables, annual temperature range and isothermality. These contributed 80.2 % and 19.8 % respectively to the model's predictive ability and generated a model with a ROC AUC of 0.993 (± 0.001).

Significant differences were found between mean annual temperature range and isothermality at the recorded occurrence locations of each European region (Fig 4.6.). UK occurrence locations showed the lowest mean annual temperature range, 19.3°C, compared to a European mean of 26.2°C, and highest mean isothermality, 3.6°C/°C, compared to a European average of 3.0°C/°C. The only mean variable value found not to be significantly different to the species mean was isothermality of the Swedish ecotype (Fig 4.6.b).

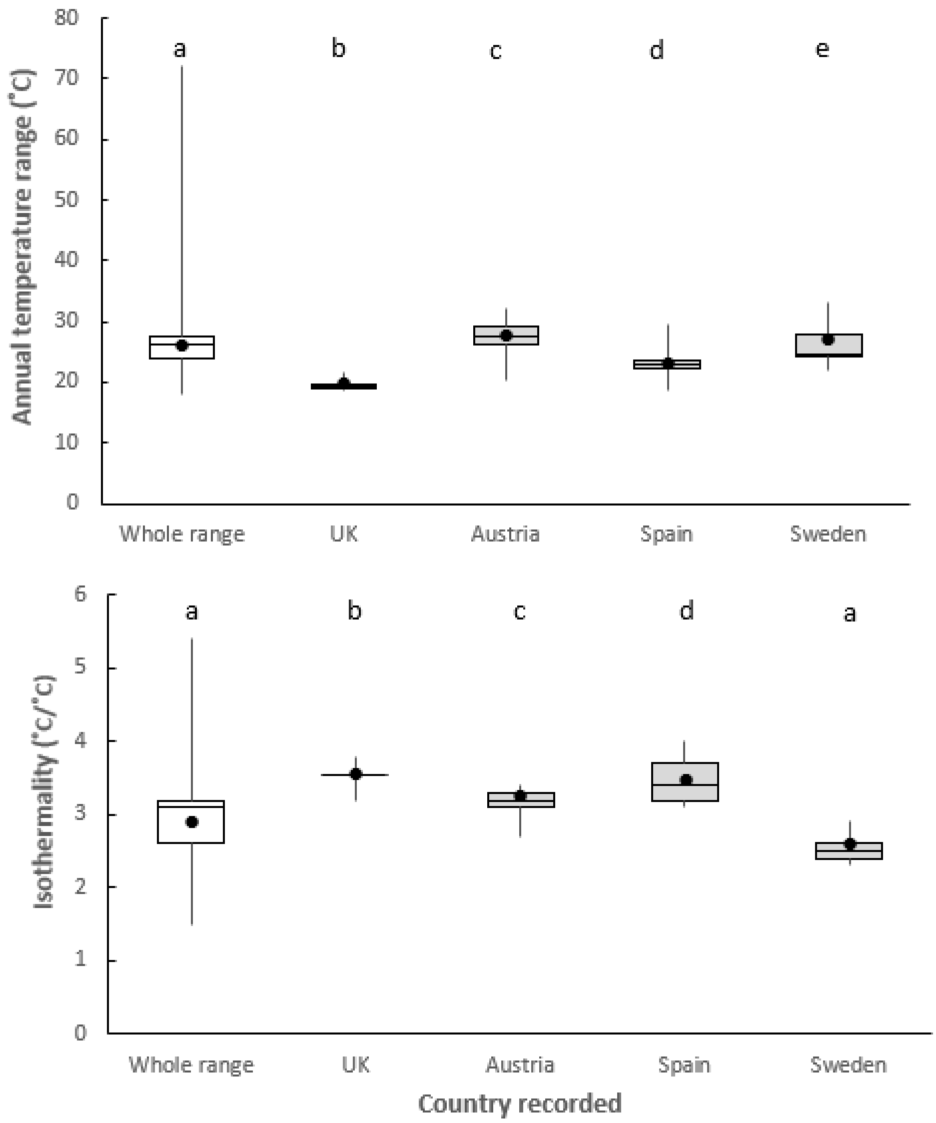

Figure 4.6. Median a) annual temperature range and b) isothermality at recorded occurrence locations of *P. farinosa* in different European countries (n = 30339, 490, 512, 847 and 8095 in the respective countries). The top and bottom of boxes represent the 75th and 25th percentiles respectively, whiskers represent maximum and minimum values within groups. Dots show mean values and letters indicate significant differences between group means, as shown by One-way ANOVA and Games-Howell *post-hoc* analysis ($P < 0.05$).

5.3.4 *Primula farinosa* UK distribution

A model constructed using all European occurrence data for *P. farinosa* shows 99.2 % of the Northern Pennines area of outstanding natural beauty (AONB) is currently suitable for the species, while 100 % is found to be suitable based on UK occurrences (Fig 4.7). Under the IPCC's RCP 6 projection, by 2050 this will have decreased to 40.3 % for the model built using all European records but will still be 100 % according to the model created with UK records only (Fig 4.7.).

a)

b)

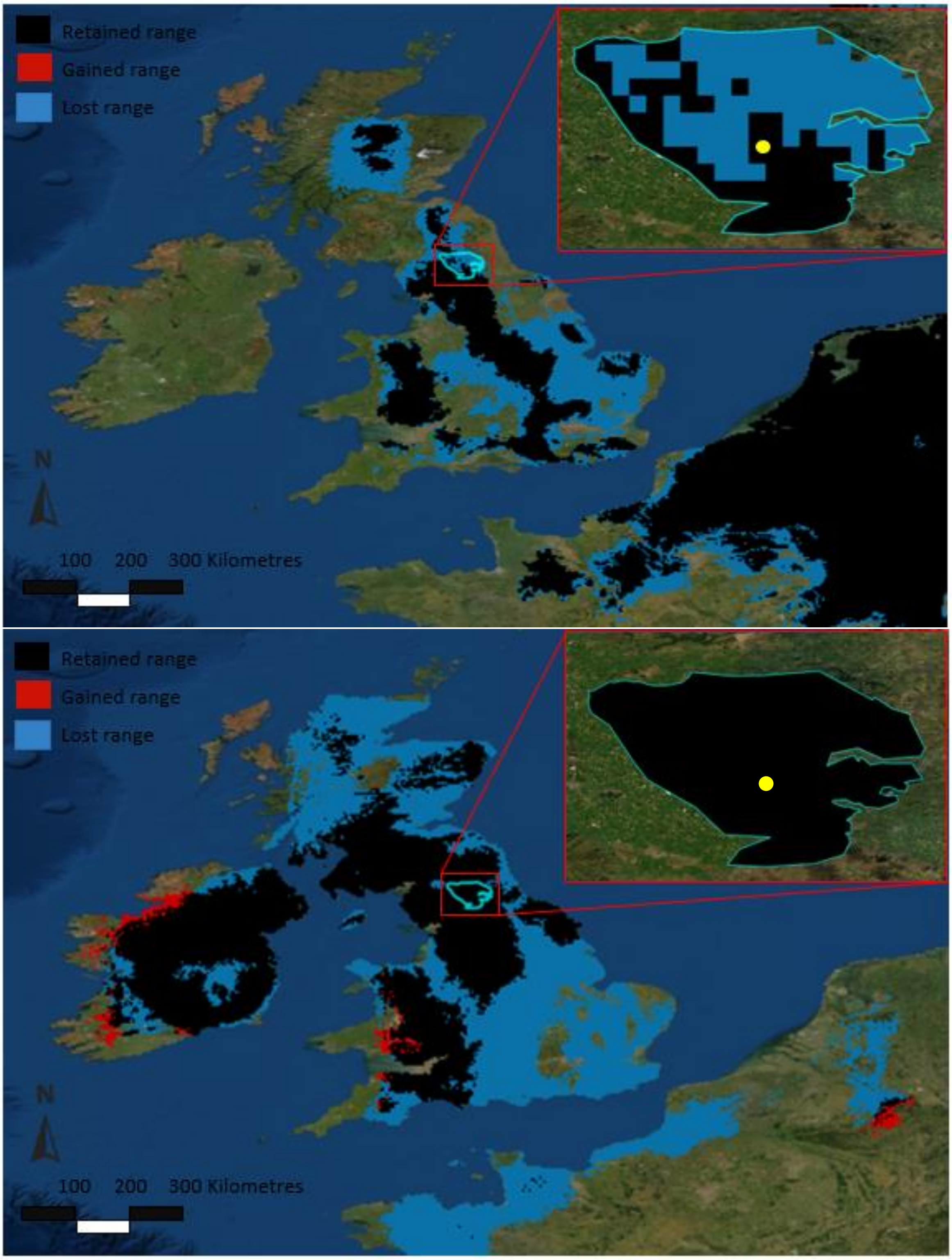

Figure 4.7. Predicted UK ranges of *P. farinosa* based on a) all recorded occurrence data and b) UK occurrence data only, showing predicted range expansion and contraction by 2050, as shown by maximum entropy modelling using the equal training sensitivity and specificity threshold (n = 10 for each model). Models are based on the IPCC's representative concentration pathway 6. Insets show enlarged images of the North Pennines area of outstanding natural beauty in which Upper Teesdale is located. Yellow dots represent the study site of chapters one and two, Widdybank Fell.

5.4 Discussion

5.4.1 Model performance

The receiver operating characteristic (ROC) area under curve (AUC) values of the models generated are all high, indicating correct predictions of presence or absence in more than 90% of cases for each species. Future work may benefit from reducing the Pearson's correlation coefficient used to classify variables as highly colinear as, in most disciplines, 0.8 is regarded as a strong relationship. Increasing strictness of the collinearity criteria may help to prevent overfitting, a common issue in models with many predictor variables (Elith *et al,* 2010; Muscarella *et al,* 2014). The optimum number of predictors needed to avoid over and underestimating model performance is still largely unknown (Radosavljevic and Anderson, 2014; Moreno-Amat *et al,* 2015) but reduction of model complexity, informed by principal component analysis may be beneficial to future research (Hirzel *et al,* 2002).

The ROC AUC is a useful measure of a model's ability to correctly categorise areas as suitable or unsuitable, as it is exempt from issues of subjective threshold choice. However, it has been shown to inflate estimates of model accuracy, when used to assess the efficacy of models which used assumed absences (as is the case in MaxEnt), rather than confirmed absences (Peterson *et al,* 2008; Jiménez-Valverde, 2012). Using this performance measure penalises models for predicting potential distribution, rather than the realized distribution i.e. with interspecific interactions (Jiménez-Valverde, 2012).

5.4.2 Current environmental suitability across Europe

MaxEnt models indicate that only small areas of the UK are currently suitable for *G. verna* and *V. rupestris*, in which the Northern Pennines are not included (Fig 4.1. a, b). This suggests that the species are indeed relicts from a previously suitable environment as concluded by several previous publications (Pigott, 1956; Bellamy *et al,* 1969; Squires, 1971) and that they are now living in a sub-optimal environment in the UK. *P farinosa* is predicted to live in a large swath of land across the UK, which is reflected by its higher abundance here. MaxEnt models the fundamental niche of a species, consistently predicting distribution larger than in reality (Yang *et al,* 2013). Predicted distributions closely resembled the actual European distributions of the study species, but overestimated ranges across France and Germany for all species. This may be due to the high agricultural intensity in these countries (Donald *et al,* 2001), which could also limit distribution. The model results suggest that, under the projections of the IPCC's RCP 6, by 2050 climate change will have had little effect on the European distribution of the study species. Largely accurate predictions of current distribution justify the projection of these models onto future climate scenarios.

5.4.3 Future environmental suitability across Europe

The IPCC's RCP 6 was chosen to represent the climate of 2050 as it is the second most severe of the IPCC's four projected scenarios (Van Vuuren *et al,* 2011). Of these four scenarios, the most severe, RCP 8.5, is more extreme than most other predictions, and the less extreme scenarios, RCP 2.6 and RCP 4.5 predict little change in global temperatures by 2050 (Riahi *et al,* 2011). RCP 6 was thus used as it represents the most severe climate change scenario which is most likely to occur.

An increase in mean global surface air temperature would cause an increase in latitude of the thermal niche of a species and, unless the species was already at the extreme of its thermal niche on Earth, should cause no significant overall change in species range area. These assumptions were tested for the three study species chosen in the present study. Contrary to the hypothesis of no change in suitable habitat area, models showed a severe overall decrease in suitable habitat of 19.7 % for *P.*

farinosa, while *G. verna* and *V. rupestris* are predicted to have small increases by 2050. No significant changes in the predicted mean latitude or longitude of any of the study species were found by 2050, in accordance with the hypothesis outlined above. While climate change is often synonymous with negative ecological impacts, the small increases in suitable habitat area for *G. verna* and *V. rupestris* are not counterintuitive. For example, a uniform increase in global temperatures simply means that species range may move, but this does not necessitate range shrinkage. In European high altitude and latitude areas, loss of plant species richness is more commonly associated with agricultural intensification (Luoto *et al,* 2003; Ren *et al,* 2009). These models indicate that, according to the IPCC's RCP 6, during the first half of the 21st Century, climate change in isolation will have little impact on the European distribution of the study species.

5.4.4 Environmental predictors of species presence

Phillips (2005) warns that variable contribution estimates should be interpreted cautiously, particularly when variables are correlated. Contribution values are given here as indicators of species requirements, rather than empirical data. It is important to note that MaxEnt is a machine-learning algorithm (Phillips *et al,* 2004), whereby the predictive ability of variables is based upon their correlation with occurrence data. This can lead to, for example, precipitation of the warmest quarter correctly predicting the majority of occurrence locations and thus heavily contributing to the overall model, whilst precipitation of the remaining three quarters may contribute relatively little or even be omitted. This should not be interpreted as the species not requiring rainfall during these periods.

Jackknife analysis showed that, for *G. verna*, the highest contributing variable in isolation, temperature seasonality, generated a model with a ROC AUC of 8.99. Temperature of the coldest quarter, which contributed only 3.8 % to the overall model, alone generated a model with a ROC AUC of 9.20. This gives two important insights into the variable contributions. Firstly, whilst temperature of the coldest quarter is not strongly correlated, relatively, with the occurrence data, it is an important determinant of *G. verna* distribution. Secondly, the contribution of temperature seasonality to the model is dependent upon interactions with other variables a common phenomenon in niche modelling (e.g. the predictive ability of temperature in conjunction with precipitation is greater than the sum of the two individually (VanDerWal *et al,* 2013)).

Across the study species, temperature seasonality was an important predictor of occurrence and variables relating to the warmest and coldest periods of the year also featured highly in models. This indicates that the occurrence of these arctic-alpine species is often dictated by the annual variation in temperatures experienced. Precipitation played a much lesser role in model predictions than the temperature variables, indicating that these species may universally inhabit damp environments.

The final inclusion of only two predictor variables in the model built using only UK *P. farinosa* occurrence data (annual temperature range and isothermality), using the same method, is most probably due to fewer variables being required to predict the distribution of a smaller, less variable, data set. No precipitation-related variables were used to predict UK occurrences. This suggests that none of the aspects of precipitation included in the Worldclim dataset are limiting to *P. farinosa* in the UK i.e. most of the UK has sufficient precipitation for *P. farinosa* to persist, so this does not convey any discriminatory ability to the model.

5.4.5 Regional adaptation of *Primula farinosa* ecotypes

Based on the observation that many species exhibit regional adaptations to their environments (Joshi *et al,* 2001; Leimu and Fischer, 2008) and often inhabit different environmental conditions in these different regions (Wasof *et al,* 2013), the hypothesised that *P. farinosa* would inhabit a different set of environmental conditions in the UK, compared to the rest of Europe, was tested.

While the boxplots for figures 4.5 and 4.6 show considerable overlap between the longitude and latitude and climatic conditions inhabited by the European populations of *P. farinosa,* it is important to note the parameters being displayed here. Boxes display the 25th and 75th population percentiles and error bars display the most extreme values of the populations. This best represents the full spatial and environmental extent of the different populations, but consequently compresses the plots. Dots should be used to interpret the population mean values from which statistical analyses were derived, and boxes are best interpreted as an indication of data skewing (for instance, a mean value higher than the median indicates a number of extremely high values within the population).

If no differentiation in environmental tolerances had occurred between the isolated regions currently inhabited by *P. farinosa*, then the plants from each region would inhabit regions of similar climatic conditions. This could still lead to corelative model predictions differing for each region e.g. plants in a maritime British environment may fill a smaller proportion of their thermal niche than their continental counterparts. This, however, would still mean that the UK would be classified as suitable for the environmental tolerances of the continental plants. As this is not the case in the models created for *P. farinosa,* this indicates that the UK, Scandinavia, Pyrenees and the Alps may be home to distinct ecotypes adapted to their local environments. The models suggest that the only other ecotype suited to the UK climate is the Pyrenean one, which inhabits a similarly maritime environment. As *P. farinosa* seeds are dispersed only short distances by hydrochory (Hambler and Dixon, 2003), however, it is unlikely that the Pyrenean adapted plants could become established in the UK currently. It is important to note that these models do not show absolutely that plants from the Alps or Scandinavia are unable to survive in the UK climate, but rather that they currently live in significantly different climates. The models generated for each region all had significantly different mean latitudes and longitudes.

In the UK, *P. farinosa* occurrence was best predicted by annual temperature range and isothermality. Isothermality is a measure of the severity of day/night temperature fluctuation, relative to winter/summer fluctuation (O'Donnell and Ignizio, 2012) and is a strong ecological predictor in maritime environments (Nix, 1986). Smaller annual temperature ranges were found at the *P. farinosa* occurrence locations in the UK and the Pyrenees than in Scandinavia or the Alps, indicative of more maritime regions (Scheitlin, 2013). The UK and Pyrenees were also found to have higher levels of isothermality than the other European regions i.e. a larger daily temperature range, relative to annual temperature range. These are the strongest environmental correlates of *P. farinosa* occurrence in the UK and, as such, should not be interpreted as the sole environmental requirements for the species in the region.

Based on the distinct environmental tolerances of *P. farinosa* in UK ecotype, compared to continental populations, a 2050 projected distribution model was created using only UK occurrence training data. According to the model created using all European occurrence data, by 2050, the proportion of the Northern Pennines AONB suitable for *P. farinosa* will have decreased by more than 50%. In contrast, the model created using only the occurrence data for the locally adapted UK plants show that by 2050, all of the Northern Pennines AONB will still be climatically suitable. This shows that, due to local adaptation, there is perhaps little concern for *P. farinosa* in the upper Teesdale under the RCP 6 predictions. This again suggests that agricultural practices are potentially a more important factor in the UK in limiting species distribution.

The higher predicted success of UK plants could be attributed to the greater resistance to climate variability at range edges predicted by the abundant centre model (Sagarin *et al,* 2006). However, it has also been shown that range centre seeds can perform better than those of locally adapted ecotypes, due to higher maternal investment in more optimum environments (Santon and Galen, 1997). These possibilities remain ripe for further investigation in the context of the findings of the present study.

5.4.6 Limitations to the present methodology

Using presence-only species occurrence data is fundamentally flawed for a number of reasons. Firstly, and most importantly, any grid cell of the map where there is no recorded occurrence is classified as an absence by MaxEnt (Elith *et al,* 2010). These assumed absences are unverified and thus may lead to the model classifying areas of suitable environmental conditions as unsuitable for the species in question. However, unless regions with one set of environmental conditions are consistently surveyed less than others, a large sample size should counteract the niche classification implications of assumed absences. Assumed absences also have detrimental implications when using model evaluation techniques based on true positive rate (proportion occurrence grid cells correctly predicted [*also sensitivity*]) and false positive rate (proportion of absence grid cells correctly predicted [*also 1-specificity*]), such as the receiver operating characteristic (ROC) area under curve (AUC). Sampling bias arising from uneven sampling intensity, pseudo replication and variation in species detectability across its range also hinder model accuracy (Phillips *et al*, 2009; Elith *et al,* 2010).

The Worldclim data set was interpolated from weather station data worldwide to a resolution of approximately 1Km^2 (Hijmans *et al,* 2005). The resolution of the data and method by which it was attained have been criticised for use in localised SDMs (Bedia *et al*, 2013; Piggio *et al,* 2018; Wango *et al*, 2018). As the distribution of the study species was analysed for general trends across Europe, these issues were avoided as no localised predictions were made.

Indirect variables, (those representing the compound effect of other environmental variables, e.g. Altitude and NDVI (Li *et al,* 2011; Körner, 2007)) were avoided in model construction in favour of individual climate components. This avoided basing projections on predictors which are only proxies for temperature and precipitation, giving more insight into the fundamental causes of species distributions. Whilst altitude was excluded from analyses, it should be noted that altitude also affects air pressure and thus CO_2 availability (Smith *et al,* 2009). Whilst this may affect plant growth (Kogami *et al,* 2001), no data are available which would allow these effects to be projected onto future emissions scenarios.

There is some disagreement in the literature as to what exactly the continuous outputs generated by MaxEnt represent (e.g. Royle *et al,* 2012; Yakulic *et al,* 2013). To avoid ambiguity, and for the purposes of spatial analysis, the logistic output was converted to a binary (suitable or unsuitable) prediction. As MaxEnt generates a value between 0 and 1 for each cell of a map, threshold choice involves deciding on a number, between 0 and 1, below which a cell is classified as unsuitable and above which it is classified as suitable for the species in question (Escalante *et al,* 2013). This is a largely is a largely subjective process, but can seriously impact model outputs (Norris, 2014). The default for many modellers is to simply use 0.5, but this neglects the fact that a species' prevalence is not uniform across its range (Freeman and Moisen, 2008). In the present study, the equal training sensitivity and specificity threshold was chosen to create binary models, due to its high prediction accuracy (Cao *et al,* 2013). This is the threshold value calculated by MaxEnt, for a situation in which the proportion of occurrences correctly predicted is equal to the proportion of absences correctly predicted in the data used to train the model. This effectively weights the threshold according to how widespread the study species is i.e. how likely a default threshold of 0.5 is to correctly classify as suitable or unsuitable.

5.4.7 Ecological explanations and implications of model results

Whilst it is hard to quantify whether a species is at the edge of its geographic range, the following table (Table 4.2.) percentiles at which the mean UK longitudes and latitudes of the study species are found. The values indicate that, in terms of both their longitude and latitude, the UK populations of the species studied herein are not at the extremes of their ranges. Although geographical coordinates cannot be used alone do not determine climate (e.g. Leroux, 1998; Grabowski, 2000; Hall, 2004), along with the large areas found to be climatically suitable for the UK ecotype of *P. farinosa*, this calls into question the thought that the Teesdale rarities are at their range margins and is an important area for future research.

Table 4.2. Population percentiles of *Gentiana verna, Primula farinosa* and *Viola rupestris* mean UK longitudes and latitudes.

Species	Longitude	Latitude
Gentiana verna	35.8	41.5
Primula farinosa	22.5	22.6
Viola rupestris	33.3	38.8

Niche models created using only climate variables can, by definition, only predict areas of suitable climate. There are many of the determinants of a species' distribution which are not factored into these models. As such, the ranges predicted here will be subject to further reduction dependent upon species interactions, agricultural practices and geomorphological restrictions. Despite this, Dullinger *et al* (2012) found environmental variables to be more important dictators of plant species distribution than distance from refugial source populations. Dullinger *et al* (2012) also reported calcicolous species and species with short seed dispersal distances filled a smaller proportion of their potential distributions. As *G. verna, P. farinosa* and *V. rupestris* are all calcicolous (Elkington, 1963; Jonsell *et al,* 2000; Hambler and Dixon, 2003) and have short seed dispersal distances (Hambler and Dixon, 2003; Hedley, 2015; Beattie and Lyons, 1975), this may cause further significant restrictions to their distributions. It is important to note that a species' distribution is dictated not just by its current surroundings, but also by historic environmental conditions (Hortal *et al,* 2008). For this reason, the results of correlative distribution models may be skewed to some extent if distribution lags behind climate change.

The differing environmental conditions that *P. farinosa* was found to inhabit across its European range lends support to the thought that the Teesdale rarities, including *Hippocrepis comosa* (Fearn, 1973), *Dryas octopetata* and *Polygala amorella* (Pigott, 1956; Gibbons, 1978) belong to ecotypes distinct from those found on the continent. Conservation efforts should, therefor, focus not just on protecting areas inhabited by the rarities, but also on allowing genetic diversity to spread by maintaining connected metapopulations (Hannah *et al,* 2014).

Alterations to ecological interactions are usually overlooked in studies on the biological effects of climate change (Post and Pedersen, 2008). For example, phenological mismatches can lead to detrimental effects on reproductive success, through the breakdown of mutualistic interactions (Toby Kiers *et al,* 2010). Under changing climatic conditions, the leading and trailing edges of species ranges often move at different rates (Anderson *et al*, 2009). Models tend to predict more stable trailing edges due to the lack of ancestral ecological interactions in newly colonised areas (Hampe and Petit, 2005).

The finding of no significant changes in latitude or longitude in the 2050 models is unexpected given the poleward trends seen in most species (Parmesan and Yohe, 2003; Root *et al,* 2003), however this is may simply be due to the limited extent of upland and alpine areas across Europe.

6. Conclusions

6.1 Effects of experimental warming and grazing simulation on Upper Teesdale plant species

For the most part, there were no observable effects of experimental warming and simulated grazing on leaf area growth of the study species. In support of the hypotheses of the study, *P. farinosa* exhibited significantly greater dry biomass accumulation in all warmed treatments, compared to the un-warmed treatments, despite being at its warmer range extremity at the study site. Finally, across all of the species studied, no significant differences were found between competition intensity under control and experimentally warmed conditions.

The importance of reproduction for future conservation efforts was recognised by Doody (1975) in her demographic study of some of the Teesdale rarities. Further work would certainly benefit from investigating the effects of experimental warming on reproductive success of the species in question.

More replicates are clearly needed to establish the effects of the treatments investigated here with greater statistical confidence, particularly the effects of warming on competition intensity, which is an understudied area of vegetation ecology.

6.2 Effect of reservoir proximity on the temperature environment of Widdybank Fell

Contrary to the hypothesised impacts of proximity to the Cow Green reservoir, no effects were observed on mean air temperature or growing degree day sum and no lag effect was observed on temperature at the daily scale. The reservoir did appear to moderate cold temperature extremes, significantly reducing exposure to freezing events.

While it is hard to relate this phenomenon directly to its impact on the local vegetation, future work could certainly benefit from using distribution data of the rarities, collected by Margret Bradshaw, to attempting to track any movement of populations post reservoir construction.

It is important to note that demographic turnover plants can vary greatly across their ranges, creating a lag between environmental changes and their biotic responses (e.g. Lönn and Prentice, 2002). For one of the species studies here, *V. rupestris*, the population turnover time was estimated at 32 years (Doody, 1975). While this could significantly delay the observable impact of climate change, it would not obscure the effects of the reservoir, which was filled in 1971 (Lewthwaite, 1999). This precludes the possibility of a local extinction debt due to the reservoir’s construction.

6.3 Responses to post-industrial climate change across their European ranges

All species studied exhibited a small trend towards lower latitudes and longitudes, representing a more maritime environment, in the post-industrial era. *G. verna* and *P. farinosa* were observed significantly later in the year and *P. farinosa* and *V. rupestris* were found to inhabit significantly higher altitudes.

Accounting for concurrent increases in mean global surface air temperature, *G. verna* and *P. farinosa* did not fully track the spatial or temporal movement of their fundamental thermal niches in the post-industrial era. Conversely, *V. rupestris* was able to track its thermal niche, even exhibiting a net shift into cooler areas, driven primarily by its movement towards higher altitudes. This is, however, a short-term solution which may lead to population isolation in the future. These findings support the intuitive logic that species would shift their ranges to higher altitudes more readily than to higher latitudes, due to the smaller distance required to experience an equivalent temperature reduction.

The delay in phenology observed is counterintuitive given that it represents a shift towards warmer summer temperature for the species studied but could be explained by alterations to the seed stratification process during winter.

As species shift their ranges it is likely that they will form novel species interactions and potentially lose ancestral interactions, further complicating predictions for their future success.

6.4 Future distributions of and variations in the study species

MaxEnt distribution models indicated that each of the study species are at their environmental limits in Upper Teesdale, with only small areas of the UK being classified as climatically suitable form them. In terms of latitude and longitude, however, the UK does not lie at the extremes of the ranges of any of the species studied, suggesting the maritime nature of the UK climate may play an important role in determining distribution of the study species.

The MaxEnt model created using only the UK occurrence data for *P. farinosa* indicates that a much larger area of the UK is currently suitable for the species, supporting the hypothesis that *P. farinosa* may have developed regional adaptation to the UK climate. The mean annual temperature range and isothermality, the most important predictors of *P. farinosa* presence in the UK, at known occurrence locations showed significant differences in mean values between inhabited regions. This further supports the notion that the species has developed regionally adapted ecotypes. This point should not be overlooked as local adaptation of plants has been shown to counteract and outweigh the effects of climatic changes (Liancourt *et al,* 2013).

Due to both the isolation of the UK populations and low seed dispersal abilities of the species studied and the apparent differences in climatic requirements of the continental ecotypes, genetic input from populations outside of the UK is unlikely. While Upper Teesdale is relatively distant from the core ranges of the species studied, such areas can be important “stepping-stones” for species range shift (Hannah *et al,* 2014).

For all models, little change is predicted in distribution by 2050 based in the IPCC’s RCP 6 climate projection. For the UK, and much of Europe, the predicted distributions are much larger than the known distributions of the species, showing that the species do not currently fill their fundamental niches. This suggests that factors other than climate are important dictators of the species ranges.

It is well established that plants can modify their microclimate (Cuddington *et al,* 2011), for instance, low-growing species can decouple from atmospheric temperature to some extent by reducing heat convection (Körner, 2007). In the present study, this was inadvertently demonstrated when bryophyte removal was shown to significantly reduce relative humidity. In light of this, an important direction for future research could be to create a fine-scale dataset, using the bioclim variables outlined by Hijmans *et al* (2005), for the Upper Teesdale region. This would facilitate much more accurate distribution modelling for the area.

6.5 Summary of the concepts investigated

The effects of the phenomena studied here on a species' distribution and persistence can be best conceptualised as a simple two-dimensional representation of a Hutchinsonian niche. Here mean and minimum temperatures were used to demonstrate the thermal niche of a hypothetical species. Units are arbitrary and are provided as examples only, as such, they do not correspond numerically to the effects of the environmental variables discussed.

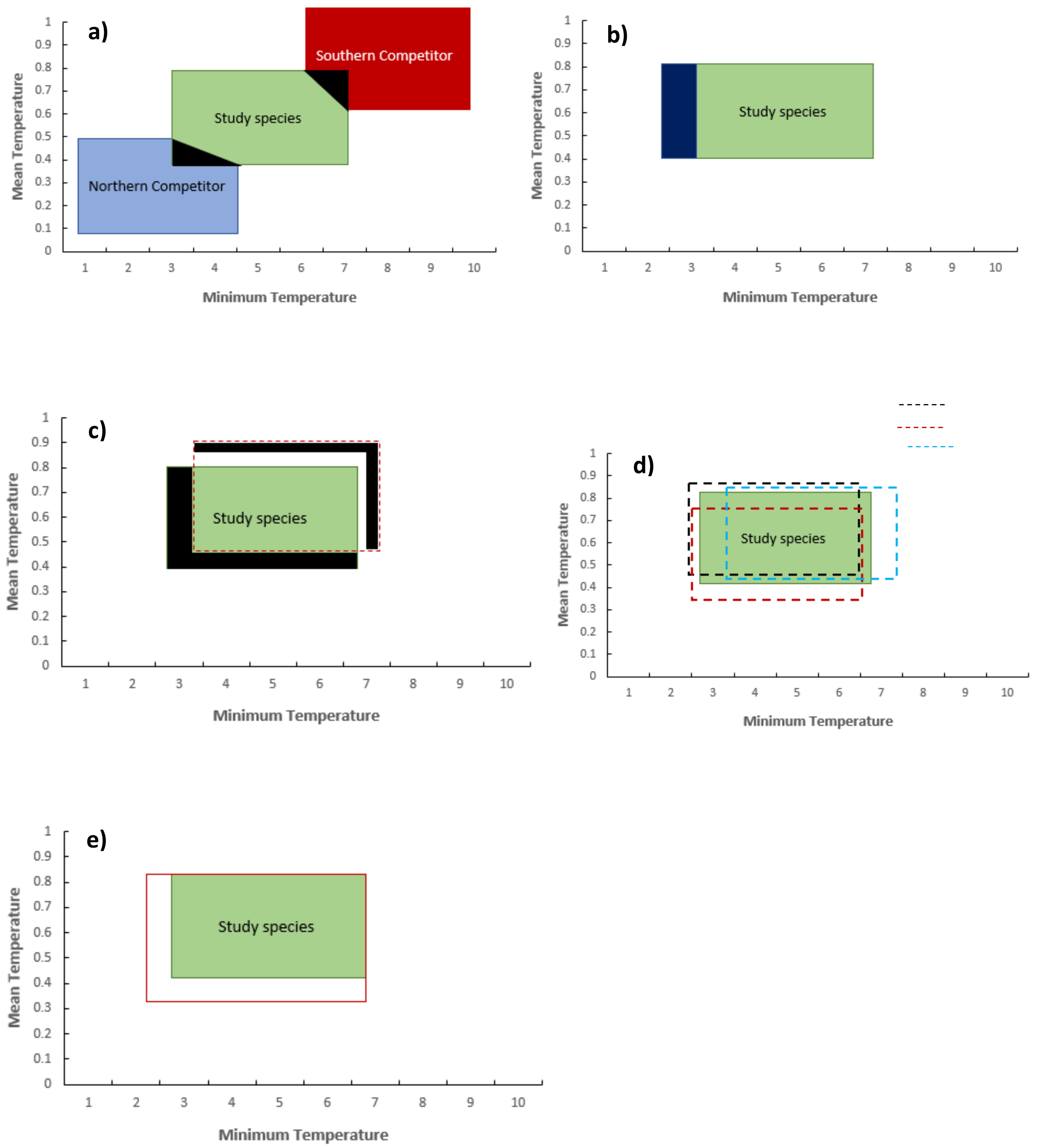

Figure 6.1 Diagrammatic representations of the impact of a) competitor species, b) lake proximity, c) range shifts, d) ecotypic variation and e) microclimate on niche breadth of a species.

The first figure demonstrates the simplified thermal niches of three northern hemisphere species, with a more northerly species better adapted to colder temperatures and a more southerly species better adapted to warmer temperatures (fig. 6.1. a). In regions where the temperature is suitable for both the study species and a competitor, i.e. the respective niche's overlap, resources must be divided between the two. Here this is simplified by splitting the region of overlap exactly in half.

The second figure illustrates how moderation of the minimum temperatures by the reservoir could allow the study species to inhabit a region which would otherwise lie outside of its thermal niche (fig. 6.1.b).

In the third figure, a representation of failure of a species to track its niche, as was the found to have occurred in *G. verna* and *P. farinosa* in chapter 3, is given (fig. 6.1.c). The green plot represents a species niche at a given point in time, while the red plot represents the same niche following a shift in environmental conditions. In this instance, the lower black section indicates the area in which the species currently lives which will no longer be suitable in the future. The white section indicates the newly suitable habitat the species has colonised and the upper black section the newly suitable habitat the species has failed to colonise.

The following figure demonstrates how ecotypes of the same species which have slightly different environmental tolerances give rise to the average thermal niche displayed in all of the figures (fig. 6.1.d).

Finally, the last figure illustrates how the insulative effects of ground-cover vegetation can allow plants to alter their own environment, making areas with temperature previously too low habitable (fig. 6.1. e).

The present study suggests that the scenarios shown in Figure 6.1 b, c and d may affect the study species so some extent in Upper Teesdale. Chapter three showed that the Cow Green Reservoir moderated temperature minima at ground level (Figs. 2.6, 2.8 a), potentially extending the species' thermal niches to include areas which would ordinarily experience temperatures too low at times. In Chapter four, *P. farinosa* and *G. verna* were found to have shifted their spatial and temporal ranges insufficiently to fully counteract the effects of post-industrial climatic warming (Table 3.1). This could lead to a reduction in overall niche breadth, as demonstrated in Figure 6.1 c, as species fail to fully exploit areas of newly favourable climate. Finally, as was shown for *P. farinosa* in Chapter 5 (Figs. 4.4, 4.6), ecotypic variation may occur in the environmental tolerances of species. This may confound the above effects on niche breadth, with plants possibly becoming better adapted to different environmental conditions in different areas. No compelling evidence was found regarding the role of interspecific interactions in determining niche breadth of the study species.

To conclude, it is hard to establish the extent to which the presence of the Teesdale rarities can be attributed to climate, past and present, geomorphology or anthropogenic land management processes, deforestation, grazing etc.

The prospect of the UK becoming climatically unsuitable for the rarities to persist creates both biological and social implications for conservation efforts. A commonly raised issue within the field of ecology is the idea of the shifting baseline syndrome leading conservationists trying to maintain an ecological state which may no longer be suited to the current environment (Papworth *et al,* 2009). While it is true that the future existence of the species investigated here is probably not dependent on the populations in the Teesdale, the unique local adaptation of these populations could provide an important source of the phenotypic diversity needed to survive in a rapidly changing environment.

No area of the present study raised any pressing concerns for the future of *Gentian verna, Primula farinosa* or *Viola rupestris* in Upper Teesdale under current climate change scenarios. The environment of the northern Pennines is climatically stable relative to the Alpine and Boreal core ranges of the species and does not appear to pose any great threat to the longevity of the populations

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