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The ecology and conservation of *Arctostaphylos uva-ursi* Bearberry heath habitats in the Burren, Western Ireland

Thesis submitted to the National University of Ireland, Galway
for the degree of Doctor of Philosophy

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Declaration

I certify that this Thesis is all my own work and that I have not obtained a degree in this University or elsewhere on the basis of any of this work.

Abstract

This thesis focuses on *Arctostaphylos uva-ursi* and co-occurring species within vulnerable habitats in the Burren region of western Ireland. The objectives of this research were: to describe the plant communities; to monitor their response to cutting as a management tool to restore overgrown heaths to good conservation-status by promoting the growth of *Arctostaphylos* and other key prostrate dwarf shrubs *Empetrum nigrum* and *Dryas octopetala*; and to explore the reproductive biology of *Arctostaphylos.*

The Burren *Arctostaphylos*-rich heaths were compared to EU protected habitats, such as Alpine and Boreal heaths and European dry heaths. Threats to these rare habitats were identified, mainly the encroachment of more vigorous species, such as *Calluna vulgaris,* at least partly due to under-grazing. Thus tall over-mature *Calluna* was cut and removed in experimental trials and the effects on the vegetation cover and species composition were monitored in the short-term study. As climate change is an added potential threat, baseline data were obtained for the reproduction of *Arctostaphylos,* its pollination mechanisms, rates of fruit and seed set in the Burren upland and lowland populations as well as its phenology; pollinator-exclusion experiments and observations were undertaken.

Four distinct communities were identified: the *Arctostaphylos – Sesleria* heathy grasslands, found throughout the Burren; the *Dryas – Empetrum* heaths and the *Calluna – Arctostaphylos* heaths, both restricted to the uplands, the latter subject to the cutting trials; and the rarest and most vulnerable *Arctostaphylos – Juniperus communis* heath in the eastern Burren lowlands. Cutting trials reduced *Calluna* cover, increased species richness and diversity; *Molinia* was reduced by the spring cut and bracken appeared to decrease following cutting in autumn. In terms of reproductive biology, *Arctostaphylos* flowers were visited mainly by bumblebees, fruit and seed production took place more in open-pollinated than in pollinator-excluded flowers, but curiously seedlings were not observed in the field.

Acknowledgements

Massive thanks first and foremost to Micheline Sheehy Skeffington for her supervision, advice, and for her constant encouragement, advice and guidance through it all. Thank you also to Mike Gormally for his support, insight and enthusiasm.

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I would like to thank all the Burren farmers who allowed me to access their land for the duration of my research, and in particular those who let us

carry out the cutting trials and helped bringing equipment up to the winterages.

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Finally I could not have completed this work without the love, support and dedication of my wonderful family and friends, in particular my husband Cillian Hanrahan and my mother Áine O'Loughlin, and also my father George Irwin, his partner Nuro, my brother Naoise Irwin and my special little girl Nancy Hanrahan who kept on telling me 'back in office mammy'.

Dedicated to the loving memory of my grandmother Nancy O'Loughlin and for Nancy Óg and the next little one whose due date is impending!

Chapter 1. Introduction

1.1 Heathlands

1.1.1. Heathlands in Europe

European heathlands are found along the Atlantic seaboard from northern Norway to the north of Portugal and also in northern continental Europe (Krzywinski et al., 2009). They are open landscapes dominated by ericaceous dwarf shrubs such as *Calluna vulgaris* and *Erica* species, typically developing on nutrient-poor soils (Fagúndez, 2013). Heathlands are important habitats in terms of cultural history, biodiversity and landscape conservation and additionally they facilitate ecosystem services such as carbon sequestration and water filtration (Fagúndez, 2013). Formerly heathlands were thought to be a natural vegetation type but it is now recognised that they are an example of habitats which have been halted in their successional stages having been shaped by traditional management/land-use practices by humans following forest clearances since at least 4,000 years ago (Gimingham, 1972, Webb, 1986, Kvamme et al., 2004). Thus they are often described as cultural landscapes (Krzywinski et al., 2009).

1.1.2. Heathland management in Europe

The management of heathlands is a long-standing practice and, although there has been a considerable amount of regional variation in the forms of management, traditional methods usually involved a number of the following: cutting of peat, mowing and/or burning of heather to promote growth of young shoots, and different grazing systems (Gimingham, 1972, Webb, 1986, Fagúndez, 2013). In many heathland areas traditional management continued up until the mid-eighteenth or early-nineteenth century when there was a shift from subsistence farming to more intensive agriculture (Webb, 1998).They were formerly a widespread vegetation type in Western Europe, extending over millions of hectares, but currently only a fraction of this area remains (Webb, 1998).

Heathlands are under threat, mainly from habitat loss due to change of land-use (afforestation, urban development, agricultural intensification), resulting in highly fragmented heathland habitats (Webb, 1998, Fagúndez, 2013). Other threats include pollution, eutrophication and climate change (Fagúndez, 2013). In recent years much research has been undertaken relating to heathland ecology, management and conservation (Fagúndez, 2013).

1.1.3. Conservation of European heathlands

The EU Habitats Directive (Council Directive 92/43/EEC) and the EU Birds Directive (79/409/EEC) provide lists of habitats and species which are rare and/or threatened within EU member states and the Directives provide for maintaining or restoring the same through the creation of a network of designated sites (Special Areas of Conservation SACs and Special Protection Areas SPAs) also known as Natura 2000 sites (Hickie, 1997). Seven distinct heathland types are protected under the EU Habitats Directive (92/43/EEC) as Annex I habitats, each with a number of sub-types, and as they are seral habitats, management is a requirement for their conservation (Gimingham, 1972); in the absence of management these habitats tend to revert to woodland (Kvamme et al., 2004). Two of the protected heath habitats in the EU are Alpine and Boreal heaths (habitat code 4060) and European dry heaths (4030) (92/43/EEC). These both contain sub-types that occur in Ireland and have specific communities found on calcareous substrate and/or within the Burren region, containing *Arctostaphylos uva-ursi* among other positive indicator species (NPWS, 2013a, NPWS, 2013b).

The focus of this thesis is on heathland communities with *Arctostaphylos uva-ursi* and therefore a review of associated plant species follows.

1.1.4. Summary of international *Arctostaphylos uva-ursi* heath communities

As a species with a far-ranging global distribution it is useful to examine some of the range of plant communities within which *A. uva-ursi* occurs.

***North America*.** In the subalpine zone of the Pacific coastal states of Washington State, USA and British Columbia, Canada, *A. uva-ursi* is dominant in occasional areas of the North Cascades at 1750 to 2250 m on well-drained southern slopes with snowmelt from late May to mid-June (Douglas and Bliss, 1977). It is also a frequent ground flora element in the Canadian and Alaskan boreal *Picea glauca* forests, often together with *Arctostaphylos rubra* (Peinado et al., 1998).

***Europe*.** Gimingham (1972) presents categories of heath communities within Europe, containing *A. uva-ursi,* as a 'northern' *Calluna-Arctostaphylos uva-ursi* community with continental distribution (Denmark and Halland in south-west Sweden) and an 'oceanic' *Calluna-Erica cinerea* heath, often with *A. uva-ursi* and a coastal distribution (north Scotland and south-west Norway).

On the Swedish island of Gotland *A. uva-ursi* is found growing beneath *Pinus sylvestris,* together with *J. communis, V. vitis-idaea* and *Melampyrum pratensis*, *Epipactis atrorubens, Antennaria dioica, Pilosella officinarum* and a well-developed moss layer composed of *Tortella tortuosa, Rhytidiadelphus triquetrus* and *Hypnum lacunosum* (Paal and Rajandu, 2014). In the boreal zone of northern Finland there is heath vegetation dominated by *Betula nana, Vaccinium vitis-idaea, Arctostaphylos alpinus, A. uva-ursi* and *Juniperus communis* (Törn et al., 2006). Most of these Scandinavian heath communities are open, i.e. without a tree canopy.

In Poland Artostaphylo - Callunetum heaths occur in the north and north-east, often in association with *Pinus sylvestris* and sometimes *Betula pendula* and *Juniperus communis*. These heaths can be rich in herbaceous species, and/or mosses and lichen, notably *Solidago virgaurea, Geranium sanguineum, Hypnum jutlandicum* and *Cladonia* species, depending on light availability (Adamska et al., 2015).

In Bulgaria *Arctostaphylos uva-ursi* occurs in mountain areas between 1000 – 2500 m altitude on soils of different acidity and structure; it is a pioneer on rocky outcrops and stony places, rooting in rock crevices and often forming 100 % cover (Genova and Russakova, 2015). In the next successional stage it most frequently occurs with *Bruckenthalia spiculifolia, Vaccinium myrtillus* and *V. vitis-idaea*; on limestone it occurs with *Anthyllis vulneraria, Asperula cynanchica, Dryas octopetala* and *Sesleria rigida*; and at lower altitudes it is a ground layer shrub under *Pinus sylvestris* and *P. nigra* subsp. *palassiana.* It is listed in the Red Data Book of Bulgaria as 'rare' and the main threat is collection of its leaves for medicinal purposes (Genova and Russakova, 2015).

In the central Pyrenees, in Spain, *A. uva-ursi,* together with *Vaccinium myrtillus,* occurs in pine forest (*Pinus sylvestris* and *P. uncinata*) on south-facing slopes at 1500-1800m elevation (Gracia et al., 2007). In the Cantabrian Mountains of north-west Spain at 1150m elevation *A. uva-ursi* occurs in a heath community with the dominant tall heather *Erica australis* ssp. *aragoniensis,* in addition to *Erica umbellata, Calluna vulgaris, Genista (Chamaespartium) tridentatum, Halimium alyssoides, Halimium umbellatum* and *Quercus pyrenaica* (Calvo et al., 2002a).

In Norway *Arctostaphylos uva-ursi* is a common species in western coastal heaths. For example, it is abundant in the *Calluna-Arctostaphylos uva-ursi-Racomitrium lanuginosum* acidic heath where *Empetrum nigrum, Vaccinium vitis-idaea, Hypnum jutlandicum* and *Cladonia arbuscula* and *C. rangiferina* are frequent; as well as in the *Calluna-Arctostaphylos uva-ursi-Carex flacca* rich heath where *Juniperus communis, Empetrum nigrum,* *Linum catharticum, Succisa pratensis* and *Hylocomium splendens* are all common species (Nilsen and Moen, 2009, Kaland and Kvamme, 2009).

In north-east Scotland the *Calluna vulgaris-Arctostaphylos uva-ursi* heaths occur in the sub-montane zone of the east-central Highlands. As well as *A. uva-ursi* and *Calluna, Erica cinerea* is often present together with *Vaccinium myrtillus, V. vitis-idaea* and *Empetrum nigrum* ssp. *nigrum* sometimes replaces *A. uva-ursi.* Common bryophytes include *Hypnum jutlandicum, Pleurozium schreberi, Hylocomium splendens and Dicranum scoparium*; additional species of northern distribution include *Pyrola media* and *Antennaria dioica* (Ward, 1971a, Ward, 1971b, Rodwell, 1991). A herb-rich and a herb-poor sub-community, and a *Cladonia*-rich sub-community have been described (Ward, 1971a).

Many of the continental heaths with *A. uva-ursi* have *Pinus sylvestris* as a canopy component, whereas the oceanic heaths of Scotland and Scandinavia are open, since grazing and exposure are more intense in those regions, thus preventing recolonization by trees.

1.2 Irish heathlands and peatlands

Peatlands are an important habitat in Ireland and formerly comprised 16% of the land surface of Ireland, or 134 million hectares (Hammond, 1979). However human activities such as peat harvesting, afforestation, land reclamation and drainage has reduced this area by approximately a fifth (Foss et al., 2001). Even less of the remaining area is of conservation importance, amounting to no more than 269 thousand hectares (Malone and O'Connell, 2009).

The earliest formation of peatlands (as fen peat) in Ireland began in the postglacial period around 9,000 years ago (Mitchell and Ryan, 2001). Peatlands develop in areas of poor drainage and/or sustained high rainfall with the presence of *Sphagnum* moss as a key species (Mitchell and Ryan, 2001). They are broadly classified into fens, raised bogs with their characteristic dome-shape and peat depths up to 12 meters, and blanket bogs with peat depths of between 2 and 7 meters (Malone and O'Connell, 2009). Shallower peatlands are usually drier and are classified as heaths, which may grade into the deeper blanket bogs. Blanket bogs require a permanent supply of moisture in the form of rainfall whereby the soil becomes progressively leached of minerals resulting in podzolisation, facilitating the invasion by *Sphagnum* moss species and peat formation (Mitchell and Ryan, 2001). The waterlogged conditions allowed for the expansion of the peaty podzol, which, over time, covered the ground with a layer of peat (Mitchell and Ryan, 2001). Blanket bogs in Ireland are confined to the western regions and the uplands.

1.2.1. Heath formation and classification in Ireland

Heath comprises the driest type of peatlands and has a peat depth of less than 1 metre (Rodwell, 1991) and > 25% cover of dwarf shrubs (Fossitt, 2000). In general there are four main types of heath in Ireland: dry siliceous heath HH1; dry calcareous heath HH2; wet heath HH3 and montane heath HH4 (Fossitt, 2000); the best examples of these heaths may be linked to conservation-grade Annex I habitats: European dry heaths (4030); *Juniperus communis* formations on heaths or calcareous grasslands (5130); northern Atlantic wet heaths with *Erica tetralix* (4010); and Alpine and Boreal heaths (4060) respectively (EU Habitats Directive 92/43/EEC). The distribution of Irish heathlands is, as in North-west Europe, largely coastal, along the Atlantic seaboard as well as on mountains (Gimingham, 1969). The formation of heathland requires relatively mild humid conditions all year round, withstanding limited periods of drought, with an annual rainfall in the range of 600mm to 1100mm (Gimingham, 1972). Historically heathland habitats in Ireland have not been as widely studied or classified as the deeper peatlands or bogs which are more extensive (Malone and O'Connell, 2009). There is however pollen evidence to support the presence of a heath understory, with *Calluna* and *Erica tetralix,* in an open *Pinus* forest during the Boreal and early Atlantic periods (8500 to 6700 B.P.) in parts of western Ireland (O'Connell, 1990).

In recent years the National Parks and Wildlife Service (NPWS) commissioned a National Upland Habitats Survey from 2009 to 2014 which targeted Annex I habitats and fed into the Article 17 report of the EU Habitats Assessment for the Republic of Ireland (NPWS, 2013a). This survey took place on lands that are designated for conservation, (e.g. Special Areas of Conservation, SACs) and on non-designated lands above 150 meters in altitude and provides the most comprehensive study of Irish heathlands to date, including an estimation for the total potential range of heathlands of conservation value: 156,600 km^2. However the areas of the habitats of EU importance are notably smaller: European Dry heath (4060): 1,094 km^2; Wet heath (4010): 1,430 km^2; and Alpine heath (4060) 170 km^2 (codes are from EU Habitats Directive 92/43/EEC; (NPWS, 2013a)). Most of these occur on acidic soils over siliceous rock formations, but in a few cases, such as in the Burren, in Counties Clare and Galway in the west of Ireland, they form over limestone.

1.2.2. Heath formation in the Burren

The Burren is well-known for its high to excessive drainage, as it is a karst landscape comprising pure and highly porous Carboniferous limestone (Feehan, 2001) and has only one permanent river and few permanent lakes, but is rich in ephemeral lakes or turloughs which typically flood in autumn with lime-rich groundwater and empty in spring, giving way to grassland (Sheehy Skeffington et al., 2006). Due to the karst nature of the bedrock in the Burren there is limited potential to retain water and thus very little potential for peatland development within the Burren region except in areas where shale persists over the limestone creating waterlogged conditions (Jeličić and O'Connell, 1992).

However, in the Burren uplands, the persistent rainfall enables peat to form on the limestone (D'Arcy and Hayward, 1992). The limestone heaths contain calcifuge (acid-loving) species as well as calcicolous (lime-loving) species in a predominantly calcareous environment. The presence of calcifuges may be related to the acidification of the soil resulting from leaching of minerals from the surface layers above the limestone due to high levels of rainfall, which may also lead to limited soil aeration in deeper peaty soils or they may occur on unleached soils with nutrient deficiencies (Grime, 1963, Jeffrey, 2003). In chalk heath where soil is between pH 5 and 6 both calcicoles and calcifuges have been found to root in loamy soil above the chalk, while other calcicole species require pH 7 or higher (Grubb et al., 1969). In contrast the presence of loess (quartz-derived non-lime air-borne material deposited from Connemara in periglacial times) may persist in pockets rich in organic matter providing areas of low pH, often occurring in close proximity to soils rich in limey material and of higher pH – these give rise to heterogeneous soil conditions where calcifuges can grow beside calcicolous species (Jeffrey, 2003). The result of these soil processes is that heath vegetation is found side by side with calcareous grasslands and limestone pavement (Jeffrey, 2003). In the lowlands, calcareous heaths may also have arisen after over-exploitation and abandonment of shallow soils in early historic times (C. Roden pers. comm).

1.2.3. Summary of Burren heath plant communities

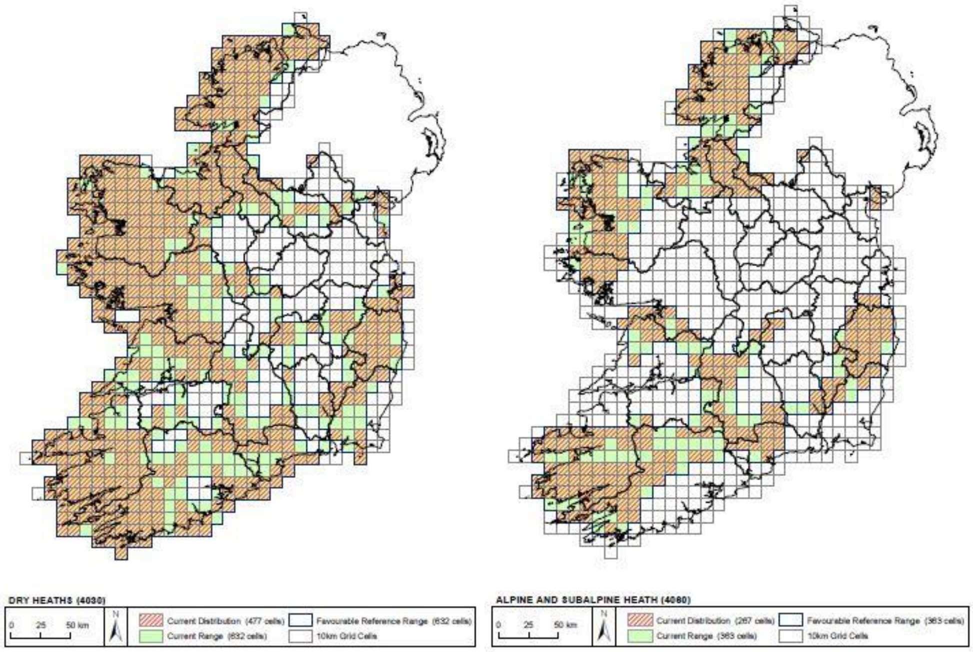
There are two distinctive types of heath found in the Burren: one on leached acidic soils in the uplands with dominant *Calluna vulgaris; Molinia caerulea* and *Erica cinerea* may also be prominent and occasionally *Arctostaphylos uva-ursi* (Ivimey-Cook and Proctor, 1966, Parr et al., 2009); the other rarer type is characterised by *Dryas octopetala,* typically hosting a range of calcareous grassland species and often also features *Arctostaphylos uva-ursi* and/or *Empetrum nigrum*, two dwarf shrubs with restricted distribution within the Burren (Parr et al., 2009). The *Calluna* heath may correspond to Annex I habitat European dry heaths (4030) and the *Dryas* heath may correspond to either Alpine and Boreal heaths (4060) or European dry heaths (4030).

1.2.4. European dry heaths in Ireland

European dry heaths (4030: EU Habitat Directive 92/43/EEC), hereafter called 'dry heaths', are protected habitats in Europe and as such their conservation is an obligation. The range and distribution of this habitat in Ireland is shown below (Fig. 1.1a). There are two regional variants: (a) siliceous heaths; (b) calcareous heaths; positive indicator species for dry heaths common to both types are: *Arctostaphylos uva-ursi, Calluna vulgaris, Erica* cinerea, and *Empetrum nigrum* (Wilson and Fernández, 2013, NPWS, 2013a, Perrin et al., 2014). The siliceous variant also comprises: *Daboecia cantabrica, Racomitrium lanuginosum, Ulex gallii, Vaccinium myrtillus* and *V. vitis-idaea* (NPWS, 2013a, Perrin et al., 2014). Additional indicator species for the calcareous variant include: *Breutelia chrysocoma, Carex flacca, C. pulicaris, Dryas octopetala, Galium saxatile, G. verum, Juniperus communis, Sesleria caerulea, Succisa pratensis,* and *Thymus polytrichus* (Wilson and Fernández, 2013, NPWS, 2013a).

1.2.5. Alpine and Boreal heaths in Ireland

Alpine and boreal heaths (4060), hereafter called alpine heaths, are afforded the same protection as dry heaths (4030) within EU member states. The range and distribution of this habitat in Ireland is shown below (Fig. 1.1b). There are two variants in Ireland (not distinguished on map) that fall into this habitat category: the more widespread is found from 350-400m OD (Ordnance Datum) on siliceous rocks in the western regions of counties bordering on the Atlantic: Galway (Connemara), Mayo, Sligo, Donegal, on mountains from Kerry in the south, and north-eastwards across to Wicklow in the east. The second type occurs below 300m and in some areas down to sea-level on the Burren limestone in south west Galway and North Clare (NPWS, 2013a, NPWS, 2013b). Positive indicator species for alpine heaths differ for the upland (Perrin et al., 2014) and lowland (Wilson and Fernández, 2013) types – species common to both comprise: *Arctostaphylos uva-ursi, Calluna vulgaris, Empetrum nigrum, Erica cinerea,* and *Solidago virgaurea.* In addition the upland variant includes: *Vaccinium myrtillus* and *V. vitis-idaea,* a number of bryophytes such as: *Diphasiastrum alpinum, Diplophyllum albicans,* and *Herbertus aduncus;* and lichens including: *Cladonia arbuscula, C. portentosa* and *C. uncialis* (NPWS, 2013a, Perrin et al., 2014). Additional indicator species for the lowland variant include a suite of calcareous species such as: *Sesleria caerulea, Juniperus communis, Thymus polytrichus, Campanula rotundifolia, Linum catharticum, Breutelia chrysocoma, Hylocomium splendens* and *Ctenidium molluscum* (Wilson and Fernández, 2013, NPWS, 2013a). It is typically defined by the presence of *Dryas octopetala* and often occurs in association with species-rich calcareous grassland and limestone pavement (Wilson and Fernández, 2013, NPWS, 2013a).



Figures 1.1 a and b. Current distribution (red cells) and range (green cells) of **(a)** European dry heath (4030) and **(b)** Alpine and Boreal heath (4060) in the Republic of Ireland based on its presence within 10 Km squares. Source: (NPWS, 2013b).

The distribution maps of both heath habitats (Figs. 1.1a and b) coincide with the topographic map of Ireland (Fig. 1.2), in particular for alpine heaths while dry heaths extend further into the lowlands.

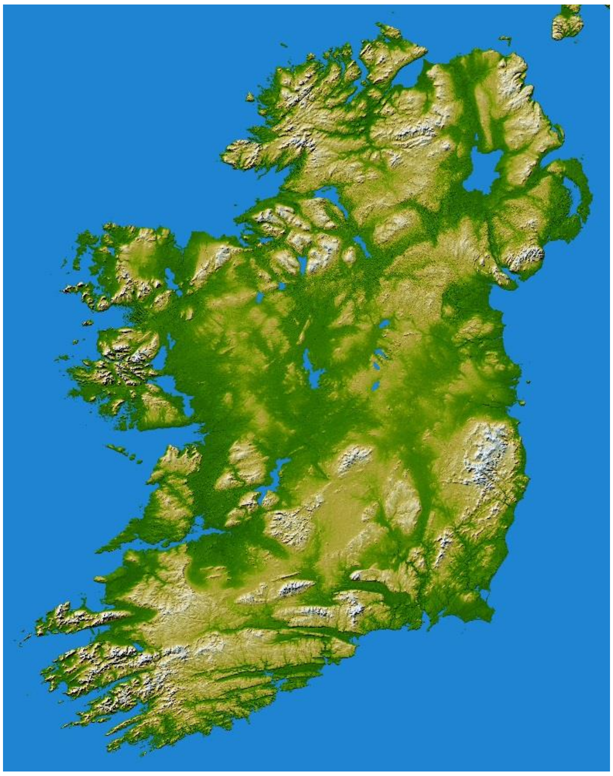


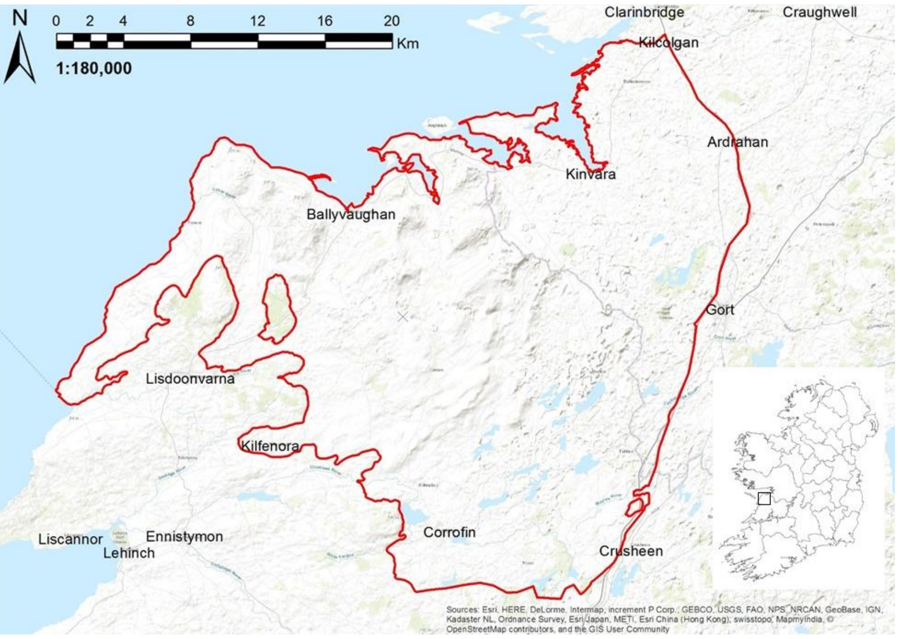
Figure 1.2. Topographic map of Ireland depicting its central lowland plain and coastal mountains. Source: (NASA, 2000).

The focus of this thesis is on Burren heath communities of conservation importance containing *Arctostaphylos uva-ursi, Dryas octopetala* and/or *Empetrum nigrum*, as these are nationally and locally rare (Parr et al., 2009) and *Arctostaphylos*-rich heaths form an important part of the vegetation on high ground in the Burren (Ivimey-Cook and Proctor, 1966, Webb and Scannell, 1983, Proctor, 2013). While the heaths in the high Burren have been studied previously to some degree, the extent of this type of heath at near-sea level are mostly smaller in size and occur in a few isolated patches in the low East Burren and these communities are as yet undocumented (C. Roden, M. Sheehy Skeffington pers. comm.).

1.3 Region of study

1.3.1. The Burren

From the Gaelic: *Boireann* meaning 'rocky place', the Burren is a region of karst landscape covering approximately 300 km^2 of counties Clare and Galway on Ireland's mid-western seaboard (Burren Programme, 2016). It is bounded by the Atlantic to the north and west, the overlying Namurian shales associated with the towns of Doolin, Lisdoonvarna, and Corofin to the south, and arbitrarily by the N18 Ennis to Galway road (between the towns of Crusheen and Kilcolgan) to the east (Fig. 1.3). To the west the 'high Burren' is composed of terraced hills of 300-330m altitude and to the east the 'low Burren' limestone plains are just 15-30m above sea level. The mean annual temperature for the Burren is between 8 and 10°C and the mean annual rainfall can vary from 1,200mm in low-lying areas to 2,000mm in upland coastal areas, south-westerly winds dominate therefore rainfall and winds are higher in the west of Ireland; especially over higher ground (Met Éireann, 2017). The landscape comprises numerous important habitats, many of which are priority Annex I habitats (EU Habitats Directive 92/43/EEC) for example, turloughs (seasonal lakes), limestone pavements and dry



Sources: Esri, HERE, DeLorme, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, Mapmyindia, © OpenStreetMap contributors, and the GIS User Community

Figure 1.3. The study area of the Burren in north Co. Clare and south-west Co. Galway, indicated by the red boundary line which is the extent of the Burren limestone (the red circle in the south-west corner is a shale outlier). Map of Ireland inset.

calcareous orchid-rich grasslands, alpine heaths, dry heaths, Juniper formations on limestone and ash woodlands.

1.3.2. Geology and soils of the Burren

The limestone of the Burren, up to 800m thick in parts, was formed during the Carboniferous Period, approximately 340 million years ago, under a shallow tropical sea; the hard calcite shells of sea creatures fell to the ocean floor and together with calcium-rich debris precipitating out of the sea water formed layers on the sea bed which eventually became the limestone rocks (Mitchell and Ryan, 2001, Hennessy et al., 2010). Sand and mud was deposited in the Upper Carboniferous forming the Clare shales which sit on top of the limestone, but much was eroded away over time though some areas of this impermeable shale remain, for example on the top of Slieve Elva (Feehan, 2001).

One of the major factors influencing the landscape was the last Ice Age which ended approximately 15,000 years ago (O'Connell, 2013). The ice moved from the north east, removing much of the shales, and depositing boulder-clay, on the valley floors and in isolated patches on the plateau; materials in the drift may have contributed to the formation of less calcareous soils than the parent material, but in general there is very little soil cover and where there is, it is very patchy (Farrington, 1965, Feehan, 2001).

The majority of the Burren soils are classified as rendzinas which are shallow (usually not more than 25cm deep but some are up to 50cm deep), neutral to calcareous, well to excessively drained, clay loams, with varying amounts of exposed rock (Finch, 1971). There are also some areas of brown earth derived from limestone till which are found on rolling hills that can be associated with tillage and grassland production except where many boulders occur (Finch, 1971).

The limestone rock in the Burren is a pure, bedded limestone and is therefore easily subject to water erosion (Sheehy Skeffington et al., 2006) as rainwater contains carbonic acid, it is slightly acidic and dissolves the calcium carbonate in the rock (Mitchell and Ryan, 2001). The Burren has been extensively weathered giving rise to countless karst landscape features such as caves, underground rivers, turloughs, clints, grykes and karren on the pavement areas (Simms, 2006).

In some cases solution cups are formed on the clints and other times the water is washed through the grykes leaching out minerals and enlarging the fissures as the water moves through the cracks (Hennessy et al., 2010). In the solution cups organic matter such as soil and/or animal faeces can build up and subsequently decompose, and where these cups are deep enough, plants may colonise (Moles and Breen, 1991, Roden, 2001). Algae are the pioneers in these solution cups (Doddy and Roden, 2014), followed by mosses, lichens and species such as *Carex flacca, Carex pulicaris* and *Juncus articulatus*, then as soil builds up the vegetation becomes more dense – the sedges remain important components along with *Sesleria caerulea, Succisa pratensis, Thymus polytrichus* and in some cases *Molinia caerulea* is present (Ivimey-Cook, 1965). The final stage of colonisation is when the surface layer of the soil, which is high in organic content, in these solution hollows begins to leach minerals creating acidic conditions and calcifuge species may be found in these micro-habitats such as *Calluna vulgaris* and *Potentilla erecta* and the bryophyte *Breutelia chrysocoma* (Grime, 1963, Ivimey-Cook, 1965).

1.3.3. The Burren and its flora

The Burren is internationally acclaimed for its unique assemblages of plant species: the only place in the world where arctic-alpine or northern species and Mediterranean or southern species grow side-by-side (Webb and Scannell, 1983). It harbours a number of species rare in Ireland and the Burren uplands are home to over 70 percent of the country’s vascular plant species on only 0.5 percent of the country’s geographic area (Webb and

Scannell, 1983, Dunford, 2002). While the arctic-alpine species have persisted since the post-glacial period (O'Connell, 2013), the Mediterranean species presumably came into Ireland more recently (Webb and Scannell, 1983, Roden, 2001).

The Burren is the most northerly latitude for some of the southern species that occur there, and also the most southerly latitude for arctic-alpine species that occur at sea-level. It is striking that these species are as abundant as they are in higher latitudes and altitudes, for example *Dryas octopetala* forms dense mats over a very large area and *Gentiana verna* can be seen flowering profusely in springtime (Roden, 2001, O'Connell, 2013). Both species are normally found in high mountains such as the Alps (Webb and Scannell, 1983).

Arctostaphylos uva-ursi is a northern montane dwarf shrub with a circumpolar boreal distribution and in the Burren forms a rare type of heath community together with *D. octopetala* and sometimes *Juniperus communis, Empetrum nigrum* and *Calluna vulgaris* on some of the hills in the west of the Burren and in the low east Burren (Ivimey-Cook and Proctor, 1966, Parr et al., 2009).

1.3.4. Climate relicts

The arctic-alpine species are examples of climate relicts; populations that persist from a time when the climate in Ireland was periglacial in character; their distributions are now disjunct and where they occur they were able to survive through climatic changes (Woolbright et al., 2014). It has been postulated that the more exposed hills and cliffs of the west Burren never became fully wooded following the last ice age and that this allowed the dwarf shrub community with *Arctostaphylos uva-ursi* and *Dryas octopetala* to remain there (Ivimey-Cook and Proctor, 1966, Roden, 2001).

Pollen evidence suggests that the woodland which developed in the Burren uplands in the early Holocene was an open pine and hazel woodland with a heath understory and there were still areas of open landscape, especially where soils were absent or very shallow (Watts, 1984, Feeser and O'Connell, 2009). Pollen core studies at Cappanawalla, a coastal upland area of the Burren which today supports *Arctostaphylos* heath, provided only a single tetrad of *A. uva-ursi* pollen, however pollen of *Empetrum nigrum* and *Erica cinerea*, often now found in association with *A. uva-ursi*, were important and continuously present from the time period c. 300 BC – AD 1100 (Feeser and O'Connell, 2009, Feeser and O'Connell, 2010); the presence of this pollen would suggest that *A. uva-ursi* was also present in the Burren continuously since not long after the retreat of the last ice cover. *A. uva-ursi* has a very enclosed flower structure (Clapham et al., 1987) that would inhibit pollen dispersal, and it produces very little pollen (Garcia-Fayos and Goldarazena, 2008), consequently its likelihood of being found in the fossil record is low. *Pinus sylvestris* together with *Corylus avellana* would have formed a well-developed woodland in the north Burren uplands between 1500 – 300 BC, however *P. sylvestris* was not present after 300 BC suggesting it had become locally extinct (Feeser and O'Connell, 2009).

Indeed the discovery of the association of the ectomycorrhizal fungi *Cantharellus aurora*, typically hosted by *Pinus sylvestris*, with key Burren species *D. octopetala, A. uva-ursi* and *Helianthemum oelandicum* spp. *piloselloides*, may provide evidence of these dwarf shrubs having originally grown underneath a pine canopy (Liston and Harrington, 2012, Woolbright et al., 2014). The diversity of fungal symbionts with *A. uva-ursi* in the Burren populations is notably lower (seven mycorrhizal types; (Liston and Harrington, 2012)) than for example in the Austrian Alps where over 80 species of mycorrhizae were recorded in association with *A. uva-ursi* (Krpata et al., 2007). As the associations with *C. aurora* are not normally found in populations of *Dryas* and *Arctostaphylos* outside of the Burren, it suggests that these ectomycorrhizae are relict species along with their host shrub populations (Woolbright et al., 2014). Three of the ectomycorrhizal species found on *A. uva-ursi* were also hosted by *D. octopetala* (Liston and

Harrington, 2012), a species with a more widespread distribution throughout the Burren. Thus current *A. uva-ursi* populations are probably relicts from sub-canopy carpets of the species that existed in the Burren under open pine forests ca. 1500 – 300 BC years ago (Feeser and O'Connell, 2009) and that may have resembled current plant communities under open pine forest in e.g. continental Europe (Gracia et al., 2007, Paal and Rajandu, 2014, Adamska et al., 2015).

1.4 Farming and the conservation of natural habitats

1.4.1. Farming and the Burren in a historical context

The Burren was colonised by Neolithic farmers approximately 6,000 years ago and gradually they began to clear the forest to provide grazing land for stock by both cutting and burning, according to pollen records and charcoal fragment evidence (Feeser and O'Connell, 2009). Since this time, there have been farming activities in the area to varying degrees, such as woodland and scrub clearance for livestock grazing and some tillage crops, most intensive in the late 18th and early 19th centuries, as represented in the pollen record by very low levels of *Corylus avellana* and an almost absence of other arboreal pollen (Keane, 1990, Feeser and O'Connell, 2010).

Sheep farming, for wool and meat, was an important activity in the Burren during the 18th and 19th centuries (Dutton, 1808 cited in Dunford and Feehan, 2001), possibly dating back as far as 800 AD, together with some cattle, pig and goat rearing (Dunford, 2002). It is likely that the present day winterage tradition (bringing stock into the uplands for the winter months) dates back to the Middle Ages and that both cattle and sheep were out-wintered in the Burren uplands (Plunket Dillon, 1985 cited in Keane and Sheehy Skeffington, 1995). Light summer grazing, mainly by sheep, was also practiced (Dunford, 2002).

During the pre-famine years there are records of a widespread 'fuel famine' when the stems of mountain avens *Dryas octopetala* were collected for fuel (Dunford, 2002), as were sods of turf or heathy soil, and dried in stone structures called turf tiles (Dunford, 2001). Throughout the famine years (1845 – 1848) and continuing until 1901 the population of the Burren decreased by over 60% while simultaneously there was an increase in the export of livestock resulting in the reduction of sheep numbers and subsequently the severity of these pressures on the land was reduced and *C. avellana* began to recolonise (Kirby, 1981 cited in Keane, 1990). In the years after the famine farm sizes increased and cattle became the more important grazer (Ní Scannláin, 1988 cited in Keane and Sheehy Skeffington, 1995), as they are today (Dunford, 2002).

Since the 1950s and especially since Ireland's entry into the EEC in 1973 there was a push for agriculture to become more productive with greater numbers of livestock and the increasing use of fertiliser (Hickie et al., 1999). This also occurred in the Burren, especially in low-lying areas particularly where the soils were deeper and derived from glacial drift, but also on rocky rough grazing pastures (Keane, 1990, Bohnsack and Carrucan, 1999). The number of cattle continued to increase while sheep numbers declined rapidly from 1970 until 1980, when the Headage payments were introduced and subsequently sheep stock nearly doubled in some areas of the Burren over the following decade (Bohnsack and Carrucan, 1999). But overall sheep numbers were kept low compared to cattle, which is just as well as intensive sheep grazing has proved to be detrimental to some of the arctic-alpine species (such as *Dryas octopetala* and *Gentiana verna*) in England and is therefore not recommended (Elkington, 1963 and 1971 cited in Bohnsack and Carrucan, 1999). The cattle breeds were also changing from smaller hardy breeds such as Angus, Hereford and Shorthorn to larger continental breeds Charolais, Limousin and Simmental following market demands; these breeds of cattle were not as well suited to the rough terrain of the winterages and they required additional nutrients (Dunford, 2002).

Between 1970 and 1990 the number of farms in the Burren area of north Clare fell by half, while the farm sizes rose and the number of farms being managed on a part-time basis with farmers having to seek an off-farm income also increased (Bohnsack and Carrucan, 1999). Part-time farmers needed increased efficiency in terms of farm operations and the use of slatted sheds became more prevalent during the winter months together with silage feeding and this meant that the more productive grasslands were required to grow silage crops and there was an increase in slurry and fertiliser use (Dunford, 2002).

Some of the consequences of these changes in farming practices were the marginalisation and reduced level of use, both in terms of livestock units and length of grazing season, of numerous upland winterage pastures. Many of these were subject to silage feeding, and the increased use of slatted sheds for the continental breeds of cattle (Dunford and Feehan, 2001). The decreased grazing level on some sites led to scrub encroachment on many of the winterages, while on winterages with increased stock levels, silage feeding was in fixed spots, becoming point sources of aquifer pollution and enrichment and leading to local changes in plant species composition and diversity. In some cases these sites were grazed throughout the year where previously they had been only winter-grazed (Bohnsack and Carrucan, 1999).

Many of the changes that have been highlighted were the driven by a number of factors notably the EU Common Agricultural Policy (CAP) and the Rural Environment Protection Scheme (REPS), the Irish scheme responding to the EU agri-environment measures (Council Regulation 2078/92) which came on-stream in the Burren in 1995, with special conditions for the Burren (Bohnsack and Carrucan, 1999, Dunford, 2002, Williams et al., 2009). The objectives of REPS were to protect wildlife habitats and species by establishing environmentally friendly and sustainable methods of farming for the production of quality food while in the Burren, grazing of winterages in the 'high Burren' was only allowed from November to April with supplementary feeding permitted where it was already taking place from mid-January onwards. Furthermore, the sensitivity of the Burren aquifer was afforded some protection by the prohibition of spraying of fertilisers and herbicides: wipe-on and spot applications were allowed on certain weed species and scrub removal by chain saw or brush cutter was allowed (Department of Agriculture, 2000).

The 1992 Habitats Directive was transposed into Irish law under the European Communities (Natural Habitats) Regulations 1997 and with this enactment a number of proposed Natural Heritage Areas were afforded legal protection as proposed Candidate Special Areas of Conservation (cSACs). Under the EU Habitats Directive the protection and conservation of the condition of listed habitats and species had to be prioritised and REPS was felt to be too generalised in its prescriptions, in particular on the issues of scrub encroachment and the intricate nature of Burren habitats and crucially the variety of winterage ‘types’ or ‘strengths’ requiring more flexibility in the timing of grazing and carrying capacity of livestock (Bohnsack and Carrucan, 1999, Dunford and Feehan, 2001, Williams et al., 2009). In 1998, The Heritage Council commissioned a report of farming under REPS in the Burren uplands (Bohnsack and Carrucan, 1999) the same year research was undertaken to examine the relationship between agriculture and the natural heritage of the Burren uplands (Dunford, 2002). This research found that traditional farming was integral to maintaining the diversity of species and habitats as well as conserving the built heritage in the Burren. It also revealed the complexity of its land management systems, identified the farmers as ‘custodians of the countryside’ and recommended that the Burren farming community be active participants in the conservation process.

1.4.2. Farming for conservation in the Burren

The first major farming for conservation programme in Ireland was the BurrenLIFE project (BLP; LIFE04 NAT/IE/000125), which ran from 2005-2010 - working with 20 Burren farms, local conservation and ecology specialists, National Parks and Wildlife Service and the Burren IFA to develop a blueprint for sustainable farming in the Burren. The monitoring of vegetation and animal health was a key component of the project; and another major factor was the involvement and influence of the farmers themselves. Following on from the success of the ‘pilot’ BLP in 2010, the Burren farming for conservation programme was rolled out to 160 farmers on 15,000 hectares across the Burren (Anon., 2014). And in 2016 a new six-year programme began, currently catering for 200 farmers and envisaged to include 500 farmers by 2020 (Anon., 2016).

The programme is a farmer-led agri-environment scheme with a focus on habitat conservation through payment for results delivered in relation to habitat health, based on a unique results-based field scoring system that specifically refers to plant communities of conservation interest, and actions completed such as farm maintenance works e.g. stone wall building, gate installation, water provisions, scrub removal and access tracks. It focuses on the conservation of prime wildlife habitats such as (Annex I) Limestone Pavements, Orchid-rich Calcareous grassland, Turloughs, *Juniperus* formations on limestone and Alpine and Boreal heath. Much of the Burren area has been designated as Special Areas of Conservation (SACs), however there are also non-SAC Annex I habitats of conservation interest. The majority of the SAC lands and much of the land covered by non-SAC Annex I habitats is included in the Burren Programme thereby ensuring that these areas are/will be managed properly for wildlife conservation. The BurrenLIFE project has received a number of accolades: most recently, in 2017 it was shortlisted as one of the top 5 best EU LIFE-funded nature conservation projects in Europe in the last 25 years; in 2013 the prestigious ‘European Diploma of Protected Areas’ award was presented by the Council of Europe to the Burren region for its sustainable management; additionally it was selected as one the ‘Best of the Best’ LIFE Nature Projects 2010.

1.4.3. Conservation of Burren heathlands

The vegetation history of the Burren has shown that in the absence of grazing, there is a reversion to scrub and woodland develops; in grassland areas *Corylus avellana* encroaches, while in heathlands it is *Calluna vulgaris* that dominates (Keane, 1990, Parr et al., 2009). Thus it is clear that management is key to the conservation of the habitats of the Burren. The majority of the Burren speciality plant species are to be found on the upland grasslands which are low-input systems and are traditionally grazed during the winter months: October to April (Dunford, 2002). The winter grazing is key to the floral diversity of the Burren as it allows the plants to set seed prior to grazing and reduces the vigour of dominant species (Bohnsack and Carrucan, 1999). In addition it aids in removing the build-up of plant litter, allowing light to get in, and creating bare soil patches where less competitive species can flourish (Keane, 1990, Dunford, 2002, Williams et al., 2009).

It is apparent that grazing must not have been a regular practice everywhere in recent years given the level of *Calluna* growth in some areas: *Arctostaphylos* heath has been encroached by tall *Calluna* and may decrease in diversity, so key species such as *A. uva-ursi* may be under threat in the absence of management. Burning is a commonly used management tool for the removal of mature *Calluna* biomass (Webb, 1998), however the thin soils of the Burren make this an unfavourable option (Parr et al., 2009).

1.5 Summary of the use of cutting in heathland management in Europe

The cutting of vegetation in heathland habitats may not be as widely used as burning but nevertheless it is an important form of management involving the removal of plant biomass and prevention of succession (Webb, 1998, Fagúndez, 2013). In Norway *Calluna* was traditionally mown in winter and early spring to provide fodder for cattle who were kept indoors (December to March), periodic burning was also practiced before the plants reached the mature-degenerative phase (Kvamme et al., 2004). In the Netherlands and Denmark heather would have also been used for winter fodder (Webb, 1998). In Britain cutting of heather was not widely practiced, burning being the preferred method (Webb, 1986).

However cutting trials have been undertaken in Britain: in lab trials *Calluna* re-growth was found to be stunted to a greater degree by summer cutting than winter cutting, resulting in a higher proportion of green shoots and less woody growth (Grant and Hunter, 1966). Field trials were undertaken on an upland moor in northern England involving burning, flailing (litter was not removed) and rolling back (large stems were cut manually and vegetation was rolled to the side of the plot), re-growth of *Calluna* and *Empetrum nigrum* was monitored for 10 growing seasons, initially re-growth was greatest following burning but over time the plot subjected to flailing rejuvenated to a similar degree (Cotton and Hale, 1994). Rolling back resulted in a significantly lower level of *Calluna* re-growth, and also saw the greatest increase in the cover of *E. nigrum* (Cotton and Hale, 1994).

In the Cantabrian Mountains of north-west Spain cutting experiments have been carried out on *Calluna*-dominant heathlands where grazing had ceased since a number of years and is no longer economically viable. Mature-phase *Calluna* was cut at ground-level and removed; re-growth was monitored at one, two, twelve and twenty-four months following cutting and within this time-scale its re-growth was slow (Calvo et al., 2005). In a ten-year study in the same area of Spain *Calluna* was found to regenerate more slowly over the period of monitoring following cutting, as compared to burning or ploughing (Calvo et al., 2002b). Similar trials were carried out in a *Calluna*-dominant heathland in southern Czech Republic involving burning, cutting and sod-cutting with a five-year monitoring period: burning and sod-cutting facilitated regeneration from seed while cutting did not, possibly due to the retention of the pleurocarpous moss layer preventing light penetrating to the seedbank (Sedláková and Chytrý, 1999).

Additionally management trials in a ten-year study were undertaken in northwest Spain on *Erica australis* heaths with *Arctostaphylos uva-ursi,* involving cutting, burning and ploughing: *A. uva-ursi* and other sprouting species were among the first woody species to reappear after burning; however it was not seen to recover following cutting; following ploughing *A. uva-ursi* recovered by germination and sprouting (Calvo et al., 2002a). However del Barrio et al. (1999) found the vegetative re-sprouting capacity of *A. uva-ursi* to be very effective within an 18-month timespan following cutting and burning.

While management of heathlands is clearly very important in terms of its conservation, it also is important to understand the requirements of the key species in relation to their reproductive biology. A review of these aspects of Ericaceous species in Britain and Ireland follows.

1.6 Reproductive biology and phenology of species of Ericaceae

Notes on the reproductive and pollination mechanisms and pollinators of select Ericaceae species in Britain and Ireland. NB apart from *Daboecia cantabrica*, the information for all species is from observations made in Britain.

Calluna vulgaris. New shoots appear in April or May and flowering may begin in late June, but the peak flowering period in Britain and Ireland is August and September. Flowers forming a raceme or panicle-like inflorescence, corolla *c.* 4 mm, bell-shaped, pale pinkish-purple. Seeds are shed from September to November and germination may occur in autumn with seedlings over-wintering and additional seedlings germinating in spring and summer. It has an abundant nectar supply and is protandrous. Numerous insect visitors, including members of the Hymenoptera: parasitoid wasps, social and solitary bees; Diptera: dance flies, hoverflies, parasitic flies; and Thysanoptera: thrips. Reproduction is amphimictic i.e. capable of interbreeding freely producing fertile offspring. Self- and cross-pollination probably both occur but a pollinating agent is required. Wind pollination may also occur but insect pollinators are important (Knuth, 1909, Gimingham, 1960, Clapham et al., 1987). *Calluna* is also known to be a clonal species, reproducing vegetatively (Callaghan et al., 1992).

Erica cinerea. Shoot growth begins in late April and early May. The main flowering period is in July and early August although open flowers may be observed from end of May to November. Flowers are in short terminal racemes, corolla 5-6 mm, urceolate or flask-shaped with a narrow opening, reddish-purple. Mature seed is shed in October and November. Leaves are shed during their second year of growth. Germination may occur in autumn following seed shedding and continue until the next growing season. Reproduction is amphimictic. Self- and cross-pollination probably occur. Abundant supply of nectar. Visited by various insects: Lepidoptera; Diptera: house flies and hoverflies; and Hymenoptera: honeybees and bumblebees; but only the Lepidoptera have long enough tongues to reach the nectar and some bumblebee species pierce the base of the corolla to rob nectar, bypassing the reproductive parts. Other insects may use these holes to rob more nectar. Fertilisation may occur before the flowers open as the receptive stigma is often covered in pollen which collects in the tip of the flower before it opens and thus the species is not totally dependent on a pollinator for fertilisation (Knuth, 1909, Bannister, 1965, Clapham et al., 1987).

Erica tetralix. Shoot growth occurs in April and May, bud development may also occur at this time or later in the growing season. Flowering begins in June with the main flowering period in July and August, continuing through September. Flowers in terminal umbel-like clusters, corolla 6-7 mm, urceolate, rose-pink. Seeds mature from September to October and are shed by December. Leaves are shed during their second year of growth. Germination may occur following seed shedding and continue until the following growing season. Seedlings are rare. Reproduction is amphimictic. Probably undergoes both self- and cross-pollination. Abundant nectar. Main insect visitors are the Hymenoptera but also less frequently visited by Lepidoptera and Diptera (Bannister, 1966). Hagerup and Hagerup (1953) consider that Thysanoptera: thrips (*Taenethrips ericae* and *Frankliniella intonsa*) act as pollinators – the wingless males inhabit the flowers and the winged females actively seek out males, moving between flowers and thereby becoming cross-pollinators; these authors also criticise the classical view of *Erica* spp. being viewed as 'bee-flowers' noting that the proboscis of most bees are too short to reach the nectaries and instead they rob the nectar by boring holes in the corolla.

Daboecia cantabrica. This species occurs mainly on the Iberian Peninsula, but is widespread in Connemara in Ireland. New leaf shoots typically appear from mid-April in Irish populations and flowering occurs from mid-June to September with a peak in July and August. Flowers last approx. two weeks. Flowers in terminal clusters, corolla 8-12 mm, urceolate, reddish-purple. Mature seeds can be found in late August and seeds are shed from then until October. Germination times in the field unknown. Some nectar is present and bumblebee visitors have been noted in Ireland including *Bombus terrestris, B. pascuorum* and *B. lapidarius.* Many flowers have been observed with perforations at the base of the corolla. Almost all flowers are successfully fertilised, but it is not known whether self-pollination occurs. Thrips have been observed inside the corolla but whether they assist in pollination is not known (Woodell, 1958, Clapham et al., 1987).

Andromeda polifolia. Flowering can occur as early as April and a second flowering period may occur in autumn. Flowering begins soon after the onset of shoot growth and peaks at the beginning of June. Flowers in terminal clusters, corolla 5-7 mm, urceolate, pink fading to whitish. Most of the growth occurs in early to mid-summer and flower buds overwinter. Homogamous. Anther pores are open in the bud but pollen is not shed until the corolla opens and anthers dry out. Self- and insect-pollination by bumblebees and butterflies occurs. Nectar is present and nectar-robbing also occurs, for example by ants. Vegetative reproduction may be more widespread than sexual reproduction (Clapham et al., 1987, Jacquemart, 1998).

Vaccinium myrtillus. New vegetative shoots appear in March/April. Over-wintered flower buds open, flowering occurring twice - in spring and early summer. Flowers are borne laterally, singly or rarely in pairs. Corolla 4-6 mm, spherical, green tinged with pink. Nectar is secreted by a swelling at the base of the style. Fruit is a berry, forming 2-4 weeks following pollination. Seedlings are rare in the wild. Vegetative spread by horizontal rhizomes is common. Flowers are insect- and self-pollinated. Pollination has been recorded by species of Hymenoptera: mining bees, cuckoo bees, social wasps, bumblebees and honeybees. Seed dispersal is by birds (Knuth, 1909, Ritchie, 1956, Clapham et al., 1987).

Empetrum nigrum. Dioecious. Flowers late March to May; fruits ripen by July and germination may occur in the following spring but seedlings are uncommon. Winter buds are formed by October, overwintering until growth re-commences in April. Flowers in axils of upper leaves, *c.* six flowers per stem in female plants, and numerous in males plants. Flowers 1-2 mm in diameter, perianth segments pinkish or purplish, in two similar whorls. Short style with 6-9 stigmas. Stamens 3-4 with long anthers. Reproduction is amphimictic; cross-pollinated, no self-pollination owing to its dioecious nature. Wind-pollinated, although possibly also visited by flies, as the stigma seems to secrete nectar (Knuth, 1909). Fruit is a drupe with 6-9 stones. Dispersal by animals and birds, for example grouse. Many fruits fall to the ground near the parent plant and seedling have been observed though there appears to be a high mortality rate during winter (Bell and Tallis, 1973).

1.6.1. Reproductive biology and phenology of *Arctostaphylos* species

The genus *Arctostaphylos* is successful and diverse, it has 67 species and a number of sub-species in a wide variety of habitats, occurring in western North and Central America, and the majority are not found elsewhere except for *A. uva-ursi* and *A. alpina* (Clapham et al., 1987, Kauffmann et al., 2015). These two species have a circumpolar distribution, and are found in the boreal-montane and arctic-montane zones, respectively (Hill et al., 2004)

Arctostaphylos spp. are known to be adapted to regeneration following fire events – they may do so either by re-sprouting from burls i.e. root crowns (*A. glandulosa* var. *mollis*) or, more commonly by seed reproduction (Fulton and Carpenter, 1979). The re-sprouter was found to have a smaller number of flowers per unit volume, a shorter flowering period and appeared to be self-incompatible, however it also produced less concentrated nectar and in smaller quantities than the seed reproducing species, and had a smaller number of insect visitors but nevertheless was still visited by solitary bees, honeybees and syrphids though rarely bumblebees (whereas they commonly visited *A. pringlei*) (Fulton and Carpenter, 1979). *Arctostaphylos glauca* and *A. pringlei* var. *drupacea* are both early flowering plants and offer nectar as well as pollen to potential pollinators, although not in great quantities, and a high proportion of buds were observed not to reach full maturity (Brum, 1975).

Arctostaphylos uva-ursi is a stress-tolerator, able to withstand periods of snow-cover and drought (Fitter and Peat, 1994), growing well in windy exposed places, and where competitive plant species' growth is reduced by rocky terrain, it may be an important pioneer species (Gimingham, 1972, Genova and Russakova, 2015). Burl-sprouting regeneration occurs in *A. uva-ursi* following disturbances by trampling (Bowles, 1983, Remphrey et al., 1983b) and fire events (Tiffney et al., 1978).

In *A. uva-ursi* populations near Alberta, Canada flowering occurred from snowmelt in early May until approximately mid-June in 1968: bumblebees were the only visitors observed, however these visits ceased with the onset of flowering of pollen-rich and nectar-rich species such as *Salix* spp. and *Taraxacum* spp. (Mosquin, 1971). In Saskatchewan, Canada, the majority of growth in *A. uva-ursi* occurs between late-April and July when plants become dormant until the following spring: floral buds typically begin to open in late

April/early May, vegetative buds begin to swell a week or two later, followed by bud burst and shoot elongation; new flowering shoots begin to form in May, for the following year, and are complete with early stage flower buds by June/July which then overwinter (Remphrey and Steeves, 1984b).

In Britain and Ireland *A. uva-ursi* flowers between May and July (Clapham et al., 1987) but was observed to flower in April in Burren populations (Chapter 4). Flowers are in terminal racemes of 5-12. Corolla 4-6 mm, urceolate, white tinged with pink or green and fruit is a red berry-like drupe (Clapham et al., 1987, Streeter et al., 2009). *A. uva-ursi* produces nectar and pollen and is capable of self-pollination (Knuth, 1909, Clapham et al., 1987) however it reproduces poorly by seed, mainly spreading vegetatively and it is capable of layering, developing roots on underground stems (Remphrey et al., 1983b, Salemaa and Sievanen, 2002).

Insect visitors to *A. uva-ursi* include bumblebees, both as legitimate visitors and nectar-robbers, occasionally butterflies and thrips (Knuth, 1909). Thrips were found in an experimental study in eastern Spain to make an important contribution to the pollination and fruit set of *A. uva-ursi*, particularly in the absence of other pollinating insects: 13% fruit set occurred where all visitors were excluded, 30% fruit set in thrips-only treatment, and 60% in open pollinated inflorescences (Garcia-Fayos and Goldarazena, 2008). One of the species of thrips commonly observed in the Spanish populations, *Ceratothrips ericae,* is known to occur in Ireland (O'Connor, 2008), while the second main species involved, *Haplothrips setiger*, a Mediterranean species (Garcia-Fayos and Goldarazena, 2008), has not been confirmed to date (O'Connor, 2008). The phenomenon of thrips pollination may be widespread because thrips are found throughout the geographical range of *A. uva-ursi* and as thrips pollination did not vary with site studied (Garcia-Fayos and Goldarazena, 2008).

1.7 Aims of the research

This study was originally formulated together with staff of the Burren Programme in order to address the conservation requirements of the *Arctostaphylos* – rich heaths in the Burren, in particular the restoration of in areas where encroachment by mature *Calluna vulgaris* was a threat to some of the rarer prostrate dwarf alpine shrubs such as *Arctostaphylos uva-ursi, Empetrum nigrum* and *Dryas octopetala.* The conservation of these calcareous heath habitats was considered in terms of three key themes: plant communities, management, and pollination biology of *Arctostaphylos uva-ursi,* which were the basis for the three research chapters. The main aims for each of these chapters are as follows:

Chapter 2:

- to describe the heathland plant communities within the Burren containing *Arctostaphylos uva-ursi* and/or *Empetrum nigrum* (including areas of heath at near sea-level in the eastern Burren previously undescribed)
- to describe any differences in species composition in relation to their geographical distribution and environmental variables
- to relate the resultant plant communities to previous Burren studies and existing classifications, both Irish and European
- to evaluate potential threats to these plant communities

Chapter 3:

- to test the effects of cutting and removal of vegetation (mainly *Calluna vulgaris*) on the regrowth of plant species, notably *Arctostaphylos uva-ursi,* over a short timescale (two years)

- to determine whether cutting of the vegetation in spring results in differences in species regrowth compared with cutting in autumn
- to identify the main factors that lead to these heaths becoming overgrown with mature *Calluna*

Chapter 4:

- to investigate the pollination requirements and effectiveness of *Arctostaphylos uva-ursi* in Burren populations
- to determine its rate fruit and seed set in open pollinated and pollinator-excluded flowers in the Burren uplands and lowlands
- to document the species' phenology in order to look for differences in flowering and fruiting patterns in the Burren uplands and lowlands

1.8 Outline of the thesis

Chapter 1 constitutes a general introduction. Chapters 2 to 4 are laid out in scientific paper format, each comprising an introduction, methodology, results and discussion section. Finally Chapter 5 comprises a general discussion.

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Chapter 2. Plant communities of Alpine and Boreal heaths (4060) and European dry heaths (4030) with *Arctostaphylos uva-ursi* in a lowland Atlantic karst region of Europe

2.1 Introduction

Alpine and boreal heaths (habitat code 4060: EU Habitat Directive 92/43/EEC) and European dry heaths (4030), are both EU Annex I habitats and are therefore vulnerable and/or rare, are protected habitat types and their conservation is an obligation within EU member states. Large declines in the extent of heathlands, as much as 90 percent, have occurred in the uplands of Britain and Ireland, since the 19th century (Thompson et al., 1995). Indeed there has been a loss of heathland habitat throughout Europe leading to habitat fragmentation and isolation, encroachment of bracken, scrub or woodland due to land abandonment, or the conversion of heathland to intensive farmland or forestry (Fagúndez, 2013).These heaths have wide variation locally and a large number of sub-types exist throughout the EU (European Commission, 2013). In Britain there are a number of corresponding heathland classifications (Rodwell, 1991), and in Ireland due to its hyperoceanic climate, montane heath vegetation is distinct from that of Britain (Hodd, 2012). In Ireland both types of Annex I heath are considered to have ‘bad conservation status’ and Burren or limestone communities are distinguished as separate sub-types (NPWS, 2013a, NPWS, 2013b). The calcareous dry heath community, not restricted to the Burren but rather to limestone areas, comprises *Calluna vulgaris*, *Erica cinerea*, *Vaccinium myrtillus* and in coastal areas also *Ulex gallii,* and the Burren alpine and boreal heath variant is distinguished by the ‘mats of mountain avens’ (*Dryas octopetala*) (NPWS, 2013b). In both of these variants, *Arctostaphylos uva-*

ursi is a positive indicator species, and heath species occur together with calcareous grassland species (NPWS, 2013a, Wilson and Fernández, 2013, Perrin et al., 2014).

Arctostaphylos uva-ursi has a wide global distribution, stretching across Canada, northern USA and northern Europe, as well as in more southerly mountain ranges on both continents where it is a plant of well-drained shallow rocky soils on open heath, sand dunes or open forest (Tutin et al., 1972, USDA NRCS Northeast Plant Materials Program, 2006, Kauffmann et al., 2015). Throughout its geographic range *A. uva-ursi* is found on both acidic and calcareous soils, in association with species of conservation interest: on calcareous soils it occurs with *Juniperus communis* and *Dryas octopetala* together with typical calcicoles *Antennaria dioica, Linum catharticum* and *Sesleria* spp. in Ireland, Finland, Norway, Poland and Bulgaria (Törn et al., 2006, Nilsen and Moen, 2009, NPWS, 2013a, Adamska et al., 2015, Genova and Russakova, 2015). On acidic soils it is often found with *Vaccinium myrtillus, Calluna vulgaris, Empetrum nigrum, Racomitrium lanuginosum* and *Erica cinerea* in Scotland, Ireland, Norway and Bulgaria (Ward, 1971a, Ward, 1971b, Nilsen and Moen, 2009, Perrin et al., 2014, Genova and Russakova, 2015).

2.1.1. European dry heath in Ireland

European dry heaths, hereafter referred to as 'dry heath', include the *Vaccinium – Calluna* heaths and the Gorse-rich heaths of the Atlantic climates (European Commission, 2013). It has two variants in Ireland: the more widespread occurs on well-drained sloping ground with poor acidic soils or shallow peats (< 50 cm deep), dominated by ericaceous dwarf shrubs, mainly *Calluna vulgaris* but *Erica cinerea, Ulex gallii* and *Vaccinium myrtillus* may also be important; the other is a calcareous dry heath comprising a mixture of heath and calcareous grassland species, forming where the leaching of minerals has occurred over shallow, base-rich soils, and is also found on limestone outcrops (NPWS, 2013a, Perrin et al., 2014).

This second type is not restricted to the Burren but does encompass some of the Burren heaths. The non-Burren calcareous dry heaths have been tentatively classified as *Calluna vulgaris – Antennaria dioica* dry heaths (Perrin et al., 2014), and the Burren variants described as *Calluna – Potentilla erecta* and *Calluna – Molinia caerulea* heath groups (Wilson and Fernández, 2013).

2.1.2. Alpine and Boreal heath in Ireland

As with the dry heaths, there are two variants of Alpine and Boreal heath in Ireland, hereafter referred to as 'alpine heath': the more widespread is found from 350 - 400 m a. s. l. and upwards on siliceous rocks in western counties (west Galway (Connemara), Mayo, Sligo, Donegal), and from Kerry in the south-west across to Wicklow in the east. It is a community of dwarf shrubs with *Calluna vulgaris* often the most frequent shrub species, together with *Arctostaphylos uva-ursi, Empetrum nigrum, Erica cinerea, E. tetralix, Juniperus communis* subsp. *nana, Salix herbacea, Vaccinium myrtillus* and *V. vitis-idaea;* the bryophyte *Racomitrium lanuginosum* is usually abundant, *Cladonia* spp. and *Carex bigelowii* are also present (NPWS, 2013a, Perrin et al., 2014).

The lowland (< 300 m a. s. l.) type is restricted to the Burren limestone of south-west Galway and north Clare and comprises unique plant community and environmental elements that increase its conservation importance. The Burren community is typically defined by the presence of *Dryas octopetala* and often occurs in association with species-rich calcareous grassland (NPWS, 2013a). This vegetation type occurs mainly between 160 - 300 m a. s. l., and unusually also near sea-level at some locations. These plant communities, described as *Dryas octopetala – Empetrum nigrum* heath (Wilson and Fernández, 2013), which are also associated with *Arctostaphylos-uva-ursi,* are nationally and locally rare (Parr et al., 2009) and *Arctostaphylos*-rich heaths form an important part of the vegetation on high ground in the Burren on the plateaux near Black Head, Carnesfin, Cappanawalla and Gleninagh (Ivimey-Cook and Proctor, 1966, Webb and Scannell, 1983, Proctor, 2013). These are arctic-alpine species and are examples of climate relicts, persisting from a time when the climate in Ireland was periglacial in character; their distributions are now disjunct and they occur where they were able to remain through climatic and vegetation changes (Woolbright et al., 2014).

2.1.3. The Burren heaths

The Burren vegetation comprises an unusual suite of species many of which are not seen growing side-by-side elsewhere in the world – there are what are termed arctic-alpines and Mediterranean species, as well as calcicole and calcifuge species (Roden, 2001). Burren habitats occur as a complex mosaic of limestone grassland, limestone heath and limestone pavement often making it difficult to isolate one habitat type from another and the Burren plant communities are notoriously difficult to compare with extant classifications as they never quite match (Parr et al., 2009). Indeed this observation may be extended further than the Burren region to encompass upland areas with montane heath where the descriptions of certain Annex I heaths (Northern Atlantic wet heaths, alpine heaths and dry heaths) did not fit with the Irish oceanic upland communities and the author of this study decided that montane heath communities were ‘any heath community occurring above 400m altitude’ (Hodd, 2012). As a result of this mismatch a comparative summary of the published classifications relevant to the Burren heaths is provided in Tables 2.1 and 2.2. When the corresponding classification was given by the author of the relevant paper or report this is indicated in the table, when not provided, an attempt has been made here to provide a comparison, based on the examination of plant species lists and is indicated by an asterisk *.

Ivimey-Cook and Proctor (1966) first described the Burren limestone heaths as communities derived from their associated grasslands of the class Festuco - Brometea (Braun-Blanquet and Tüxen, 1943): the *Dryas octopetala*

- *Hypericum pulchrum* association is common throughout the Burren on organic soils over exposed limestone, and the *Antennaria dioica - Hieracium pilosella* nodum which is also widespread on drift-derived soils – lowland limestone heaths may develop from either of these grassland types where soils have become acidified due to leaching processes (Ivimey-Cook and Proctor, 1966). The *Empetrum nigrum - Epipactis atrorubens* nodum was found to replace the *Dryas - Hypericum* heathy grassland on exposed coastal plateaux, and the *Arctostaphylos uva-ursi - Dryas octopetala* nodum (notable for the presence of the northern montane species *A. uva-ursi* which in the Burren occurs mainly above 200 m but also descends to sea level in some areas) replaces the *Antennaria – Hieracium* grassland; in the uplands it may merge into the more acidic *Calluna vulgaris - Carex binervis* heath association of the class Nardo - Callunetea where soils are deeper and more peaty (Ivimey-Cook and Proctor, 1966).

Parr et al. (2009) described the upland grasslands and heaths of the Burren – dividing the heaths into two main communities: one characterised by *Dryas octopetala* and the other by *Calluna vulgaris*. The *Dryas* heaths were divided into three sub-communities: the *Antennaria dioica - Asperula cynanchica* sub-group, containing *Empetrum nigrum, Arctostaphylos uva-ursi* and *Juniperus communis;* the *Teucrium scorodonia* sub-group; and the *Galium verum - Lathyrus pratensis* sub-group. The *Calluna* heaths were divided into three sub-groups: typical *Calluna* heath; calcareous *Molinia* sub-group; and the *Molinia - Erica cinerea* sub-group, which contained *Arctostaphylos uva-ursi* as a companion species. Wilson and Fernández (2013) also described Burren heath communities, combining relevés from Parr et al. (2009) together with their own, as *Dryas octopetala - Empetrum nigrum* heath, *Calluna vulgaris - Potentilla erecta* heath and *Calluna vulgaris - Molinia caerulea* heath – all of these heath types may contain *A. uva-ursi* as a companion species and may have affinities to (4060) alpine heaths or (4030) dry heaths.

Table 2.1. Comparison of relevant classifications of Burren heath communities based on localised studies and equivalent classification scheme habitats associated with these heaths, i.e. Burren: Ivimey-Cook & Proctor 1966, Parr et al. 2009; Irish: Fossitt 2000; British: NVC, Rodwell 1991, Rodwell 1992; and EU Annex I habitats: NPWS 2013b, EC 2013. Asterisk * indicates the comparisons made in this study that were not provided by the author referenced. See also Table 2.2.

Ivimey-Cook & Proctor 1966*	Parr et al 2009	NVC communities associated with Parr et al 2009 descriptions	Fossitt 2000*	EU Annex I habitats associated with Fossitt 2000, NPWS 2013	Relevant NVC classifications associated with EU Annex I habitats: Rodwell 1991, 1992; EC 2013
Class Festuco - Brometea, Order Brometalia erecti, Alliance Bromion erecti, Sub-alliance Mesobromion erecti, *Dryas octopetala - Hypericum pulchrum* (Asperulo - Dryadetum) Association; *Empetrum nigrum - Epipactis atrorubens* nodum	*Dryas* heath, *Antennaria - Asperula* sub-community	(CG9) *Sesleria caerulea - Galium sterneri* grassland; (CG13) *Dryas octopetala - Carex flacca* heath	Dry calcareous heath (HH2); Montane heath (HH4); Dry calcareous and neutral grassland (GS1)	European dry heaths (4030); Alpine and Boreal heaths (4060); *Juniperus communis* formations on heaths or calcareous grasslands (5130); Semi-natural dry grasslands and scrubland facies on calcareous substrates (6210)	Heaths: (H7) *Calluna vulgaris - Scilla verna* heath; (H10) *Calluna vulgaris - Erica cinerea* heath; (H12) *Calluna vulgaris - Vaccinium myrtillus* heath; Calcareous grassland: (CG2) *Festuca ovina - Helictotrichon pratense* grassland; (CG9) *Sesleria caerulea - Galium sterneri* grassland
Class Festuco - Brometea, Order Brometalia erecti, Alliance Bromion erecti, Sub-alliance Mesobromion erecti, *Dryas octopetala - Hypericum pulchrum* (Asperulo - Dryadetum) Association; *Arctostaphylos uva-ursi - Dryas octopetala* nodum	*Dryas* heath, *Antennaria - Asperula* sub-community	Communities as above (CG9; CG13)	Communities as above (HH2; HH4; GS1)	Communities as above (4030; 4060; 5130; 6210)	Communities as above (H7; H10, H12; CG2; CG9)
Class Nardo - Callunetum, Order Calluno - Ulicetalia, Alliance Ulicion nanae, *Calluna vulgaris - Carex binervis* heath Association	*Calluna* heath, *Molinia - Erica cinerea* sub-community	(CG13) *Dryas octopetala - Carex flacca* heath; (H10) *Calluna vulgaris - Erica cinerea* heath; (H7) *Calluna vulgaris - Scilla verna* heath	Dry calcareous heath (HH2)	European dry heaths (4030)	Heath communities as above (H7; H10, H12)

Table 2.2. Comparison of relevant classifications of Burren heath communities based on localised studies and relevant classification schemes habitats associated with these heaths, i.e. Limestone habitats: Wilson & Fernandez 2013; Irish: Fossitt 2000; British: NVC, Rodwell 1991, Rodwell 1992; and EU Annex I habitats: NPWS 2013b, EC 2013. See also Table 2.1. This second table is provided as the NPWS (2013) publications refer to Wilson & Fernandez 2013 and thus should be considered as the current definitive descriptions for Ireland.

Wilson & Fernandez, 2013	**Fossitt, 2000 habitats associated with Wilson & Fernandez, 2013**	**EU Annex I habitats associated with Wilson & Fernandez, 2013**	**Parr et al., 2009 habitats associated with Wilson & Fernandez, 2013**	**Relevant NVC classifications associated with Wilson & Fernandez 2013**
Dryas octopetala - Empetrum nigrum heath	Dry calcareous heath (HH2), re-classified as HH2 Dryas variant (of Fossitt habitat description)	European dry heaths (4030); Alpine and Boreal heaths (4060); Semi-natural dry grasslands and scrubland facies on calcareous substrates: *Festuco - Brometalia* (6210/6211)	*Dryas* heath association	(CG9) *Sesleria caerulea - Galium sterneri* grassland; (CG13) *Dryas octopetala - Carex flacca* heath
Calluna vulgaris - Potentilla erecta heath	Dry calcareous heath (HH2); (GS4) Wet grassland	European dry heaths (4030); Alpine and Boreal heaths (4060)	*Calluna* heath association: typical sub-group	(H10) *Calluna vulgaris - Erica cinerea* heath; (CG13) *Dryas octopetala - Carex flacca* heath
Calluna vulgaris - Molinia caerulea heath	Dry calcareous heath (HH2); (GS4) Wet grassland	European dry heaths (4030); Alpine and Boreal heaths (4060)	*Calluna* heath: calcareous *Molinia* sub-group; Calluna heath: calcareous *Molinia - Erica cinerea* sub-group	(H10) *Calluna vulgaris - Erica cinerea* heath; (CG13) *Dryas octopetala - Carex flacca* heath

In terms of the Heritage Council classification of habitats in Ireland (Fossitt, 2000) the heaths in the Burren may be classified as dry calcareous heath HH2 occurring on well-drained shallow basic soils with some leaching causing localised acidic conditions; Wilson and Fernández (2013) suggest a *Dryas* heath sub-type of HH2. Species associated with this habitat are: *Calluna vulgaris, Molinia caerulea, Potentilla erecta* together with species of dry calcareous grassland GS1 and other dwarf shrubs *Empetrum nigrum, Arctostaphylos uva-ursi* and *Erica cinerea* (Fossitt, 2000). Fossitt (2000) links HH2 to EU Annex I Habitats European dry heaths (4030) and *Juniperus communis* formations on heaths or calcareous grasslands (5130). NPWS (2013a) describes dry heaths in the Burren where heath has formed on leached soils but does not include the *Arctostaphylos - Dryas* heaths. On the other hand, montane heath HH4 comprises a heath community of very exposed high altitude or coastal areas with dwarf shrubs *Empetrum nigrum, C. vulgaris, A. uva-ursi* and/or *Salix herbacea* (not present in the Burren) and *J. communis* where these shrubs are stunted by exposure (Fossitt, 2000). This heath may also be found in the Burren although some elements of the herb and bryophyte flora are not present; it corresponds to Annex I alpine heaths (4060) sub-types *Dryas* heaths of the British Isles and mountain aven mats in 'isolated Atlantic outposts' (European Commission, 2013). The description for dry heaths (4030) includes the *Vaccinium - Calluna* heaths of the northern and western British Isles (European Commission, 2013); these correspond to relevant National Vegetation Classification (NVC) system of Great Britain (Rodwell, 1992) H10 *Calluna vulgaris – Erica cinerea* heath and H12 *Calluna vulgaris – Vaccinium myrtillus* heath (Table 2.1).

In addition to the difficulties of classifying plant communities in the Burren in relation to existing classification schemes the distribution of *Arctostaphylos*-rich heaths within the Burren region poses questions in itself: the fact that it is part of these relict plant communities may add an element of chance as to where it survives. In some areas there is seemingly suitable habitat yet *A. uva-ursi* is absent - could this be due to the absence of its associated mycorrhiza (Liston and Harrington, 2012)?

This research focuses on heath communities, focusing on *Arctostaphylos uva-ursi* and/or *Empetrum nigrum* as the defining species, within the greater Burren region. While the Burren upland communities have been previously described, those in the eastern lowlands have not and therefore this study fills a knowledge gap and provides a useful comparison between the two, together with environmental factors and a distribution map of the plant communities. In addition it is important to identify potential threats, for example species with the potential to invade or encroach on these rare heaths (e.g. *Corylus avellana, Pteridium aquilinum, Molinia caerulea* and *Calluna vulgaris* in a mature to degenerate state) and thus lower their conservation value.

2.1.4. Aims

- To describe the plant communities of *Arctostaphylos* and *Empetrum* heaths in the karst limestone landscape of the Burren, western Ireland.
- To identify any differences in species composition and environmental factors between upland (> 100 m) communities, chiefly in the western Burren and lowland (< 50 m) communities, occurring to the east.
- To plot the geographical distribution of the different plant communities identified in the study.
- To evaluate potential threats to these plant communities and their habitats.

2.2 Materials and methods

2.2.1. Site description

From the Gaelic: *Boireann* meaning ‘rocky place’, the Burren is a region of karst landscape covering approximately 300 km^2 of counties Clare and Galway on Ireland’s mid-western seaboard (Burren Programme, 2016). It is bounded by the Atlantic to the north and west, the overlying Namurian shales to the south, and arbitrarily by the N18 Ennis to Galway road (between the towns of Crusheen and Kilcolgan) to the east (Fig. 2.1). To the west the ‘high Burren’ is composed of terraced hills of 300-330 m altitude and to the east the ‘low Burren’ limestone plains are just 20-30 m above sea level. The mean annual temperature for the Burren is between 8°C and 10°C and the mean annual rainfall can vary from 1,200 mm in low-lying areas to 2,000 mm in upland coastal areas, winds are predominantly from the south-west (Met Éireann, 2017).

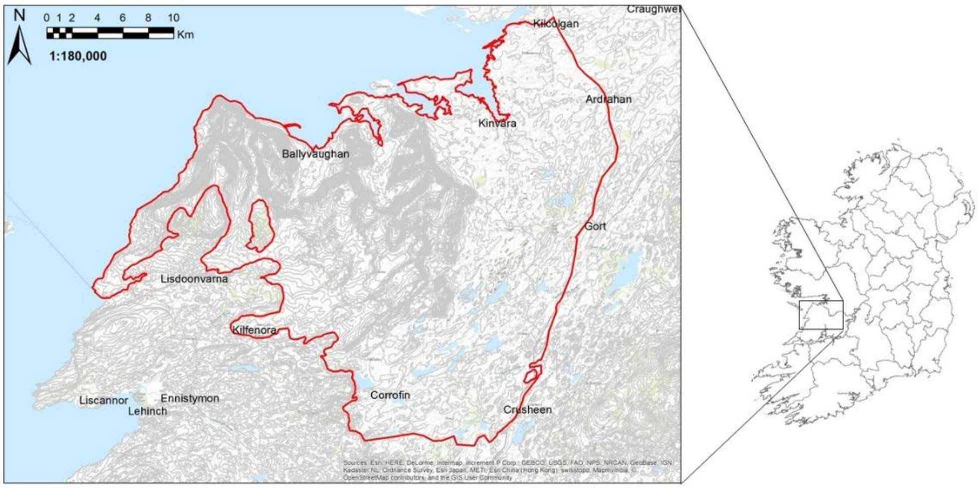

Figure 2.1. Map of study area. Red outline indicates the area of Carboniferous (Burren) bedrock (Geological Survey of Ireland, 2012) with shale outlier to the southwest; the boundary to the east arbitrarily defines the karst region (GSI, 2012). Contour lines in grey indicate areas of steep terrain and upland areas where they are close together. Map of Ireland inset.

2.2.2. Field methods

Sites for a vegetation survey were chosen for their presence of *Arctostaphylos uva-ursi* heath and additional sites were selected to survey *Empetrum nigrum* heath where *A. uva-ursi* was absent e.g. Moneen

Mountain. In order to locate populations of the target species a review was done of relevant literature (Grime, 1963, Ivimey-Cook and Proctor, 1966, Webb and Scannell, 1983, Parr et al., 2009), flora records (Preston et al., 2002, Botanical Society for Britain and Ireland, 2012), Special Area of Conservation (SAC) Site Synopses (NPWS, 2013a) within the study area, and the specialist knowledge of local botanists and BSBI vice county recorders for H15 south east Galway and H9 County Clare (S Parr, S. D. Ward, M. Sheehy Skeffington, and C. Roden pers. comm.). Where the plant community patch was of sufficient size (i.e. > 20 m^2) a maximum of five relevés was taken at a given location (typically there were small patches of *Arctostaphylos* or *Empetrum* heath within larger areas of *Dryas* heath, *Calluna* heath, calcareous grassland or limestone pavement rather than large continuous areas). Relevé size was 2m x 2m as is recommended for dwarf heath (Rodwell, 1991). In total 114 relevés were taken during the field seasons of 2013 and 2014, comprising 39 relevés in the east ‘low’ Burren (below 50 metres a. s. l.) and 75 in the west ‘high’ Burren (above 100m a. s. l.). Lowland sites were insufficient in number and size for more relevés to be taken without over-sampling. All vascular plant and bryophyte species were recorded and their percentage cover was estimated. Nomenclature follows Stace (2010) for vascular plants and Atherton et al. (2010) for bryophytes. The soil depth and vegetation height were recorded at each corner and the centre of each quadrat and subsequently averaged for each quadrat. Vegetation height may be used as a proxy for grazing level (Parr et al., 2009b). Slope and aspect were noted, aspect was later transformed to aspect category in order to give an indication of heat load which is an important factor for arctic-alpine species (Hodd, 2012), and the percentage cover for bare ground, exposed rock, leaf litter and total cover of plant functional groups i.e. graminoids, forbs, shrubs, ferns and bryophytes were visually estimated. Soil samples were collected in 2013, using a trowel, from the four corners of the relevé plot and from the centre, to a maximum depth of 15 cm; samples from each quadrat were bulked for analysis. Soil depth was often < 5 cm and, where insufficient soil was present within the quadrat due to the very rocky terrain, additional soil was collected from as close to it as possible. Soil samples were frozen on the day of collection and then de-frosted for analysis.

Gemini TGP-4500 Tiny tag Plus 2 Dual Channel temperature and relative humidity data loggers were placed in key locations throughout the study area. These are known to have some issues regarding humidity readings, often reading 100 % relative humidity when placed within vegetation or in an exposed location in the field and therefore can be housed inside a Gemini ACS-5050 Stevenson-type screen which is designed to protect Tiny tag data loggers from adverse weather conditions – two such screens were used, one at an upland site and one at a lowland site. These were secured as close to the low-growing vegetation as possible while the unhoused data loggers were placed within *Arctostaphylos* vegetation. Additional temperature-only TGP-4017 Tiny tag Plus 2 data loggers were used in the final year of data collection. Eleven data loggers were deployed in total in the final year of data collection, five at lowland sites and six at upland sites.

2.2.3. Soil analysis

Soil samples were de-frosted prior to analysis, soil pH was obtained using a Hanna pH meter; see Allen et al. (1986) for methods. Soils were sieved to remove stones and roots, then air dried at 105°C in a drying cabinet and weighed at room temperature before firing in a muffle furnace at 550°C and then re-weighed at room temperature in order to calculate the percentage loss on ignition, as a measure of percent organic matter (Nelson and Sommers, 1996).

2.2.4. Plant community analysis

Vegetation data were analysed initially using TWINSPAN (Two-Way Indicator Species Analysis) and preliminary results presented in Hanrahan and Sheehy Skeffington (2015). However as TWINSPAN is known to have a number of failings (McCune and Grace, 2002) a more robust analysis was performed for the purpose of this chapter. This analysis was hierarchical, agglomerative, polythetic clustering with quantitative Sørensen (Bray-Curtis) distance measure and flexible beta linkage method ($\beta = -0.25$) as deemed most suitable for ecological data sets (Perrin et al., 2006). Cluster analysis was performed repeatedly with a step-wise increase in the number of clusters specified and the group membership variable was added to the second matrix on each run (Perrin et al., 2006). Indicator species analysis (ISA: (Dufrene and Legendre, 1997)) was used to give an objective indication of the appropriate stopping point for the cluster analysis and thus the optimum number of groups. ISA uses the abundance and frequency of species to calculate Indicator Values (IV) for each species within each group (0 = species absent from all samples in that group, 100 = present in all samples in that group and not found in other groups), the statistical significance of species within each group is determined by Monte Carlo randomisation tests (Perrin et al., 2006, Kent, 2011). The optimum number of clusters can be defined by the highest number of significant ($p < 0.05$) indicator species and the lowest average p-value for all species (Fig. 2.2). Outliers were removed prior to the final ISA, and left out of further analyses. Outliers comprised one relevé and four species (*Potentilla erecta, Viola riviniana, Campanula rotundifolia* and *Hypericum pulchrum*), selected by the Outlier analysis; this detects sample units that are more than 2 standard deviations from the mean and therefore could be disproportionately influential (Peck, 2010). In order to remove 'noise' in the data set those species only occurring in 1 sample were also removed – this resulted in an additional 40 species being removed and the total number of species being reduced from 153 to 113.

Multi-response permutation procedures (MRPP) were performed on seven environmental variables soil pH, aspect category (after Hodd (2012) where a categorical scale, from 1 for south-facing up to 17 for north-facing, is used based on heat load; see Table 2.3), vegetation height, soil depth, %

bare ground, % exposed rock and % litter), using Sørenson distance measure, to test for differences between the vegetation groups determined by the cluster analysis. MRPP is a useful non-parametric tool in the analyses of ecological datasets as it does not make assumptions about distributions which ecological data rarely meet (McCune and Grace, 2002). The resulting p-value is a measure of the likelihood of the observed difference between groups being due to chance; a small p-value indicates the similarity of sample units within groups (McCune and Grace, 2002, Peck, 2010).

Table 2.3. Aspect categories used, after Hodd (2012).

Category	Aspect
1	South
2	South-southwest
3	South-southeast
4	Southwest
5	Southeast
6	West-southwest
7	East-southeast
8	West
9	No Aspect
10	East
11	West-northwest
12	East-northeast
13	Northwest
14	Northeast
15	North-northwest
16	North-northeast
17	North

The test statistic A indicates how (dis)similar relevés are, A = 1 when samples are identical, A = 0 when heterogeneity equals expectation by chance. Values of $A < 0.1$ are common in community ecology and $A > 0.3$ is relatively high for ecological datasets (McCune and Grace, 2002). The Kruskal-Wallis test was used to test for differences between groups in regard to environmental variables, where the test yielded significant ($p < 0.05$) results pairwise Mann-Whitney tests were run to determine which groups' means were significantly different.

Non-metric multidimensional scaling (NMS) ordinations were run in order to test the multidimensional relationships between relevés and the environmental and derived variables. This is deemed the most suitable ordination method for ecological datasets where data often do not conform to assumptions of normality and linearity between samples and are therefore not assumed (McCune and Grace, 2002, Peck, 2010). NMS was run using the autopilot slow and thorough setting, Sørensen (Bray-Curtis) distance measure with random starting configurations, 250 runs with real data, 250 runs with randomised data and an initial step length of 0.20. The stability of the solution was assessed using the stress vs. iteration number plot. The environmental matrix contained % cover values for plant functional groups (shrubs include low-growing woody species and dwarf shrubs such as *Rubus* spp., *Rosa pimpinellifolia, Dryas octopetala* and *Arctostaphylos*), soil depth, soil pH and % LOI, vegetation height, altitude, slope, aspect category and % cover for bare ground, exposed rock, leaf litter, faeces; additional factors assessed were species richness (*S*), Shannon diversity index (*H*), Simpson's index of diversity (*D*') – the inverse of Simpson's original index of dominance (*D*), evenness, and Ellenberg L (Light) and F (Moisture) values; the last two factors were derived by calculating the Ellenberg values, corrected for use in the British Isles, for each relevé (Hill et al., 2000). Simpson's index (*D*') and Shannon's index (*H*) both account for the abundance and evenness of the species present, evenness (equitability) is calculated by dividing H by H_{max} (here $H_{\text{max}} = \ln S$) (McCune and Mefford, 2006). For the final ordination additional rare species (i.e. those present in ≤ 5 relevés) were removed in order to improve the clarity of the ordination plot, further reducing the species number from 113 to 80; this did not substantially alter the nature of the plot. All plant community analyses were undertaken in PC-ORD Version 5.10 (McCune and Mefford, 2006).

MAVIS (Modular Analysis of Vegetation Information System) Plot Analyser Version 1.04 (Smart and DART Computing, 2016) was used in order to compare vegetation groups with the NVC (National Vegetation Classification), which is more comprehensive than current Irish classifications for heathlands.

2.2.5. Microclimate data analysis

Tiny tag data were uploaded using Tiny tag Explorer 4.4 software and mean monthly temperature values were obtained and graphed in Microsoft Excel in order to compare mean upland and lowland values. Relative humidity data were disregarded as being largely unreliable, including readings from the data-loggers housed in Stevenson-type screens, as records for all data-loggers, these included, alternated mostly between the two readings of 0% and 100% humidity.

2.3 Results

2.3.1. Vegetation survey

During the course of the vegetation survey historically recorded sites for *Arctostaphylos uva-ursi* were investigated. At the majority of these sites the species still occurred, however, there were a few sites where it was not re-found. For example a herbarium sample in the National Botanic Gardens, Dublin is recorded as having been collected from Turlough Hill, County Clare in 1892 (Webb and Scannell, 1983); the species was recorded on a cliff top at Slieve Carran Nature reserve, County Clare (Goodwillie, 1972); it is described in the SAC (Special Area of Conservation) Site synopsis for the East Burren Complex (site code 001926) as occurring on the western shores of Lough Bunny, County Clare (NPWS, 2001); and there was anecdotal evidence of its occurrence at Castletaylor woodland, south County Galway (Coillte woodland restoration site; A. O'Loughlin pers. comm.) – but it was not found at any of these sites during this survey, despite several searches. Webb and Scannell (1983) note that the species appears to be in decline, as nineteenth century records suggest a greater abundance. Other sites were brought to the author's attention where *Arctostaphylos* was present and these were added to the survey.

2.3.2. Vegetation analysis

The cluster analysis and Indicator Species Analysis resulted in a number of options with a high number of significant indicator species and low average p-value (Fig. 2.2): 4 or 6 groups were the best options based on a high number of significant indicator species (41 species for both 4 and 6 clusters) and a low average p-value ($p = 0.2656$ for 4 clusters; $p = 0.2721$ for 6 clusters). However the '6 groups' option was not as ecologically interpretable, particularly as one of the groups had just a single significant indicator species. Considering the ecology of the species, classification into 4 groups appeared to have merit and was therefore chosen. The MRPP test results indicate that there are significant differences ($p < 0.001$) between groups based on the environmental factors though within-group heterogeneity was relatively high ($A = 0.167$) for 4 groups but still within the acceptable range. The groups were established based on the dominant species and the significant indicator species for each group.

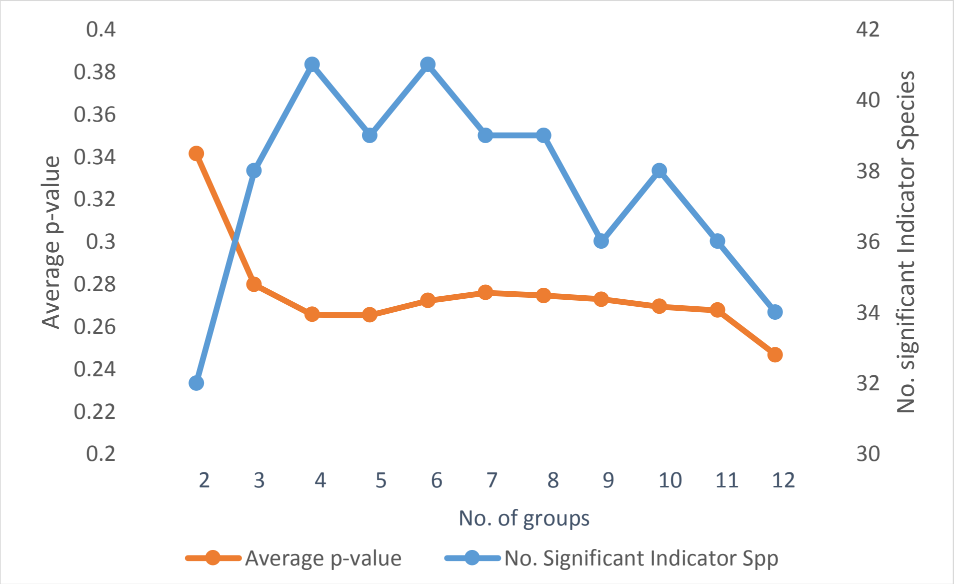

Figure 2.2. Indicator Species Analysis (ISA) groupings. The ideal number of groups is based on a high number of significant indicator species and a low average p-value (indicating the statistical significance of the observed maximum IV for each species from Monte Carlo randomisation tests).

2.3.3. Plant community composition

The four relevé groups are presented in the vegetation table (Table 2.4); species with low constancy values (values I to R, i.e. <20% frequency) which also have low indicator values are not included, except for *Hypnum cupressiforme* and *Salix repens*. Mean percent cover values for these species are presented in Table 2.5. Mean values for environmental and derived variables for the groups are also provided (Table 2.6) with any statistical differences between the groups as indicated (Kruskal-Wallis and Mann-Whitney test results in Appendix 2.1).

Group 1. *Arctostaphylos uva-ursi - Sesleria caerulea* heath

This is a broad ranging group, as it occurs in both upland and lowland areas (Table 2.4). Its dominant species in terms of mean % cover values (Table 2.5) ± standard deviation (SD) within this group are *Arctostaphylos uva-ursi* (52.6% ± 24.5) and *Sesleria caerulea* (21.6% ± 24.3). While these two species are common to all four groups, they are constant and significant indicator species for group 1 and their mean % cover values are highest in this group. *Rubus saxatilis,* although present in low cover values (0.35% ± 1.07) and an occasional species, is nearly confined to, and is a significant indicator species, for this group (IV = 20). Other (non-significant) indicator species which are frequent to occasional include *Pteridium aquilinum* (2.56% ± 4.3)*, Lotus corniculatus* (4.86% ± 8.64) and *Fissidens dubius* as well as *Corylus avellana, Polygala vulgaris, Rosa pimpinellifolia* and *Eurhynchium striatum*; *Hypnum cupressiforme* is scarce. Of the four groups, this group has the highest mean % cover of shrubs and the lowest mean % cover of forbs and graminoids (Table 2.6). The mean soil pH is highest and soils are the shallowest. This group also has the lowest mean species richness per relevé and lowest Evenness, Shannon diversity and Simpson diversity, as well as Ellenberg L which is a proxy for light (Table 2.6).

Table 2.4. Constancy table of relevés and species (outliers and species occurring in < 2 samples removed) for Alpine heath in the Burren, Western Ireland. Constancy values are as follows: R = ≤ 5%; + = 5.01-10%; I = 10.01-20%; II = 20.01-40%; III = 40.01- 60%; IV = 60.01-80%; V = 80.01-100%. Numbers given in superscript are Indicator Values (IV) from ISA of each species for each group based on their relative abundance and frequency; significant ($p < 0.05$) indicator species are highlighted.

Groups	1	2	3	4
No. of relevés	32	26	17	38
% relevés from lowland sites	46.9	88.5	5.9	0
% relevés from upland sites	53.1	11.5	94.1	100
1. *Arctostaphylos - Sesleria* heath				
Arctostaphylos uva-ursi	V ^{51}	V ^{27}	V ^{14}	IV ^{5}
Sesleria caerulea	V ^{40}	V ^{26}	V ^{10}	V ^{22}
Pteridium aquilinum	III ^{24}	II ^{3}	IV ^{23}	I ^{1}
Lotus corniculatus	III ^{23}	V ^{18}	IV ^{12}	IV ^{16}
Fissidens dubius	III ^{17}	II ^{9}	II ^{5}	II ^{6}
Rubus saxatilis	II ^{20}	R		R
Corylus avellana	II ^{17}	II ^{16}	+	+
Polygala vulgaris	II ^{15}	II ^{9}	I ^{1}	III ^{14}
Rosa pimpinellifolia	II ^{15}	II ^{13}	II ^{4}	II ^{2}
Eurhynchium striatum	II ^{11}	I	I ^{4}	I ^{4}
Hypnum cupressiforme	I ^{6}	I ^{2}	I ^{4}	I ^{1}
2. *Arctostaphylos - Juniperus* heath				
Juniperus communis	II ^{3}	V ^{80}	I	II ^{1}
Briza media	I ^{7}	V ^{39}	II ^{3}	I ^{1}
Ctenidium molluscum	IV ^{22}	V ^{30}	IV ^{5}	IV ^{18}
Carex flacca	V ^{23}	V ^{24}	V ^{22}	V ^{22}
Frullania tamarisci	I ^{2}	IV ^{49}	+	III ^{7}
Teucrium scorodonia	III ^{11}	IV ^{49}		I ^{3}
Neckera crispa	III ^{8}	IV ^{39}	I	IV ^{21}
Carex pulicaris	III ^{8}	IV ^{24}	IV ^{11}	IV ^{22}
Dicranum scoparium	II ^{5}	III ^{32}	III ^{3}	III ^{11}
Asperula cynanchica	+	III ^{22}	I ^{2}	II ^{13}
Leontodon saxatilis	R	II ^{30}		
Gymnadenia conopsea	+ ^{2}	II ^{23}		I ^{3}
Hypochaeris radicata	I ^{1}	II ^{22}	I ^{2}	II ^{5}
Rhytidiadelphus triquetrus	+	II ^{22}	III ^{22}	I ^{1}
Plantago maritima	+ ^{2}	II ^{21}		I ^{1}
Carex caryophyllea	+ ^{2}	II ^{15}		I ^{4}
Centaurea nigra	I ^{3}	II ^{14}	II ^{7}	R
Koeleria macrantha	+ ^{1}	II ^{14}	+ ^{1}	R
Pilosella officinarum	I ^{8}	II ^{13}		+

3. *Calluna- Arctostaphylos* heath

Calluna vulgaris	III ^{10}	V ^{6}	V ^{62}	V ^{15}
Hylocomium splendens	III ^{2}	IV ^{12}	V ^{62}	IV ^{8}
Molinia caerulea	III ^{3}	IV ^{18}	V ^{58}	II ^{3}
Festuca ovina	IV ^{6}	IV ^{17}	V ^{42}	V ^{20}
Succisa pratensis	III ^{6}	IV ^{13}	V ^{41}	V ^{22}
Geranium sanguineum	IV ^{18}	V ^{26}	V ^{29}	II ^{2}
Pseudoscleropodium purum	IV ^{12}	V ^{27}	V ^{27}	V ^{19}
Erica cinerea	I ^{1}	I	IV ^{48}	II ^{8}
Lathyrus linifolius	+ ^{1}	II ^{6}	IV ^{30}	II ^{9}
Hypnum jutlandicum	II ^{13}	I ^{1}	IV ^{25}	II ^{1}
Cirsium dissectum	R	R	III ^{28}	+ ^{3}
Anthoxanthum odoratum	II ^{3}	III ^{17}	III ^{21}	II ^{3}
Rhytidiadelphus squarrosus		II ^{14}	III ^{16}	I ^{2}
Festuca rubra	II ^{5}	I ^{5}	III ^{14}	II ^{6}
Plantago lanceolata	+ ^{4}	II ^{4}	III ^{14}	II ^{2}
Thuidium tamariscinum	+ ^{1}	I ^{5}	III ^{12}	I ^{3}
Agrostis capilaris		R	II ^{28}	R
Agrostis canina	+	+ ^{3}	II ^{9}	I ^{2}
Galium verum	R ^{1}	+ ^{2}	II ^{9}	R
Salix repens			I ^{18}	

4. *Dryas- Empetrum* heath

Thymus polytrichus	IV ^{19}	IV ^{11}	IV ^{6}	V ^{52}
Dryas octopetala	IV ^{18}	IV ^{10}	IV ^{10}	V ^{47}
Breutelia chrysocoma	V ^{31}	III ^{2}	V ^{11}	V ^{44}
Carex panicea	II ^{5}	III ^{8}	IV ^{28}	V ^{30}
Empetrum nigrum	I ^{1}	+		IV ^{60}
Linum catharticum	+ ^{1}	II ^{6}	I ^{3}	IV ^{32}
Tortella tortuosa	IV ^{17}	III ^{14}	II ^{2}	IV ^{26}
Solidago virgaurea	II ^{9}	III ^{12}	III ^{8}	IV ^{22}
Racomitrium lanuginosum	I ^{1}		I	III ^{39}
Euphrasia sp.	I ^{1}	II ^{9}	II ^{7}	III ^{19}
Hypnum lacunosum	II ^{5}	II ^{15}	I ^{1}	III ^{19}
Antennaria dioica	+ ^{1}	II ^{5}	+ ^{1}	II ^{24}
Epipactis atrorubens	I ^{6}	+ ^{1}	+ ^{1}	II ^{12}
Rhinanthus minor	+ ^{2}	I ^{3}		II ^{10}
Scapania aspera	I ^{5}		II ^{7}	II ^{9}

When compared with the NVC classification using MAVIS, this group has strong affinities (33 to 46%) for calcareous grassland communities: CG9 *Sesleria caerulea - Galium sterneri* grassland (37.9% affinity), and CG9c *Carex pulicaris - Carex panicea* sub-community (38.8%); CG13 *Dryas octopetala - Carex flacca* heath (37.5%), and CG13a *Pilosella officinarum - Ctenidium molluscum* sub-community (38%); CG10 *Festuca ovina - Agrostis capillaris - Thymus polytrichus* grassland (37.3%), and CG10b *Carex pulicaris - Carex panicea* (37.6%) and CG10a *Trifolium repens - Luzula campestris* (33.1%) sub-communities; and also has affinities for the heathland community H10 *Calluna vulgaris - Erica cinerea* heath (33.4%) and H10c *Thymus polytrichus - Carex pulicaris* (33.78%) and H10d *Festuca ovina - Anthoxanthum odoratum* (33.8%) sub-communities. CG9 occurs on moist free-draining Carboniferous limestone-derived soils and, in the U.K., is restricted to the montane and sub-montane climates of the northern Pennines, often forming an important part of upland hill pastures (Rodwell, 1992). CG10 is a sub-montane community of base-rich moist brown earths occurring from sea-level in north-west Scotland to 750m on calcareous bedrock, and CG13 is an oceanic lowland community of calcareous soils in north-west Scotland (Rodwell, 1992). H10 occurs on acid to neutral generally free-draining soils in the cool oceanic lowlands and upland fringes of north and western Britain (Rodwell, 1991).

Group 2. *Arctostaphylos uva-ursi - Juniperus communis* heath

This group comprises 88.5% lowland relevés (Table 2.4). It is defined mainly by a high % cover (38.77% ± 26.08) of the significant indicator species *Juniperus communis* (Table 2.5), which is constant here but is scarce to occasional in the other groups and rarely present in upland relevés. Although *A. uva-ursi* has a stronger affinity to group 1, it is also constant in this group (21.68% ± 17.18) as is *S. caerulea* (13.73% ± 6.82), *Calluna vulgaris* (5.20% ± 10.14), and *Molinia caerulea* (12.66% ± 17.07), *Corylus avellana* and *Pteridium aquilinum* are occasional; but they are not indicator species for

Table 2.5. Mean % cover of species with over 0.20% cover in at least one Group (except for *Epipactis atrorubens*) and standard deviation per species per vegetation group (outliers and species occurring in < 2 samples removed) in decreasing order of % cover values for the species assigned vegetation group. Significant indicator species are highlighted with the cover values for their respective vegetation group.

Vegetation Groups	1		2		3		4	
No. of relevés	32		26		17		38	
% of relevés from lowland sites	46.9		88.5		5.9		0	
% of relevés from upland sites	53.1		11.5		94.1		100	
	Mean % cover	St. Dev.	Mean % cover	St. Dev.	Mean % cover	St. Dev.	Mean % cover	St. Dev.
1. *Arctostaphylos - Sesleria* heath								
Arctostaphylos uva-ursi	52.59	24.52	21.68	17.18	15.85	13.70	7.21	6.59
Sesleria caerulea	21.64	24.30	13.73	6.82	6.26	7.67	12.11	9.00
Lotus corniculatus	4.86	8.64	2.75	3.70	1.88	2.48	2.75	3.00
Pteridium aquilinum	2.56	4.31	0.93	2.31	1.71	1.66	0.29	0.65
Corylus avellana	1.70	7.79	2.27	5.56	0.03	0.12	0.03	0.11
Rosa pimpinellifolia	1.64	2.92	0.68	1.25	0.74	2.34	0.28	0.44
Eurhynchium striatum	1.30	5.34	0.05	0.14	0.56	1.88	0.72	2.30
Helictotrichon pubescens	0.47	2.61	0.02	0.10	0.03	0.12	0.00	0.00
Fissidens dubius	0.36	0.88	0.25	0.29	0.15	0.23	0.16	0.23
Rubus saxatilis	0.34	1.07	0.02	0.10	0.00	0.00	0.01	0.08
Polygala vulgaris	0.33	0.87	0.18	0.24	0.06	0.16	0.24	0.25
Hypnum cupressiforme	0.20	0.87	0.09	0.24	0.09	0.19	0.05	0.15
2. *Arctostaphylos - Juniperus* heath								
Juniperus communis	5.75	12.63	38.77	26.08	0.06	0.16	2.36	7.54
Ctenidium molluscum	4.66	8.08	5.93	10.04	0.94	1.22	3.39	4.01
Carex flacca	6.45	9.02	5.34	4.46	5.35	6.65	5.38	6.47
Carex pulicaris	1.39	2.38	3.48	3.08	1.47	1.94	2.58	3.68
Neckera crispa	1.19	2.41	3.45	4.77	0.12	0.32	2.07	3.08
Frullania tamarisci	0.41	1.74	2.55	5.18	0.06	0.24	0.54	1.02
Dicranum scoparium	0.42	0.76	1.86	2.25	0.21	0.25	0.64	1.03
Rhytidiadelphus triquetrus	0.03	0.12	1.30	4.18	0.91	1.37	0.13	0.37
Briza media	0.72	2.61	1.02	0.83	0.18	0.24	0.09	0.25
Teucrium scorodonia	0.55	0.78	0.93	1.12	0.00	0.00	0.37	1.47
Leontodon saxatilis	0.02	0.09	0.82	2.10	0.00	0.00	0.00	0.00
Hypochaeris radicata	0.11	0.27	0.77	1.55	0.12	0.27	0.25	0.51
Plantago maritima	0.23	1.22	0.68	1.34	0.00	0.00	0.13	0.45
Carex nigra	0.22	0.70	0.55	1.41	0.00	0.00	0.03	0.16
Centaurea nigra	0.13	0.28	0.52	1.06	0.21	0.35	0.05	0.32
Trifolium pratense	0.03	0.17	0.43	1.66	0.00	0.00	0.13	0.80
Agrostis vinealis	0.00	0.00	0.41	1.66	0.00	0.00	0.03	0.11
Asperula cynanchica	0.03	0.12	0.34	0.28	0.09	0.19	0.29	0.71
Pilosella officinarum	0.52	2.61	0.34	0.63	0.00	0.00	0.03	0.11
Leontodon hispidus	0.00	0.00	0.30	0.75	0.00	0.00	0.00	0.00
Carex caryophyllea	0.06	0.21	0.23	0.45	0.00	0.00	0.09	0.23
Gymnadenia conopsea	0.06	0.21	0.20	0.25	0.00	0.00	0.07	0.17
Hedera helix	0.45	1.13	0.18	0.63	0.00	0.00	0.07	0.20
Danthonia decumbens	0.33	1.74	0.18	0.47	0.12	0.21	0.11	0.49
3. *Calluna - Arctostaphylos* heath								
Calluna vulgaris	12.16	13.45	5.20	10.14	46.18	23.87	11.78	7.26
Hylocomium splendens	2.45	6.27	7.39	12.98	28.56	17.10	5.01	7.16
Molinia caerulea	2.52	4.03	12.66	17.07	28.50	22.16	3.83	8.84
Succisa pratensis	3.19	5.60	5.14	6.14	10.47	10.57	6.01	4.44
Festuca ovina	1.56	2.26	4.36	3.21	8.18	6.22	3.76	4.12
Pseudoscleropodium purum	4.92	7.52	9.84	8.00	8.18	6.07	6.36	7.61

Erica cinerea	0.53	1.85	0.14	0.34	5.53	5.91	2.00	4.76
Geranium sanguineum	2.92	7.25	3.48	3.20	3.53	2.85	0.64	1.19
Cirsium dissectum	0.09	0.52	0.05	0.21	1.18	2.30	0.70	3.56
Festuca rubra	0.53	1.26	0.59	2.15	1.06	1.55	0.64	2.46
Anthoxanthum odoratum	0.30	0.93	1.02	1.84	0.97	2.32	0.33	0.73
Rhytidiadelphus squarrosus	0.00	0.00	1.41	2.66	0.91	1.35	0.25	0.73
Hypnum jutlandicum	1.14	3.44	0.14	0.43	0.85	1.21	0.12	0.21
Lathyrus linifolius	0.25	0.87	0.43	0.76	0.74	0.60	0.51	1.05
Loeskeobryum brevirostre	0.03	0.12	0.00	0.00	0.59	2.35	0.03	0.16
Agrostis capilaris	0.00	0.00	0.02	0.10	0.53	1.23	0.01	0.08
Agrostis canina	0.05	0.19	0.50	1.64	0.41	1.18	0.18	0.71
Plantago lanceolata	0.50	2.61	0.20	0.33	0.32	0.48	0.12	0.24
Salix repens	0.00	0.00	0.00	0.00	0.26	0.73	0.00	0.00
Thuidium tamariscinum	0.14	0.55	0.34	0.92	0.26	0.35	0.20	0.59
Galium verum	0.31	1.74	0.18	0.57	0.18	0.24	0.01	0.08
4. *Dryas - Empetrum* heath								
Dryas octopetala	11.55	16.53	5.75	8.23	6.18	8.27	23.37	18.61
Breutelia chrysocoma	19.06	21.53	2.02	3.50	6.65	8.45	22.21	12.43
Thymus polytrichus	3.02	3.67	1.86	2.18	0.94	0.95	6.26	6.40
Empetrum nigrum	0.67	1.99	0.55	2.10	0.00	0.00	6.12	8.76
Carex panicea	1.20	3.12	1.84	2.39	3.59	5.08	3.62	3.14
Racomitrium lanuginosum	0.11	0.24	0.00	0.00	0.09	0.26	2.46	4.81
Trichophorum cespitosum	0.00	0.00	0.00	0.00	0.26	0.73	1.84	8.99
Hypnum lacunosum	0.67	2.62	1.36	2.65	0.15	0.48	1.11	1.81
Solidago virgaurea	0.77	2.61	0.73	0.78	0.56	1.17	1.03	1.75
Tortella tortuosa	0.59	0.76	0.52	0.73	0.18	0.29	0.82	0.82
Antennaria dioica	0.05	0.15	0.14	0.27	0.06	0.24	0.38	0.66
Linum catharticum	0.05	0.15	0.16	0.23	0.09	0.19	0.30	0.24
Euphrasia sp.	0.08	0.22	0.25	0.29	0.26	0.71	0.30	0.31
Epipactis atrorubens	0.09	0.20	0.05	0.14	0.03	0.12	0.14	0.25

this group. Other significant indicator species are the constant *Briza media*, *Frullania tamarisci, Teucrium scorodonia,* and *Neckera crispa,* the frequent *Dicranum scoparium* and *Asperula cynanchica,* occasional *Hypochaeris radicata, Plantago maritima* and *Koeleria macrantha,* and scarce *Leontodon hispidus* and *Rubus fruticosus* agg.; these species all occupy a low mean % cover within the quadrats (< 5%). This group has the highest mean species richness of the four groups. It also has the lowest mean soil organic matter (37.48% ± 19.54 loi) content. This group has relatively high mean % cover of shrubs, graminoids and forbs (Table 2.6).

The NVC affinities for this group, similar to group 1, are for CG9 (43.4%), CG9c (42.44%), CG9e (33.55%); CG13 (42.2%), CG13a (44.84%); CG10 (38.54%), CG10b (39.12%), CG10c (34.77%); CG2d *Festuca ovina - Helictotrichon pratense* grassland, *Dicranum scoparium* sub-community

(34.53%); and H10d *Calluna vulgaris - Erica cinerea* heath, *Thymus polytrichus - Carex pulicaris* sub-community (33.64%). CG9, CG10, CG13 and H10 are described above. CG2 is characteristic of free-draining calcareous soils in lowland areas of Britain and depends on grazing to maintain a close sward; the *Dicranum* sub-community is largely restricted to steep slope in the north and west (Rodwell, 1992), and a number of species in this sub-community are absent from Ireland.

Group 3. *Calluna vulgaris - Arctostaphylos uva-ursi* heath

This group is composed of 94% upland relevés (Table 2.4). It is defined by a high cover of the following constant significant indicator species: *Calluna vulgaris* (46.2% ± 23.9; Table 2.5), *Molinia caerulea* (28.5% ± 22.2), *Hylocomium splendens* (28.6% ± 17.1), *Succisa pratensis* (10.5% ± 10.6), *Festuca ovina* (8.2% ± 6.2) and *Erica cinerea* (5.5% ± 5.9). *Arctostaphylos uva-ursi,* although not a significant indicator species for this group, is constant species (15.6% ± 13.7), as is *Sesleria caerulea* (6.3% ± 7.7), and *Pteridium aquilinum* (1.17% ± 1.66); *Corylus avellana* is rare. Additional significant indicator species include constant *Lathyrus linifolius* and *Hypnum jutlandicum,* occasional *Cirsium dissectum,* frequent *Agrostis capillaris,* and rare species *Salix repens* and *Polygala serpyllifolia.* Other (non-significant) indicator constant species include *Geranium sanguineum* and *Pseudoscleropodium purum* (Table 2.4). Mean soil depth is the deepest for this group of relevés, and mean soil pH is the lowest. The mean % cover of bryophytes, graminoids and forbs are highest in this group. Mean vegetation height is the greatest and Ellenberg F which is a proxy for moisture is also highest for this group (Table 2.6).

The NVC affinities for this group are largely for the same communities as groups 1 and 2: CG13 (45.88%), CG13a (45.33%), CG10 (41.76%), CG10a (39.79%), CG10b (42.11%) and CG9c (41.02%), as well as heath communities H10 (36.62%), H10c (41.09%), H10d (40.67%) and H12c *Calluna vulgaris*

Table 2.6. Mean values for environmental variables recorded from relevés in vegetation groups 1 to 4 and mean values for derived values of diversity and Ellenberg indices. Highest values are shown in bold. Superscript letters are given for variables where $p < 0.05$ in Kruskal-Wallis test (Appendix 2.1, Table 2.1) and whose mean values are significantly different where letters are not shared; Mann-Whitney posthoc test results in Appendix 2.1; Table 2.2. Aspect categories are given in Table 2.3; in general the higher the number the more northerly-facing the site and therefore the lower the heat load (1 = south, 17 = north; (Hodd, 2012)).

	Group 1		Group 2		Group 3		Group 4	
	Mean	St. Dev.	Mean	St. Dev.	Mean	St. Dev.	Mean	St. Dev.
Altitude (m a.s.l.)	116.97 ^{a}	90.34	53.04 ^{a}	67.53	193.31 ^{b}	56.90	**239.33** ^{b}	45.38
Slope	8.63	11.96	7.89	8.39	11.88	13.15	**12.97**	13.83
Aspect Category	8.69	4.80	7.81	4.10	9.71	4.53	**10.87**	4.31
Mean Vegetation height (cm)	11.05 $^{a, c}$	7.16	13.40 ^{a}	7.77	**26.82** ^{b}	12.73	8.41 ^{c}	6.55
Mean Soil depth (cm)	3.45 ^{a}	3.07	3.63 ^{a}	2.61	**11.06** ^{b}	8.09	4.55 ^{a}	4.04
Soil pH	**7.03** $^{a, c}$	0.62	6.99 ^{a}	0.39	6.26 ^{b}	0.60	6.75 ^{c}	0.52
Soil % LOI	57.35 ^{a}	22.14	37.48 ^{b}	19.54	38.53 ^{b}	13.38	**71.73** ^{c}	16.55
% bare ground	1.03 ^{a}	1.70	0.75	1.21	1.53	2.40	**2.13**	1.96
% exposed rock	**9.89** ^{a}	11.43	9.44 ^{a}	15.34	2.12 ^{b}	3.89	7.74 ^{a}	10.00
% litter	11.16	11.51	8.69	7.50	8.29	7.77	**14.03**	8.93
% faeces	0.17	0.32	0.42	0.66	0.71	0.88	**1.96**	9.07
% bryophytes	41.44	24.41	41.15	18.88	**49.00**	24.11	45.05	17.07
% shrubs	**71.44** ^{a}	18.45	66.27 ^{a}	22.36	62.59 $^{a, b}$	22.37	52.92 ^{b}	19.08
% graminoids	29.94 ^{a}	24.06	39.92 $^{b, c}$	18.39	**49.18** ^{b}	21.22	32.24 $^{a, c}$	18.00
% forbs	14.22	11.71	18.35	13.76	**19.71**	10.40	16.91	7.30
% lichen	0.23	0.41	**0.56**	1.53	0.03	0.12	0.38	1.28
% bracken	**2.58** ^{a}	4.30	0.83 ^{b}	2.14	1.71 ^{a}	1.66	0.32 ^{b}	0.65
Species richness	25.63 ^{a}	5.81	**34.92** ^{b}	7.55	32.47 $^{b, c}$	4.97	31.58 ^{c}	4.84
Evenness	0.67 ^{a}	0.09	0.73 $^{b, c}$	0.08	0.69 $^{a, b}$	0.06	**0.77** ^{c}	0.05
H (Shannon index)	2.15 $^{a, c}$	0.39	2.57 $^{b, c}$	0.37	2.41 ^{c}	0.22	**2.64** ^{b}	0.22
D` (Simpson index)	0.80 $^{a, c}$	0.09	0.87 $^{b, c}$	0.05	0.85 ^{c}	0.05	**0.89** ^{b}	0.03
Ellenberg L (light)	6.89 ^{a}	0.24	7.06 ^{b}	0.12	7.04 ^{b}	0.12	**7.10** ^{b}	0.15
Ellenberg F (moisture)	5.21 $^{a, c}$	0.23	5.17 ^{a}	0.16	**5.50** ^{b}	0.27	5.30 ^{c}	0.21

- *Vaccinium myrtillus* heath, *Galium saxatile - Festuca ovina* sub-community (37.91%). H12 is the most common heath type outside of the oceanic zone of the British uplands, it is a sub-shrub community of acidic to neutral, free-draining mineral soils through the cold and wet sub-montane zone (Rodwell, 1991).

Group 4. *Dryas octopetala - Empetrum nigrum* heath

The relevés in this group are all located in the Burren uplands (Table 2.4). Although not indicator species *Arctostaphylos uva-ursi* and *Sesleria caerulea* are still constant in many relevés (Table 2.4), their mean % cover values (Table 2.5) are lower, particularly for *A. uva-ursi* (7.2% ± 6.6) and in these relevés *Empetrum nigrum* is an important component of the vegetation and a significant indicator species for this group although its mean % cover remains low (6.1% ± 8.8). Other significant indicator species include the constant species *Dryas octopetala* (23.4% ± 18.6), *Breutelia chrysocoma* (22.2% ± 12.4), *Thymus polytrichus* (6.3% ± 6.4), *Carex panicea* (3.6% ± 3.1), *Linum catharticum* (0.3% ± 0.2), and the frequent species *Racomitrium lanuginosum* (2.5% ± 4.8) is almost confined to this group; *Antennaria dioica* (0.4% ± 0.7) is occasional. Other non-indicator species of interest are constant *Calluna,* occasional *Molinia,* while *Pteridium aquilinum* and *Corylus avellana* are rare. This group has the lowest mean vegetation height and the highest mean soil organic matter content. Its values for Evenness, Shannon diversity and Simpson diversity are the highest of the groups, and Ellenberg L is the highest (Table 2.6).

The NVC affinities for this group are again for calcareous grassland and heath communities and sub-communities: CG13 (43.48%), CG13a (45.82%), CG10 (40.19%), CG10a (34.77%), CG10b (41.48%), CG10c (36.37%), CG9 (39.82%), CG9c (43.36%), and CG14 *Dryas octopetala* - *Silene acaulis* ledge community (33.22%), as well as H10d (35.55%). CG14 is a community of calcareous rock outcrops and ledges, mainly confined to the Scottish montane regions from 300 - 900m altitude (Rodwell, 1992).

2.3.4. Plant communities in relation to environmental variables

The NMS analysis recommended a 3-dimensional solution. Stress levels stabilised after 42 iterations with a final stress level of 16.154 and a final instability of 9×10^{-5}. Monte Carlo test result: $p = 0.0040$. The three axes explained 78.5% of the variance in the data: axis 1 explained 13.9%; axis 2 explained 27.5%; and axis 3 explained 37.1%. The ordination plots (Figs 2.3: relevés; and 2.4: species) are for axes 2 and 3 as these explain the most variation in the data and are the easiest to interpret ecologically. The relevés are coded in relation to the vegetation group they were classified into from the cluster analysis and ISA (as per Table 2.4).

The plant communities (Fig. 2.3) are well separated from each other – group 1: *Arctostaphylos* - *Sesleria* heath occupies the bottom right and middle of the plot, group 2: *Arctostaphylos* - *Juniperus* heath is in the middle of the plot, group 3: *Calluna* - *Arctostaphylos* heath is in the middle left and group 4: *Dryas* - *Empetrum* heath is in the middle and right of the top of the plot.

Group 4 in particular is strongly positively correlated with axis 3, which explains 37.1% of the variation in the ordination. Group 3 is negatively correlated with axis 2. Group 1 is positively correlated with axis 2 and negatively correlated with axis 3. Group 2 is variable in relation to axes 2 and 3, some plots having positive and others negative correlations, and it is

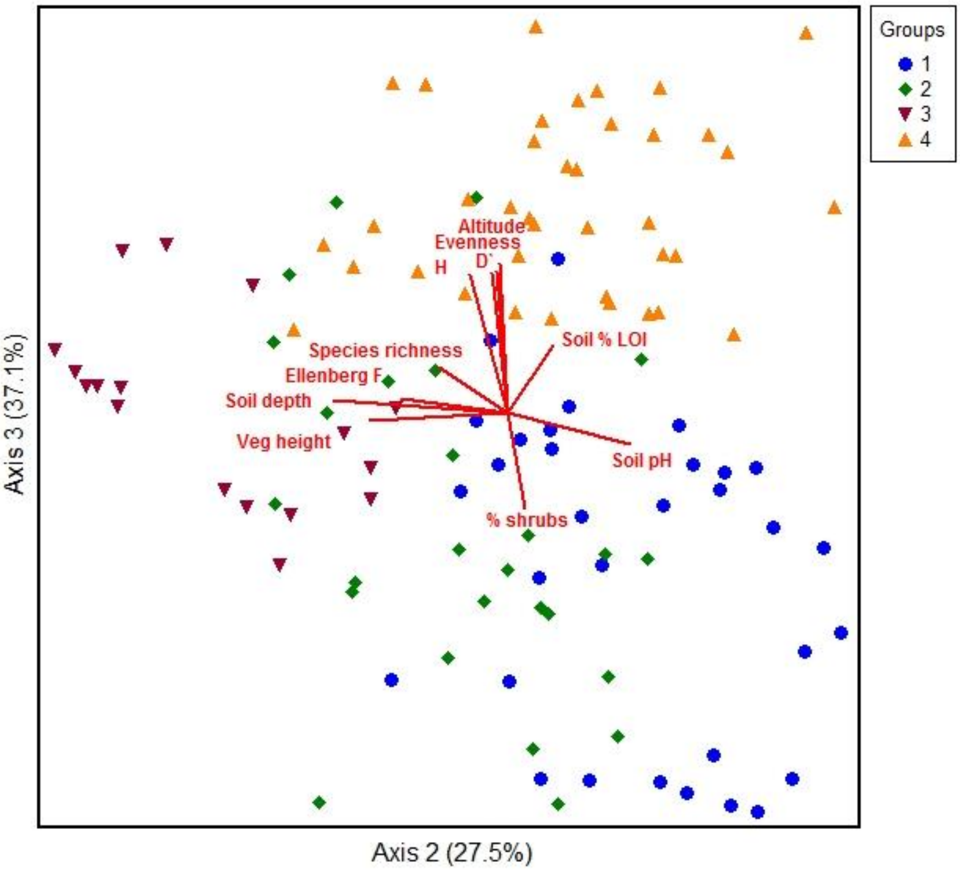

Figure 2.3. NMS ordination of relevés colour coded for vegetation groups 1-4 as per Table 2.3. Group 1 (blue circles), 2 (green diamonds), 3 (wine inverted triangle) and 4 (orange triangle) with biplot of % cover of life forms, environmental variables and derived variables D' = Simpson's index of diversity; H = Shannon diversity; and Evenness = species richness/ln (H). Only those variables with r^2 correlations with one of the axes > 0.15 are plotted (Table 2.7).

however positively correlated with axis 1. The strongest positive correlation with axis 3 is altitude (Table 2.7; $r^2 = 0.379$); Evenness and the diversity indices of Shannon (H) and Simpson (D’) also have strong correlations ($r^2 > 0.35$); soil % LOI has a weaker positive correlation ($r^2 = 0.172$). Group 4 is associated with high altitude, high values for Evenness, H and D’ and high soil organic content and its corresponding relevés are located at the top of the ordination plot. Percent cover of shrubs is negatively correlated with axis 3, i.e. relevés and species associated with high shrub cover (group 1) are at the bottom of the ordination. Relevés with low altitude (group 2), low Evenness and low Shannon (H) and Simpson (D’) diversity values are also at the bottom of the ordination (group 1). Axis 2 has the strongest positive correlation with soil pH ($r^2 = 0.313$) and strong negative correlations with mean soil depth ($r^2 = 0.443$), mean vegetation height ($r^2 = 0.351$) and Ellenberg F ($r^2 = 0.271$), and a weaker correlation with species richness ($r^2 = 0.175$). Group 1 is associated with high soil pH and short vegetation and therefore is positively correlated with axis 2, it also has a negative correlation with axis 3 associated with low altitude and a high % cover of shrubs. Group 3 however, is associated with deep soils, tall vegetation, and low soil pH in addition to high Ellenberg F, thus it is negatively correlated with this axis. Group 2 is also negatively correlated with axis 2 as it has high species richness and low Ellenberg F values, in addition to having a strong negative correlation with axis 3 as it is a low altitude group. Group 4 has strong correlations with high altitude, high soil organic matter, and high values for evenness and diversity indices (H and D’) (axis 3). Axis 1 (not shown on the plots) explains the least amount of variation in the data, it is negatively correlated with altitude ($r^2 = 0.206$) and soil % LOI ($r^2 = 0.161$; Table 2.7).

In the species plot (Fig. 2.4) many of the species associated especially with groups 3 and 4 are easily seen, though many of the group 1 species are intermixed with group 2 species and so they are harder to pick out. For group 1 (*Arctostaphylos - Sesleria* heath) to the bottom right of the plot, species include the indicator species *Rubus saxatilis* which plots clearly near the bottom of the plot and *Arctostaphylos uva-ursi* occurs further up near the small shrub *Rosa pimpinellifolia*. As Group 2 (*Arctostaphylos - Juniperus* heath) relevés are scattered from the bottom right and upwards towards the centre of the plot, the species are not easily seen, though scrub species *Ulex europaeus, Prunus spinosa*, the climber *Hedera helix,* and the indicator species *Juniperus communis* can be found towards the bottom of the central cluster and near *R. pimpinellifolia* and *A. uva-ursi*. These assemblages comprise low shrubs mixed with rocky calcareous grassland species. Species

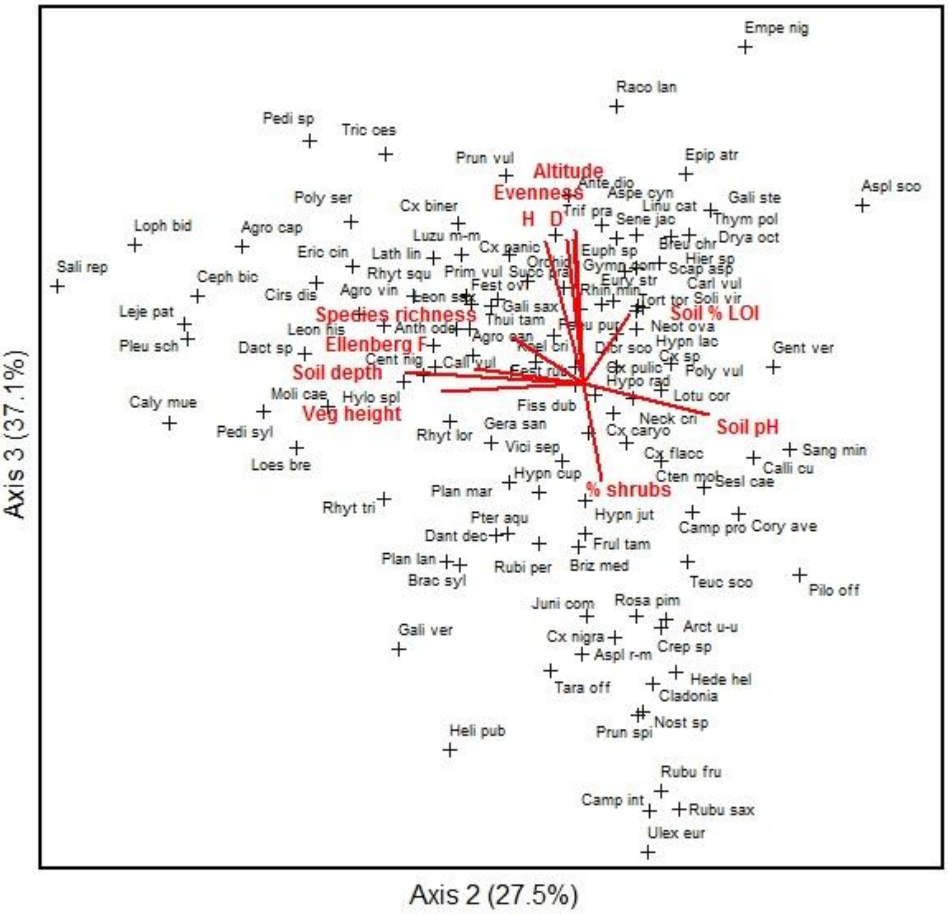

Figure 2.4. NMS ordination of species with biplot of % cover of life forms, environmental variables and derived variables. D' = Simpson's index of diversity; H = Shannon diversity; and Evenness = species richness/ln (H). Only those variables with r^2 correlations with one of the axes > 0.15 are plotted (Table 2.7). Full species names in Appendix 2.2.

associated with Group 3 (*Calluna - Arctostaphylos* heath) plot mainly to the top left and centre of the plot; *Calluna* and a number of the grasses, notably *Molinia* are plotted in the centre of the upper left quadrant with indicator species *Erica cinerea* and *Cirsium dissectum* occurring further towards the top left within a cluster of group 3 species and *Salix repens* is at the farthest left side of the plot. Group 4 (*Empetrum nigrum – Dryas* heath) species are all in the upper half of the plot, mainly to the right with few species located left of the centre. *Empetrum nigrum, Racomitrium lanuginosum* and *Epipactis atrorubens* are clearly plotted at the top right of the plot, the indicator species *Dryas octopetala, Thymus polytrichus, Linum catharticum* and *Breutelia chrysocoma* are all located lower down at the right of the plot and then group 3 species overlap with group 2 species assemblages – abbreviations of species names and their full names are in Appendix 2.2.

Table 2.6. Pearson (r^2 - parametric) and Kendall (tau – non-parametric) correlation coefficients between each axis (1 to 3) of the NMS plot and environmental variables and life forms, r^2 and tau values > 0.15 and < -0.15 are shown in bold. The r value indicates whether the Pearson correlation is positive or negative.

Axis:		**1**			**2**			**3**	
	r	r^2	tau	r	r^2	tau	r	r^2	tau
Altitude (metres a.s.l.)	-0.454	**0.206**	-0.18	-0.148	0.022	-0.112	0.616	**0.379**	**0.39**
Slope	0.052	0.003	0.005	0.106	0.011	0.05	0.183	0.034	0.126
Aspect category	-0.274	0.075	**-0.245**	0.005	0	-0.003	0.17	0.029	0.137
Mean vegetation height (cm)	-0.102	0.01	-0.03	-0.592	**0.351**	**-0.437**	-0.139	0.019	-0.132
Mean Soil depth (cm)	-0.24	0.057	-0.174	-0.665	**0.443**	**-0.532**	0.173	0.03	0.147
Soil pH	0.304	0.092	**0.225**	0.56	**0.313**	**0.357**	-0.281	0.079	-0.19
Soil % loss-on-ignition	-0.401	**0.161**	**-0.245**	0.342	0.117	**0.219**	0.415	**0.172**	**0.278**
% bare ground	-0.177	0.031	-0.114	-0.071	0.005	-0.028	0.156	0.024	**0.249**
% exposed rock	0.129	0.017	0.03	0.238	0.057	**0.308**	-0.025	0.001	0.047
% litter	-0.125	0.016	-0.047	0.066	0.004	0.019	0.217	0.047	**0.211**
% faeces	-0.064	0.004	-0.006	-0.046	0.002	-0.073	0.082	0.007	0.188
% bryophytes	-0.24	0.058	-0.172	-0.006	0	-0.029	0.141	0.02	0.083
% shrubs	0.144	0.021	0.103	0.211	0.044	0.161	-0.494	**0.244**	**-0.364**
% graminoids	0.335	0.112	**0.314**	-0.231	0.053	-0.13	-0.113	0.013	-0.061
% forbs	0.176	0.031	0.049	-0.233	0.054	**-0.228**	0.295	0.087	**0.247**
% lichen	0.05	0.002	0.073	0.05	0.002	0.149	-0.091	0.008	-0.058
% bracken	-0.27	0.073	**-0.233**	-0.153	0.023	**-0.207**	-0.232	0.054	-0.137
Species richness	0.245	0.06	0.125	-0.418	**0.175**	**-0.305**	0.339	0.115	0.188
Evenness	0.057	0.003	0.046	-0.163	0.027	-0.143	0.599	**0.358**	**0.375**
H (Shannon index)	0.151	0.023	0.108	-0.309	0.096	**-0.229**	0.593	**0.351**	**0.366**
D` (Simpson index)	0.082	0.007	0.077	-0.202	0.041	-0.167	0.597	**0.357**	**0.373**
Ellenberg L (light)	0.138	0.019	0.104	-0.258	0.067	-0.162	0.372	0.138	**0.213**
Ellenberg F (moisture)	-0.249	0.062	-0.144	-0.521	**0.271**	**-0.325**	0.195	0.038	0.134
% variance explained		**13.7**			**27.5**			**37.1**	

Potential (scrub invasion) threat species *Corylus avellana* is located in the lower right-hand side of the ordination; this correlates with shallow soils and relatively high pH and low altitude. *Pteridium aquilinum* is located centrally in the lower half of the plot not showing a strong correlation for any of the variables displayed. *Molinia caerulea* is located in the middle of the left-hand side of the plot and is correlated with somewhat deeper more acidic soils. *Calluna* is located right in the middle of the ordination with just a slight preference for the left-hand side of the plot, probably due to lower soil pH and intermediate vegetation height.

2.3.5. Geographical distribution of relevés and their associated communities

The location of relevés as represented by their vegetation groups are indicated on the maps (Figs. 2.5 and 2.6). Group 1 *Arctostaphylos - Sesleria* relevés are located both in the west Burren 'uplands' i.e. above 100m, and in the east 'lowlands' i.e. below 100m, group 2 *Arctostaphylos - Juniperus* relevés are found almost entirely in the 'low' Burren and groups 3 and 4 relevés are confined to the 'high' Burren with the *Dryas - Empetrum* group (4) having a more widespread distribution than the *Calluna - Arctostaphylos* group (3).

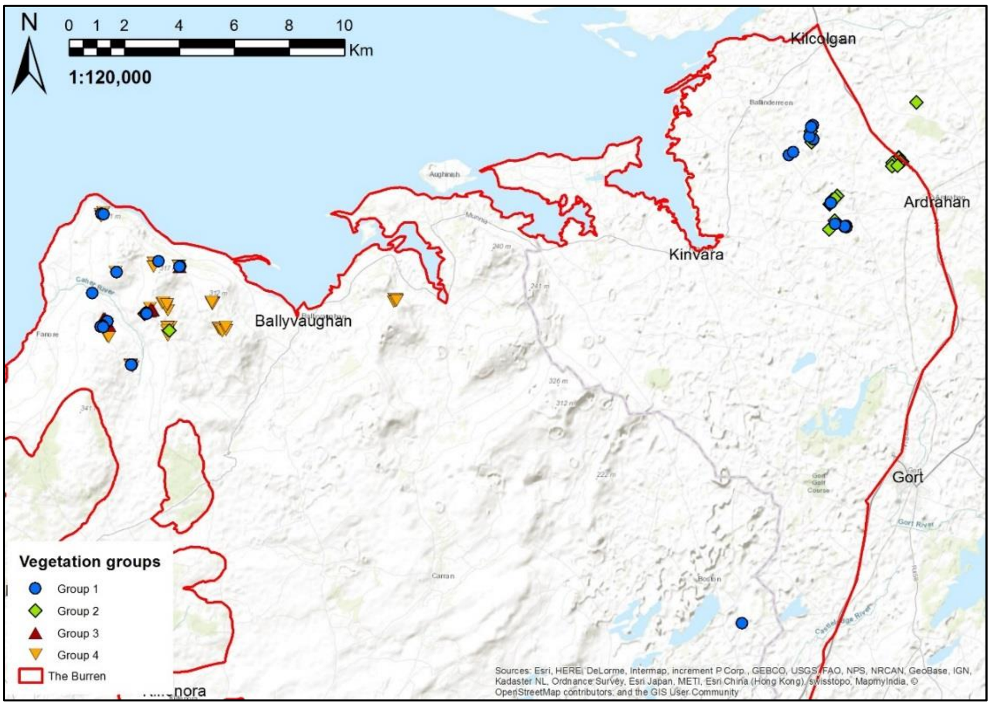

Figure 2.5. Map of study area showing relevés and their assigned vegetation group. Legend indicates the area of Carboniferous (Burren) bedrock (red outline; Geological Survey of Ireland 2012) with shale outlier to the southwest; vegetation group 1 *Arctostaphylos* - *Sesleria* (blue circle), group 2 *Arctostaphylos* - *Juniperus* (green diamond), group 3 *Calluna* - *Arctostaphylos* (red inverted triangle) and group 4 *Dryas* - *Empetrum* (orange triangle) as per Table 2.3.

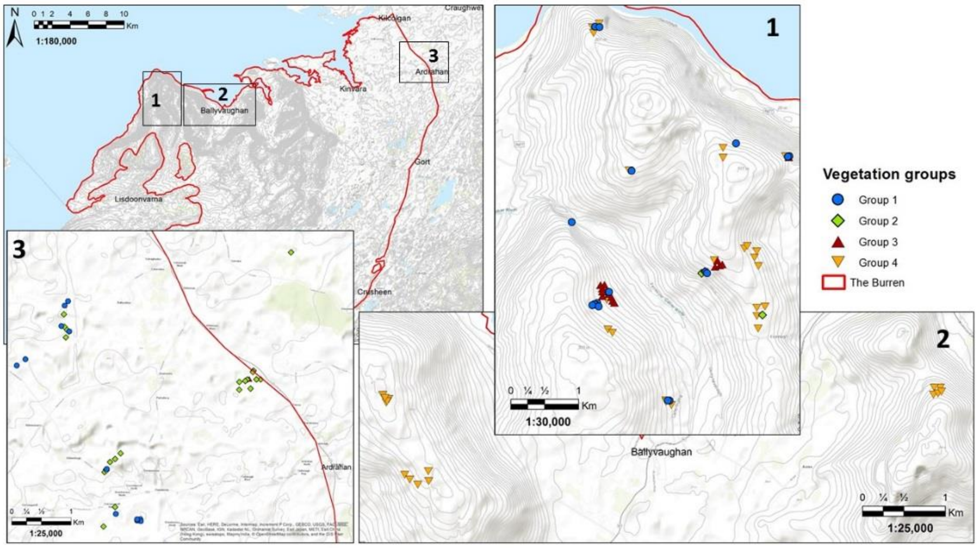

Figure 2.6. Detailed maps of study area showing relevés and their assigned vegetation group. Contour lines are in grey, darker grey indicates steep terrain. Legend indicates the area of Burren bedrock (red outline) with shale outlier to the southwest; vegetation group 1 *Calluna* - *Arctostaphylos* (blue circle), group 2 *Arctostaphylos* - *Juniperus* (green diamond), group 3 *Calluna* - *Arctostaphylos* (red inverted triangle) and group 4 *Dryas* - *Empetrum* (orange triangle) as per Table 2.3. Study regions 1, 2 and 3 enlargements inset, scale bars are 1 Km. Scale bar on main map is 10 Km. Outside the three map areas above, *A. uva-ursi* was only recorded at Attyslaney (blue circle for two relevés just southwest of Gort in Fig 2.5).

2.3.6. Microclimate data in relation to upland and lowland sample areas

The temperature data from data-loggers were calculated as mean monthly temperature averaged separately for lowland (mean altitude: 29.4 m a.s.l.; n = 5) and upland (mean altitude: 205.3 m a.s.l.; n = 6) data-loggers (Fig. 2.7). The range in mean temperature for the upland data is from 4.11 °C to 15.65 °C and for the lowland sites from 4.66 °C to 17.53 °C between August 2013 and October 2015. There is a mean difference of 1°C between upland and lowland data-logger values through the period of recording with the greatest difference in temperature between sites occurring in the spring/summer/autumn months (significant differences for months August, September and October 2014 and February to August 2015, $p < 0.05$; see Appendix 2.3, Table 2.1) and the smallest difference in autumn/winter months where in some months the upland mean monthly temperature was actually slightly warmer than in the lowlands (in November and December 2014, the mean difference was -0.13°C and -0.03°C, respectively; Fig. 2.8).

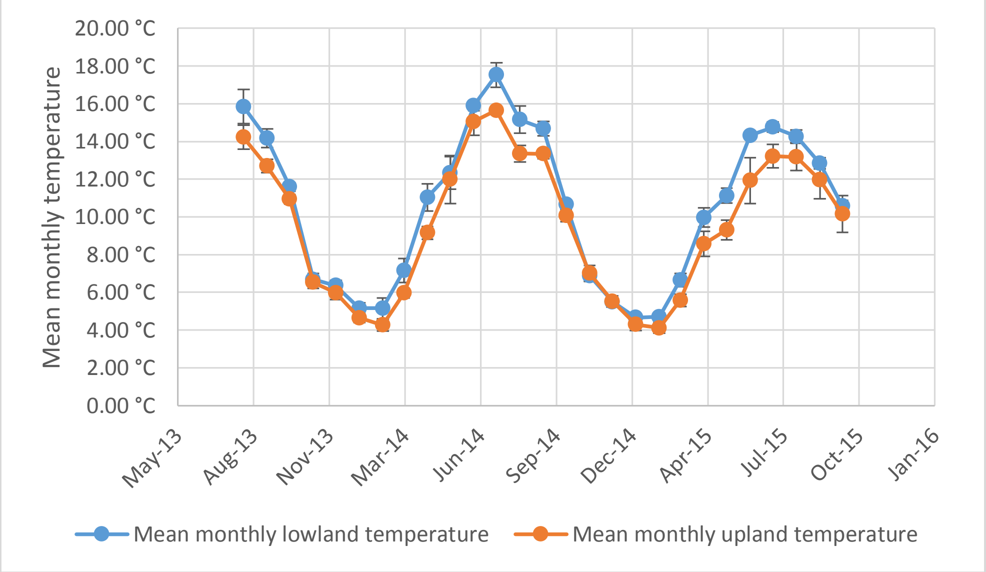

Figure 2.7. Mean monthly temperature averaged for all lowland and all upland data-loggers with standard deviation indicated as bars.

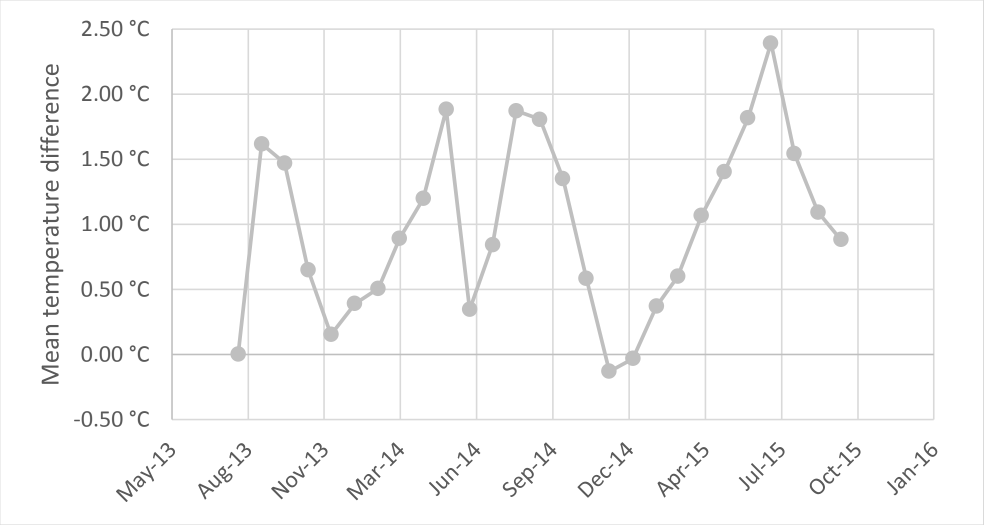

Figure 2.8. Mean monthly temperature difference between lowland data-loggers (n = 5; mean altitude = 29.4 m) and upland data-loggers (n = 6; mean altitude = 205.3 m). A positive temperature difference results from higher temperatures in the lowlands. See Appendix 2.3, Table 2.1 for Kruskal-Wallis test results.

2.4 Discussion

The lowland limestone heaths of the eastern Burren have not been studied or classified previously and this study has shown these heaths to be distinctive from those in the western upland Burren, while they do have elements in common. The plant communities will be compared with relevant existing classifications in the sections below.

2.4.1. Comparison of plant community classifications and environmental factors

1. The *Arctostaphylos uva-ursi* – *Sesleria caerulea* community is distinguished by constant *A. uva-ursi* and *S. caerulea* with occasional *Rubus saxatilis*. These are species of short, grazed, unimproved, dry, neutral to basic grasslands and dwarf shrub heath (Clapham et al., 1987). This community is composed of both upland and lowland relevés (15 relevés were taken < 40 m and 17 were taken > 100 m a.s.l.), it is associated with relatively high shrub cover (mainly *Arctostaphylos,* but also *Dryas, Calluna* and some *Juniperus*) but short vegetation (shrubs were defined as all woody species, including low-growing dwarf shrubs such as *Dryas, Arctostaphylos* and *Juniperus*), shallow soils with high pH and relatively high cover of exposed rock. It is most associated with *Pteridium aquilinum* and has the lowest species richness, diversity and evenness values.

In terms of related NVC communities, this group has affinities (33% to 39%) with CG9 *Sesleria caerulea – Galium sterneri* grassland, CG10 *Festuca ovina – Agrostis capillaris – Thymus polytrichus* grassland, CG13 *Dryas octopetala – Carex flacca* heath, and H10 *Calluna vulgaris – Erica cinerea* heath (Rodwell, 1991, Rodwell, 1992). CG9 corresponds to the Annex I habitat (6210) Semi-natural dry grasslands and scrubland facies on calcareous substrates (*Festuco - Brometalia*), hereafter referred to as *Festuco - Brometalia*; CG10 is linked to (6230) Species-rich *Nardus* grasslands, on siliceous substrates in mountain areas, however this does not occur on the limestones of the Burren; CG13 is linked to (6170) Alpine and subalpine calcareous grasslands (European Commission, 2013), but this habitat is not known to occur in the Republic of Ireland (Perrin et al., 2013); these are essentially grassland communities and the affinity is due to the relative abundance of grassland species in this group. Finally, H10 corresponds to (4030) dry heaths (European Commission, 2013).

In contrast, comparison with relevant Irish plant community classifications this group corresponds to so-called heath communities (as the cover of dwarf shrubs exceeds 25%), such as Dry calcareous heath HH2 (Fossitt, 2000), the *Arctostaphylos uva-ursi - Dryas octopetala* nodum (Ivimey-Cook and Proctor, 1966), the *Dryas octopetala* heath (Parr et al., 2009), and the *Dryas octopetala – Empetrum nigrum* heath (Wilson and Fernández, 2013); due to the predominance also of heath species such as *Arctostaphylos, Calluna* and *Dryas.* This group has affinities to both grassland and heath habitats and thus with the Annex I habitats (4030) dry heath – calcareous community and (6210) *Festuco – Brometalia,* and to a lesser extent, (4060) alpine heath - lowland community (NPWS, 2013b, Perrin et al., 2014).

2. The *Arctostaphylos uva-ursi – Juniperus communis* community comprises nearly 90% lowland relevés, i.e. 23 of 26 relevés were taken below 40 m a.s.l., and it is defined by the prostrate form of the shrub *J. communis*. *Briza media, Carex flacca, C. pulicaris, Teucrium scorodonia* and bryophytes *Frullania tamarisci, Neckera crispa* are constant species with frequent *Dicranum scoparium* and *Asperula cynanchica* and occasional *Leontodon saxatilis, Hypochaeris radicata, Plantago maritima* and *Koeleria macrantha* is scarce. A number of grasses are also constant, even if not indicator species: *Sesleria, Molinia Festuca ovina;* as are the calcicoles *Thymus polytrichus, Geranium sanguineum* and *Dryas,* and the calcifuge *Calluna.* Many of these are species of limestone grassland with the notable exception of *J. communis* ssp. *nana* which occurs on rocky heaths with thin soils (Clapham et al., 1987). As for the *Arctostaphylos uva-ursi – Sesleria caerulea* community, this is also associated with relatively high shrub cover (mainly due to *Arctostaphylos* and *Juniperus* with a little *Calluna, Dryas* and *Thymus*), short vegetation, and a relatively high cover of exposed rock. It has the lowest soil organic matter i.e. the most mineral-rich soil, and the highest species richness. It also has the lowest aspect category (7.8 ≈ West, Table 1) of the groups, meaning that it has the highest heat load. It is a community of open unimproved rocky grassland, where *J. communis, Arctostaphylos* and to some extent *Dryas*, benefit from the frequent boulders and rocky outcrops that prevent the formation of a dense closely-cropped sward.

This group has affinities (33% to 45%) for NVC communities CG9, CG10, CG13 and CG2d *Festuca ovina-Helictotrichon pratense* grassland, *Dicranum scoparium* sub-community, and H10 (Rodwell, 1991, Rodwell, 1992); in addition to the links to Annex I habitats detailed above for CG9, CG10, CG13 and H10, CG2 also corresponds to (6210) *Festuco – Brometalia* (European Commission, 2013). Thus the community has affinities to dry heaths and *Festuco – Brometalia* as it has strong grassland and heathland elements. But

H10 does not feature *Juniperus communis* and this is one of the defining species of this community, therefore the affinity to dry heaths may not be very strong. In terms of Irish classification it fits with the broad Dry calcareous heath HH2 (Fossitt, 2000), however it does not correspond well to other Burren classifications i.e. the *Arctostaphylos uva-ursi - Dryas octopetala* nodum (Ivimey-Cook and Proctor, 1966), nor does it fit in to the *Dryas octopetala* heath of Parr et al. (2009), or indeed with the *Dryas octopetala – Empetrum nigrum* heath (Wilson and Fernández, 2013). This is partly because one of the main constant shrub species in this group is *J. communis* which was rarely found in the upland heaths, and *E. nigrum* is rare in this group as it does not occur in the lowland relevés and has not been recorded from the Burren lowlands (Webb and Scannell, 1983).

This group could have affinities with the Annex I habitat (5130) *Juniperus communis* formations on heaths or calcareous grasslands - however there are generally not a sufficient number of shrubs (≥ 50 individuals of *J. communis*) to fulfil the definition of ‘formation’ (Cooper et al., 2012) therefore it is more likely to correspond to (4060) alpine heath - lowland community (NPWS, 2013b). Although *Dryas* was a constant species, it had low cover values and therefore did not appear to constitute the ‘mats of mountain avens’ of alpine heath, nonetheless the predominance of prostrate *Juniperus* together with *Arctostaphylos* does still relate to alpine heaths (Perrin et al., 2013).

3. The *Calluna - Arctostaphylos* community is defined by constant *Calluna vulgaris, Hylocomium splendens, Molinia caerulea, Festuca ovina, Succisa pratensis, Erica cinerea, Lathyrus linifolius* and *Hypnum jutlandicum; Cirsium dissectum* is frequent, *Agrostis capillaris* and *Galium verum* are occasional and *Salix repens* is rare. Many of these species are associated with dry to moist, mildly acidic peaty soils (Clapham et al., 1987). Additional, non-indicator, constant species include *Arctostaphylos, Sesleria, Pteridium aquilinum, Lotus corniculatus, Carex panicea, C. flacca, C. pulicaris, Breutelia chrysocoma, Dryas* and *Thymus polytrichus.* This is a Burren upland community (only one of the 17 relevés occurs below 170 m a.s.l.), occurring between 170 and 280 m a.s.l. It is associated with a high cover of graminoids, forbs and bryophytes, its vegetation is tall and the soils are relatively deep, moist and slightly acidic with very little exposed rock. This group is comprised mostly of relevés (13 of 17 relevés) taken to describe the vegetation in sites chosen for the need for management of tall over-mature *Calluna* (chapter 3).

This vegetation group has affinities (36% to 46%) for the NVC communities CG9, CG10, CG13, H10 and H12c *Calluna vulgaris - Vaccinium myrtillus* heath, *Galium saxatile - Festuca ovina* sub-community (Rodwell, 1991, Rodwell, 1992). In addition to the links discussed above (for CG9, CG10, CG13 and H10) H12 correspond to (4030) dry heath (European Commission, 2013). This community is somewhat intermediate between the Dry calcareous heath (HH2) and Wet heath (HH3) classification (Fossitt, 2000), but the wet heaths are found on deeper soils and *Erica tetralix* is usually one of the dominant species, not present here. This group does not fit into the communities described by Ivimey-Cook and Proctor (1966). However it does correspond quite well with the *Calluna vulgaris* community, *Molinia - Erica cinerea* sub-community of Parr et al. (2009) and the *Calluna vulgaris – Molinia caerulea* heath of Wilson and Fernández (2013).

This community contains elements of (4060) alpine heath and (4030) dry heath as it comprises a number of positive indicator species for each of these Annex I habitats (Wilson and Fernández, 2013, NPWS, 2013a) but it appears to relate more to dry heath. It has less grassland elements than the previous two communities and is more heathy, resulting in its having greater affinities with the NVC dry heath communities of H10 and H12 (Rodwell 1991) than the previous two groups. Both of these heathland communities are at least partly maintained by burning or grazing (Rodwell, 1991). It has a relatively low cover of *Dryas,* even though it is constant, and although *Arctostaphylos* cover is still high it appears to be closer to the dry heath classification.

4. The *Dryas octopetala - Empetrum nigrum* community is defined by constant *Thymus polytrichus, Dryas octopetala, Breutelia chrysocoma, Carex panicea, Empetrum nigrum, Linum catharticum, Solidago virgaurea* and *Tortella tortuosa*; *Racomitrium lanuginosum* is frequent and *Antennaria dioica* is occasional, as is *Epipactis atrorubens*. These species are associated with exposed upland heath and mountain habitats with varying degrees of soil moisture and calcareous soils (Clapham et al., 1987). Additional, non-indicator constant species include *Calluna, Arctostaphylos, Sesleria caerulea, Lotus corniculatus, Carex flacca, C. pulicaris, Festuca ovina, Succisa pratensis, Hylocomium splendens, Neckera crispa* and *Ctenidium molluscum.* This community only occurs in the Burren uplands and has quite a wide range of altitude: 140 m to 310 m a.s.l. It has a relatively low cover of shrubs, graminoids and forbs, short vegetation, shallow soils, and high soil organic content; it also has the highest values for aspect category (10.9 ≈ west-north-west, Table 1) meaning that it has the lowest heat load in comparison to the other groups described here.

This group has affinities (33% to 46%) with NVC communities CG9, CG10, CG13 and CG14 *Dryas octopetala - Silene acaulis* ledge community, as well as H10d (Rodwell, 1991, Rodwell, 1992); for links to relevant Annex I habitats see above, CG14 is also linked to (6170) Alpine and subalpine calcareous grasslands, but this habitat is not known to occur in Ireland. In terms of Irish classifications it may be described as Dry calcareous heath HH2 with elements of Montane heath HH4 (Fossitt, 2000) but it is not Montane heath proper as it is not at high altitude and therefore lacks some of the key species of that community. It corresponds to the *Empetrum nigrum - Epipactis atrorubens* nodum (Ivimey-Cook and Proctor, 1966), *Dryas octopetala* community, *Antennaria dioica - Asperula cynanchica* sub-community (Parr et al., 2009), the *Dryas octopetala – Empetrum nigrum* heath (Wilson and Fernández, 2013); and may correspond to (4060) alpine heath - lowland community, (4030) dry heath - calcareous community, and (6210) *Festuco - Brometalia* (NPWS, 2013b).

The *Calluna – Arctostaphylos* heath and the *Dryas – Empetrum* heath are both upland groups. Constant species common to both groups include *Calluna vulgaris, Molinia caerulea, A. uva-ursi, Sesleria caerulea, Thymus polytrichus, Dryas octopetala, Breutelia chrysocoma, Festuca ovina* and *Succisa pratensis* although the mean cover values differ greatly between the groups. There are however differences in species composition between them: *Empetrum nigrum,* and calcicoles *Linum catharticum* and *Tortella tortuosa* are absent or rare in the former, but constant in the latter; whereas *Molinia* and calcifuge species *Erica cinerea* and *Hypnum jutlandicum* are constant in the former but occur in less than half of the latter group's relevés.

In summary, while the difficulties in defining these Burren habitats in regards to other classifications has been highlighted, and in light of this, the communities here described are only tentatively placed into the following Annex I habitats:

1. *Arctostaphylos – Sesleria* community relates to dry heaths (4030) and *Festuco – Brometalia* (6020); this comprises dry heath species with a mixture of calcareous grassland species.
2. *Arctostaphylos – Juniperus* community has elements of both *Festuco – Brometalia* (6020) and alpine heaths (4060), while lacking some of the montane species.
3. *Calluna – Arctostaphylos* community has affinities to both alpine heaths (4060) and dry heaths (4030) but relates more to dry heaths.
4. *Dryas – Empetrum* community has elements of dry heaths (4030), alpine heaths (4060) and *Festuco – Brometalia* (6020) classifications.

2.4.2. The Burren *Arctostaphylos* heaths - their distribution and conservation

The first group described has the highest mean cover of *Arctostaphylos uva-ursi* and its cover then decreases across the groups with the *Dryas* – *Empetrum* group having the lowest mean cover, being in part at least replaced by *Empetrum nigrum* in the most exposed locations (Fig. 2.6) on the highest north-facing slopes. Ivimey-Cook and Proctor (1966) suggested that the *Arctostaphylos* - *Dryas* heaths may be the climax vegetation in some parts of the Burren uplands, given the right exposure and altitude. The *Empetrum* – *Epipactis atrorubens* nodum described by them also occurs on more exposed coastal slopes where there is more bare rock and very little soil (Ivimey-Cook and Proctor, 1966). This research has found the *Dryas* – *Empetrum* group occurring on shallow soils at high altitude, but not significantly higher than the *Calluna* – *Arctostaphylos* heath. While there are areas where *Empetrum* and *Arctostaphylos* co-occur it is interesting to note that in some *Arctostaphylos* habitats *Empetrum* is absent and the reverse is also true. *E. nigrum* mainly occurs in short swards on acid soils (Averis, 2013), it does not occur in the *Calluna* – *Arctostaphylos* heath, it may be outcompeted by the tall grasses and *Calluna* that are present in this heath type. It seems unlikely to be related to low soil pH as the species appears to prefer acidic soils. This may however explain its absence from any lowland relevés.

Since *Arctostaphylos* was a target species, it occurs in all of the vegetation groups described in this chapter, however its geographical distribution within the region is curious – it occurs in the western Burren uplands and also in the eastern Burren lowlands (with one outlying population to the southeast) but is absent from the central Burren area and from Moneen mountain (where *Empetrum* is present). Both of these species are sclerophyllous and therefore drought-tolerant so it is unlikely that water availability is the main factor involved. It could be that in the uplands *Arctostaphylos* is out-competed by other more competitive species, such as

Calluna, except in areas of high coastal exposure, but this seems unlikely given the presence of the heaths in the Burren lowland areas which are in much less exposed locations than the uplands where *A. uva-ursi* is absent. Given *A. uva-ursi* is part of a relict plant community, however, previous vegetation dynamics and competition may have resulted in the shrinking of the extent of the species in the uplands.

It is also possible that the ectomycorrhizal fungi associated with *A. uva-ursi* are absent from these areas and therefore so is their host species. Three of these fungal species, however, are also common to *Dryas octopetala* (Liston and Harrington, 2012), widespread throughout the Burren, so could the distribution of certain mycorrhizal species not associated with *D. octopetala* impact on the distribution of its host? This is a question which would be worth further research, especially in the light of conservation measures for the species.

In the summer months there may be a mean temperature difference of only 1 °C despite the difference of altitude being up to 300 m. This, however, coupled with the higher moisture in the uplands, results in the development of more peaty soils there and in part explains the absence of the true heath communities in the lowlands. In the winter months the temperature in the Burren uplands may be practically the same as in the lowlands, but there may be other factors such as cloud cover, wind exposure and rainfall that are higher in uplands, and as the uplands are also more westerly they will receive the brunt of these Atlantic weather conditions coming (Met Éireann, 2017).

Chapter 3 deals in detail with the management of *Calluna* in these heaths, however as management is an integral aspect to the conservation, and in some cases restoration, of heathlands and relates to the species composition, it is important to mention here. The majority of the Burren heaths may be found at higher altitudes due to the higher levels of exposure; these typically grade into grasslands at lower altitudes where grazing levels can be higher, often involving both summer and winter grazing (Parr et al., 2009b). In the absence of management, or under low grazing conditions in the Burren, generally taller vegetation develops and there is a greater threat of encroachment from *Calluna* and/or *Molinia caerulea* in the uplands and *Corylus avellana* and/or *Molinia* in the eastern lowlands. (Parr et al., 2009).

Many of the lowland heath sites in this study had high levels of shrub cover, although the main contribution is from species of dwarf shrubs, there was also relatively higher levels of *Corylus avellana,* and in some cases *Molinia caerulea,* than was present in the uplands*.* As they are not subject to the same level of exposure as the heaths in the uplands, they probably could sustain more grazing, however they are often grazed as 'winterage' pastures. Thus there were a number of lowland sites where the habitat condition appeared to be in decline due to a lack of management, in particular at the Ardrahan grassland SAC (site code 002244) in south County Galway. *Arctostaphylos* is abundant there, together with *Juniperus communis* on rocky outcrops, but *Molinia caerulea* is also rather dominant, with a high quantity of *Molinia* litter, and at the time of the survey the site was only grazed during the winter months. The other notable site to mention is the Lough Fingall SAC complex (site code 000606) in south County Galway where lowland alpine heath with *A. uva-ursi* and *Dryas octopetala* occurs on limestone pavement and appears to be under threat of encroachment by *Corylus avellana* scrub, as does the Coillte LIFE woodland restoration site at Attyslaney, the most south-easterly location shown on the map (Fig. 2.5).

2.4.3. The Burren *Arctostaphylos* heaths in an international context

The heaths that have been classified here are quite different from those found in some areas of Europe. In Scotland the communities described are similar to a certain degree in that *A. uva-ursi* co-occurs with *Calluna, Erica cinerea, Empetrum nigrum* ssp. *nigrum* (which may replace *A. uva-ursi), Antennaria dioica,* and the bryophytes *Hypnum jutlandicum, Pleurozium schreberi, Hylocomium splendens and Dicranum scoparium* in both regions, but the Scottish sites support species more tolerant of acidic soils and therefore *Vaccinium myrtillus* and *V. vitis-idaea* are more dominant and the sites are also of higher altitude (Ward, 1971a, Ward, 1971b). In the Cantabrian mountains in Northern Spain (Calvo et al., 2002a), the species composition is more southern; species such as *Erica australis* and *E. umbellata* are more dominant there together with *Calluna* and species of the rock rose family (Cistaceae). The heaths possibly most similar to the Burren heaths are the *Arctostaphylos* heaths on limestone in Bulgaria where *A. uva-ursi* occurs with *Dryas octopetala, Asperula cynanchica* and *Sesleria rigida* in mountain areas (Genova and Russakova, 2015). The Burren heaths are also comparable to similar heath in north-east Poland where *A. uva-ursi* occurs with *Calluna, Juniperus communis* and *Geranium sanguineum* (Adamska et al., 2015), and to Norwegian coastal heaths where it co-occurs with *Calluna, Empetrum nigrum* and *Racomitrium lanuginosum* (Nilsen and Moen, 2009).

This study provides an in-depth review of Burren heath habitat classifications (Ivimey-Cook and Proctor, 1966, Parr et al., 2009b, NPWS, 2013a, NPWS, 2013b, Wilson and Fernández, 2013) in relation to NVC plant communities (Rodwell, 1991, Rodwell, 1992) and EU Annex I habitats (European Commission, 2013) in an attempt to clarify where within the extant classifications the heaths described here are best placed.

2.5 Conclusions

The *Arctostaphylos* - heath plant communities of the Burren are described in detail in this chapter and placed both in an Irish and an international context. They are quite rare and appear to be declining, therefore they are of conservation concern. Four heath communities are presented in terms of their correspondence to Annex I habitats and are tentatively classified as follows:

1. The *Arctostaphylos – Sesleria* community was found throughout the Burren region on rocky ground with shallow soils, with elements of heath and grassland. It corresponds to dry heaths (4030) and *Festuco – Brometalia* (6020).
2. The *Arctostaphylos – Juniperus* community was restricted to the lowland areas of the eastern Burren, it is also a mixed heath and grassland community and has elements of both *Festuco – Brometalia* (6020) and alpine heaths (4060).
3. The *Calluna – Arctostaphylos* community was found only in the uplands of the southwestern Burren, on deeper somewhat peaty soils with relatively tall vegetation, and this community relates most to dry heaths (4030) but also has some elements of alpine heaths (4060).
4. The *Dryas – Empetrum* community was restricted to upland areas, mainly located on summits and seaward-facing slopes, on shallow mineral-rich soils in a short sward. It has affinities to dry heaths (4030), alpine heaths (4060) and *Festuco – Brometalia* (6020).

These rare heaths are essentially relict plant communities and have affinities to important habitats on a European level. Heathlands are generally considered to be under threat from a number of factors, as discussed previously, and the rare heaths described here are vulnerable and thus protected habitats. Therefore their apparent decline is worrying, in particular as they are located for the most part within Special Areas of Conservation (SACs), and are one of the qualifying interests that these SACs are designated for. One key threat to these habitats is that of a lack of management, resulting in the encroachment of taller more vigorous species such as *Calluna, Molinia, Pteridium* or *Corylus avellana.* In order to restore and/or maintain these habitats in good conservation status the management of the sites mentioned above needs to be addressed by the relevant land managers before some of the rarer species disappear from these sites.

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Chapter 3. A short-term experimental cutting regime study for the restoration of Annex I *Arctostaphylos* - heath plant communities in a lowland Atlantic karst region of Europe

3.1 Introduction

The Burren, in the west of Ireland, is a prime example of a karst limestone landscape in Europe (Parr et al., 2009a). It is an open landscape, though formerly covered by woodland, and it has been influenced and transformed by farmers since Neolithic times (Dunford, 2002). It is particularly renowned for its abundant and diverse rare plant communities (Webb and Scannell, 1983, Roden, 2001). It is a cultural landscape and its management is integral to the conservation of its biodiversity and archaeology. The region includes several Special Areas of Conservation (SACs) designated under the EU Habitats Directive (Council Directive 92/43/EEC), many of which are priority habitats that Ireland is obliged to sustainably manage. Since the 1950s and more so following the entry into the EEC in 1973, the Burren, along with Ireland as a whole, was subject to industrialised farming focused on productivity (Keane, 1990, Hickie et al., 1999). In the Burren, as elsewhere, this led to many areas being either intensified or abandoned, resulting in increased fertiliser use and silage feeding or on the other hand scrub encroachment and a reduction in the size grazing areas, with many of the farming families depending on off-farm incomes and the conservation status of the lands being reduced (Bohnsack and Carrucan, 1999, Dunford, 2002).

In 2005 a results-based farming for conservation programme was initiated in the Burren (Burren LIFE Project (2005-2010); the first of its kind in Ireland. It was then called the Burren Farming for Conservation

Programme (2010-2014) and now the Burren Programme (2014-2020) and is in place in order to protect not only the habitats but also to preserve the farming tradition. This recognises that appropriately managed farming practice is key to the conservation of the unique rare Burren habitats (Parr et al., 2009a). Currently there are ca. 300 farmers involved in the Programme across the Burren region (Anon., 2016).

One of the Burren Programme's objectives in terms of the sustainable management of the Burren is to improve the 'habitat health' of species-rich limestone grasslands – over the years this has resulted in a marked improvement in the quality of these Annex I habitats (Anon., 2014). Limestone heath is another important Burren habitat especially when the arctic-alpine species *Arctostaphylos uva-ursi* and/or *Empetrum nigrum* are present together with *Dryas octopetala,* corresponding with the Annex I habitats Alpine and Boreal heath (EU habitat code: 4060) and European Dry heath (4030) (NPWS, 2013a) – typically found in close association with one another. European Dry heaths occur in Ireland from sea level up to 400 m where they may transition into Alpine and Boreal heaths, except in the Burren where there is a lowland Alpine heath community (NPWS, 2013a). These Burren heath communities are described in detail in chapter 2 and historically were classified under the Class Festuco - Brometea, Alliance Bromion erecti, Association *Asperulo - Dryadetum, Arctostaphylos uva-ursi - Dryas octopetala* Nodum (Ivimey-Cook and Proctor, 1966). These heaths are of European importance yet in a number of sites where these plant communities occur, there is a dominance of tall mature *Calluna vulgaris* encroaching on the prostrate mats of *A. uva-ursi, E. nigrum* and *D. octopetala* and threatening the conservation value of the plant community. Therefore some form of management is required to restore these habitats, but to date little or no work has addressed their management requirements in the Burren or elsewhere in Ireland.

3.1.1. Farming practices in the Burren uplands

In the Burren uplands there is a long-standing tradition of out-wintering stock –‘winterage’- on the limestone hills typically from October to April, sometimes even May. Currently stock comprise mainly cattle, and sometimes also ponies, though formerly sheep were the main stock; goats were also previously farmed, but now goat herds are feral (Dutton, 1808 in Keane (1990)). The out-wintering is made possible by the availability of water which is abundant in winter, but scarce in dry periods, especially in summer, but also due to the presence of such a large amount of exposed rock which, after taking in heat during the summer months, releases it during the cooler months and thereby provides relative warmth and a ‘dry lie’ for livestock (Dunford, 2002). These low-input grazing practices have been key to maintaining the species-rich grasslands by keeping competitive species in check (Bohnsack and Carrucan, 1999). The removal of plant litter by grazers permits light-dependent species to grow (Williams et al., 2009) while allowing flowering plants to set seed prior to grazing (Keane, 1990). *Arctostaphylos*-heaths occur as a mosaic with species-rich calcareous grasslands and limestone pavement and thus they are largely grazed as part of the ‘winterage’ grazing regime. Parr et al. (2006) describe the unimproved Burren grasslands in terms of their productivity and ability to support grazing: strong winterages are ‘more productive, calcareous to neutral on deeper soils including wet grassland, short *Calluna* heath and some improved grasslands on thin soils’; while weak winterages are ‘less productive, calcareous, on rocky thin soils including *Sesleria*-dominated grassland and *Dryas*-dominated heath. While the weaker winterages sustain a winter-only grazing regime, it is recommended that the stronger winterages may require higher levels of grazing, in particular in the late summer months (Parr et al., 2009b). Mature and/or senescent *Calluna* heath tend to be found on high exposed ground and north-facing slopes (Parr et al., 2006).

In the Burren heathlands where there has been regular grazing it appears to be sufficient to keep in check the vigorous growth of *Calluna*, but in sites where grazing has ceased or been at a very low intensity for a number of years or even decades, restorative measures are required to bring the habitats back to conservation value.

3.1.2. Control of *Calluna vulgaris* in heathlands

Calluna enters its mature phase after 15 years and the degenerative phase after 25 years (Gimingham, 1972), so restorative measures involving control of the heather also improve the grazing value of the land as over-mature heather is less palatable to large herbivores (Clarke et al., 1995). *Calluna* is most productive and also palatable when in its building phase, however when left unmanaged it passes into its mature or degenerative phase which is not only less palatable but is less accessible to grazers as it is tall and leggy (Gimingham, 1995). Young *Calluna* may be an important food source for grazers and browsers, even in winter when grasses may be scarce, but its nutrient value drops in plant material over 4 years old (Gimingham, 1972).

The traditional management of European heathlands has ceased nearly everywhere leading to a massive decline in the extent and quality of existing heaths (Webb, 1998). Traditionally heaths were used for grazing animals, turf was cut for fuel and woody plants, such as *Calluna,* were cut and the stems used for many purposes including thatching, bedding and fuel (Webb, 1986, Kvamme et al., 2004). In addition, in the British uplands, vegetation was burnt to improve the quality of the fodder (Webb, 1998). The majority of remaining heathlands in Europe are now designated as nature conservation sites with much research being undertaken into their management (Webb, 1998). Currently in many areas of Europe controlled burning, cutting and grazing (used in conjunction with cutting or burning) are well-established management practices for the removal of plant biomass from heathlands and the rejuvenation of *Calluna* (Fagúndez, 2013). In

Calluna heathlands in the Cantabrian Mountains, in northern Spain, in areas where grazing is no longer undertaken, cutting has been found to be beneficial to plant species diversity (Calvo et al., 2005). Re-sprouting is the main response of *Calluna* following cutting whereas burning promotes germination as well as re-sprouting. However in experimental research, no significant differences were observed 10 years after undergoing disturbance between the type of management – cutting, burning, ploughing – or the level of recovery (Calvo et al., 2002b). Ilkley moor in northern England, a heath dominated by *Calluna* and *Empetrum nigrum,* was subject to trials involving flail cutting (cut litter was left on the ground), burning and rolling back the vegetation (spades were used to cut main stems and material above-ground, vegetation was rolled to the sides of the plots) - in this case the objective was to reduce *Empetrum* and restore *Calluna*: after five years burning was considered the most beneficial to *Calluna* restoration, followed by flail cutting while rolled plots had the effect of reducing *Calluna* regrowth; in terms of regrowth of *Empetrum* rolled plots saw an increase in cover, likely to be due to the creation of bare ground, while burning and flail cutting reduced it (Cotton and Hale, 1994). In the literature all the studies relating to the control of *Calluna* related to its regeneration and none aimed to hinder its regrowth in order to promote the growth of other plant species such as prostrate alpine shrubs, which is the objective in this case.

Arctostaphylos uva-ursi has been seen to respond well to cutting, trampling and burning as dormant buds present on surviving stems sprout within three months following the disturbance (Mallik and Gimingham, 1985). In the Cantabrian mountains in *Erica australis* heathlands with *Arctostaphylos uva-ursi*, cutting and burning were both favourable to the vegetative re-growth of *A. uva-ursi* and its recovery was rapid, achieving 70% recovery in 30 months following treatment (del Barrio et al., 1999). *Calluna* is also likely to show regrowth within this timeframe, although this is expected to be quite slow as the capacity of *Calluna* to re-sprout declines in plants over 15-20 years old (Webb, 1986, Calvo et al., 2005).

3.1.3. Management of heathlands in Ireland

There is very little in the literature regarding heathland management in Ireland. But in terms of land clearance palaeoecological sediments containing charcoal fragments suggest burning was an important factor during the Neolithic period (O'Connell and Molloy, 2005) however it has not been established whether these fires were set intentionally or occurred naturally (Mitchell and Ryan, 2001). Later charcoal deposits found in the Burren uplands suggest that burning of vegetation in association with pastoralism was practised from the Iron Age until approximately the 17th Century (Feeser and O’Connell, 2009, Feeser and O’Connell, 2010). In the last few years there has been much news coverage of burning Gorse in Connemara, Cork and the Wicklow uplands; many of these fires were not controlled and caused enormous damage to wildlife, some even spreading to adjacent forestry (Devine, 2017, Pollack, 2017); although there is a Code of Practice issued by the Department of Agriculture (Nugent, 2012) this was not followed and the burning occurred during dry summer months. In the Burren in recent times burning has not been widely undertaken nor is it recommended due to the soils being so thin and the potential to damage the limestone pavement (Parr et al., 2009b). Furthermore, as most of the Burren region is designated as SACs, burning is a notifiable action requiring National Parks and Wildlife Service (NPWS) approval (European Communities (Birds and Natural Habitats) Regulations 2011, S.I. 477/2011). Any burning or cutting must not take place within the bird nesting season (1 March – 31 August) (Wildlife (Amendment) Act 2000).

In the west Burren uplands, near Fanore, in County Clare, farms have been identified with *Arctostaphylos* heaths, some of which have become dominant in mature to degenerate-phase *Calluna vulgaris* (Parr, S. pers. comm.) due to a lack of management (Parr et al., 2009b).

3.1.4. Aims

In order to find a method of controlling the *Calluna* that did not involve burning this study focused instead on cutting as a tool to remove the tall over-mature heather canopy and allow the alpine community to regenerate thereby restoring these habitats to conservation value, with the following aims:

- To monitor plant species recovery and/or expansion, notably *Arctostaphylos*, in the first few years after *Calluna* cutting
- To determine whether cutting in spring or autumn resulted in differences in terms of the regrowth of key species
- And whether these different cutting times yielded differences in terms of species diversity and evenness

3.2 Materials and methods

Three sites were selected in the west Burren uplands which had significant encroachment of over-mature *Calluna vulgaris* on *Arctostaphylos uva-ursi* and associated low-growing alpine heath species. Site characteristics are summarised below (Table 3.1). The farmers/landowners are all participants in the Burren Life Programme and therefore were fully supportive of this study and kindly took part in a questionnaire to provide information of the land use/management history.

3.2.1. Study area

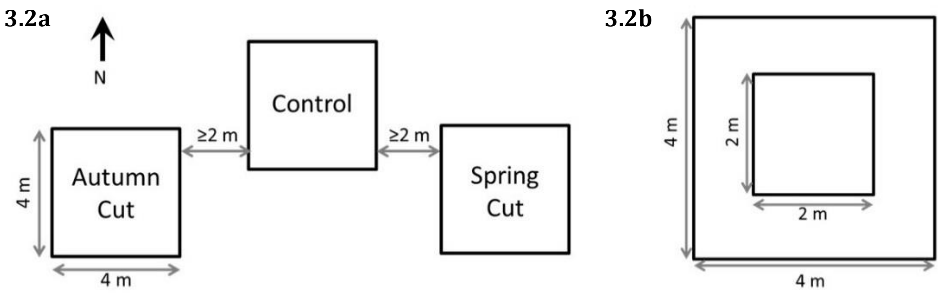
The study sites are situated in the hills above the Caher valley near Fanore in the south-west corner of the Burren region of County Clare in the west of Ireland (GPS Coordinates: 53°06'51"N 9°14'40"W; Fig. 3.1), located within the SAC Black Head-Poullsallagh Complex (site code: 000020). Sites L and N are on the southern side of the valley facing north-east and are at

Figure 3.1. Location of study site on the slopes above the Caher River valley near Fanore, Co. Clare; plots are grouped in clusters of three.

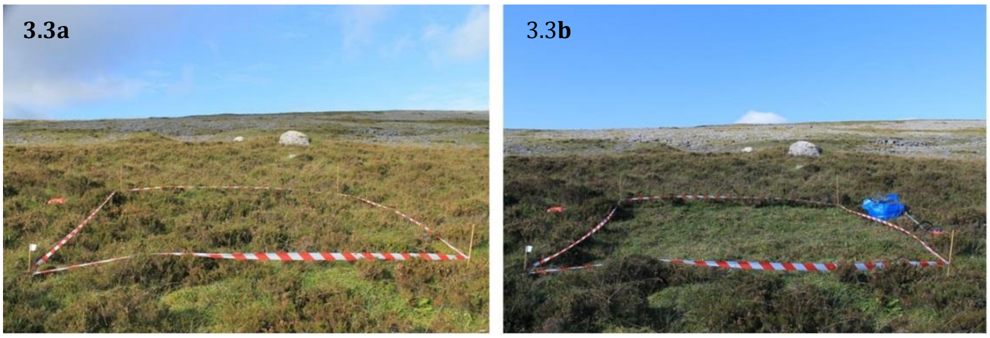
approximately 160m above sea level (a.s.l.); Site M is on the northern side of the valley facing south-west and is at approximately 260m a.s.l. The soils of the Burren are mainly Rendzina-like soils in addition to shallow organic soils with limestone rock outcrops and shallow brown earths, all derived from Carboniferous limestone (Gardiner and Ryan, 1969). The climate is mild with mean daily temperatures of 5°C in January and February and 14°C in July and August (between 1961 and 1990), the annual average rainfall is 1525mm with the wettest months being October to January (Parr et al., 2009a). While the sites all have over-mature heather they also all have areas of typical Burren exposed limestone outcrops and pockets of grassland; site N also has some peaty habitat. Site M appears to have not undergone any form of management in a number of years. Site L had the most visibly active management i.e. ponies were grazing in the adjacent field and there was cattle dung in the final year of survey, the farmer was also very keen to cut the heather with the advice and supervision of the Burren Life team.

3.2.2. Experimental design

The study took place between 26th August 2013 and 4th September 2015. At each site, in August/September 2013, fifteen permanent 4m x 4m plots were marked out in clusters of three; each plot was oriented north-south, in order to aid re-locating plots in subsequent survey years, and placed at least 2m apart within each cluster (Fig. 3.2a) that in turn were more than 5m apart. Each cluster contained one each of three treatments, randomly assigned: autumn cut; spring cut and the uncut Control (Fig. 3.2b). Autumn and spring plots were cut in October 2013 and February 2014, respectively, outside of the bird-nesting season. All vegetation was cut with a brush-cutter to a maximum of 5 cm above the ground and cut material was removed from the plots (Figs. 3.3a and 3.3b).



Figures 3.2a & b. (a) Schematic diagram of cutting trial plot layout. Each 4m x 4m plot was placed a minimum of 2m apart and randomly assigned a management regime. **(b)** Diagram showing the positioning of 2m x 2m quadrat for relevé sampling within a plot.



Figures 3.3a & b. Example of one of the 45 plots at site M **(a)** before and **(b)** after cutting with a brush-cutter – all cuttings were removed.

3.2.3. Vegetation sampling

Prior to carrying out cutting, all plots were surveyed in order to establish the baseline characteristics of the plots. 2m x 2m quadrats were centrally placed in each of the 45 4m x 4m plots (Fig. 3.2b); these were surveyed between 26th August and 27th September 2013 (Year 0). A comprehensive species list was compiled and the percentage cover of each vascular and bryophyte species was estimated. The soil depth and vegetation height were recorded at each corner and the centre of each quadrat and subsequently averaged for each quadrat; in 2015, the final year of sampling, the maximum height of *Calluna vulgaris* was also recorded. Slope and aspect were noted and the percentage cover for bare ground, exposed rock, leaf litter and total cover of plant groups i.e. graminoids, forbs, shrubs, ferns and bryophytes were visually estimated. All plots were re-surveyed between 26th August and 1st October 2014 (Year 1), 11 months after cutting of autumn plots and 7 months after cutting of spring plots. This was repeated (25th August to 4th September) in 2015 (Year 2), 23 months and 19 months after cutting of Autumn and Spring plots respectively. Nomenclature follows Stace (2010) for vascular plants and Atherton et al. (2010) for bryophytes.

3.2.4. Soil sampling

Soil samples were collected with a trowel to a maximum depth of 15 cm from each corner and at the centre of each quadrat between 26th August and 27th September 2013; samples from each quadrat were bulked for analysis. Soil depth was often < 5 cm and, where insufficient soil was present within the quadrat due to the very rocky terrain, additional soil was collected from as close to the plot as possible. Soil samples were frozen on the day of collection and then de-frosted for analysis. Soils were analysed for pH (Allen et al., 1986) and percentage loss on ignition, as a measure of organic content (Nelson and Sommers, 1996); they were ignited at 550°C in a muffle furnace (Allen et al., 1986). Soils were sieved before analysis, however it was not possible to remove all of the rooting material, so this may have added bias to the results using % LOI as a measure of organic matter.

3.2.5. Statistical analysis

In order to look at between-site differences (Table 3.1) General linear models (GLMs) were built in Minitab 17 (Minitab Inc. 2013) and a number of factors were tested with site as a fixed factor. All percent cover data were arcsine transformed before analysis took place. Residuals of the response variables were tested for normality using the Ryan-Joiner test. Where data fulfilled the criteria of normality – Altitude, soil pH, vegetation height, % *Calluna vulgaris*, % *Erica cinerea,* % shrubs, % forbs, % graminoids, % bryophytes, % litter, % bare ground, species richness, evenness, H and

Ellenberg L- parametric tests could be run and the Tukey post-hoc test was run to determine which sites were different before cutting took place. Where data were not normal – soil depth, soil % LOI, % *Arctostaphylos uva-ursi, %* *Dryas octopetala, %* *Empetrum nigrum, %* *Juniperus communis*, % lichen, % bracken, D’ and Ellenberg F - a Kruskal-Wallis test was run instead. Where p was < 0.05, pairwise Mann-Whitney tests were run to determine which groups were significantly different from one another (Dytham, 2011).

For the final analysis, to examine changes in vegetation before and after cutting and any patterns in regrowth, data from the middle year of survey was omitted, because, as the study was over a short time frame, the comparison would be greater between the pre-cutting (2013) survey and two years after cutting (2015).

Non-metric multidimensional scaling (NMS) ordinations were run in PC-ORD Version 5.10 (McCune and Mefford, 2006) on autopilot using the slow and thorough setting with random starting configurations. The Sørensen (Bray-Curtis) distance measure was used as this is the most recommended for ecological data (McCune and Grace, 2002) with 250 runs with real data, 250 runs with randomised data and a step-length of 0.20. The stability of the solution was assessed using the plot of stress v. iteration number. Environmental variables were superimposed on the NMS plots as a biplot and the Pearson and Kendall correlation coefficients between the variables and the axes of the plot were calculated. NMS was used as it is now considered the most appropriate ordination method for non-parametric data and does not assume linearity between samples (McCune and Grace, 2002).

Additional factors assessed were species richness, evenness, Shannon diversity index (H) which accounts for both abundance and evenness of the species present, Simpson’s index of diversity (D’), and Ellenberg L (Light) and F (Moisture) values; the last two factors were derived by calculating the modified Ellenberg values for each relevé (Hill et al., 2000). A two-factor PerManova was also run in PC-ORD in order to determine whether there were differences between cutting regimes before and after carrying out the cutting (Peck, 2010). In addition, a PerManova was run on cutting regimes for individual sites to test whether the effects of site were masking any vegetation responses to the cutting.

In order to analyse the effects of cutting in the second year post-treatment compared with its pre-treatment state on species richness, evenness and percentage cover of shrubs, forbs, graminoids, bryophytes in addition to key diagnostic species as well as species selected by Pearson and Kendall correlations (Table 3.2), bare ground and exposed rock GLMs were run where appropriate with site as a random factor, year and cutting regime as fixed factors, with the Tukey post hoc test. Treating site as a random factor in the GLMs enables the effects of cutting to be generalised to all sites (Grace-Martin, 2016). Data did not conform to a normal distribution in the case of % exposed rock, D' (Simpson's evenness) and all individual species cover that were tested*,* a Kruskal-Wallis test was run instead with Mann-Whitney pairwise testing as post hoc (Dytham, 2011).

3.3 Results

Statistical tables, where not in the body of the text, are in Appendix 3.1.

Vegetation correlation. Relevé data from 2013 for experimental plots were pooled with additional relevés (n = 144) carried out for a general study of alpine heath plant communities in the Burren uplands and lowlands (Chapter 2) in order to determine the relationship between *Arctostaphylos uva-ursi* and *Calluna vulgaris* by way of a simple regression plot of their respective cover (Fig. 3.4). There is a weak negative correlation between the two species ($y = -0.1821x + 27.111$; $r^2 = 0.0304$): where *Calluna* is > 40% there is a noticeable decrease in % *A. uva-ursi,* where its cover is rarely > 30%.

3.3.1. Variation in sites before cutting trials (Table 3.1)

Altitude. The plots in site N are approximately 100m higher than sites L and M ($p < 0.001$).

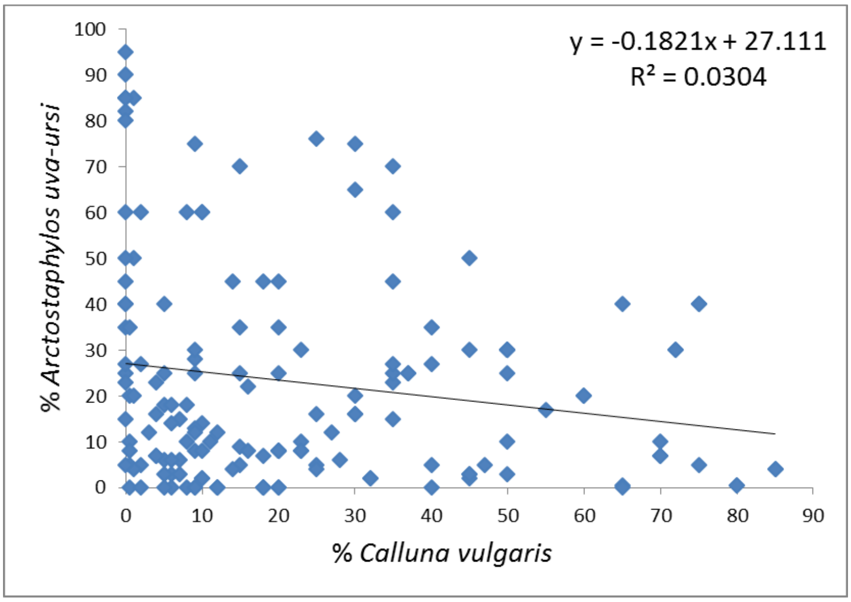


Figure 3.4. Regression plot of % *Calluna vulgaris* vs % *Arctostaphylos uva-ursi* cover. N = 144; y = -0.1821 + 27.111; $r^2 = 0.0304$.

Soils. All three sites have quite variable soil characteristics in terms of depth, pH and organic matter. Site N has deeper soils ($p < 0.001$) and lower soil pH ($p < 0.05$) than the other two sites; % loss on ignition was not significantly different ($p = 0.183$). Sites L and M are located side-by side and have very similar soil characteristics and were not significantly different in terms of soil characteristics measured.

Vegetation. Site N has lower mean vegetation height than sites L or M but this was not statistically different ($p = 0.13$). Percent cover of *A. uva-ursi* was highest in site M ($p <0.001$), the other two sites were not significantly different. Percent cover of *Dryas octopetala* was highest in site L; this was significantly different from site N ($p < 0.01$) but not from site M ($p = 0.059$). Percent cover of *Empetrum nigrum* and *Erica cinerea* were not significantly different between sites ($p = 0.554$; $p = 0.065$ respectively). *Juniperus communis* was not present within the plots in sites L and M but it was in N. Percent cover of *Calluna* was significantly higher in sites L and M than site N ($p < 0.001$). Site N has the lowest % shrubs ($p < 0.001$) and % bracken (p <

0.001). There is no significant difference between sites in terms of % forbs ($p = 0.153$), % bryophytes ($p = 0.117$) and % exposed rock ($p = 0.7$). Site N has the most % litter ($p < 0.001$) and % graminoids ($p < 0.05$) of all three sites. Site L has the most % bare ground ($p < 0.001$) and highest species richness of the three sites but this is not statistically significant ($p = 0.097$).

Table 3.1. Summary of site characteristics in 2013 before cutting. A different letter indicates a statistically significant difference between sites per variable. For statistical test results see Appendix 3.1, Tables 3.1 to 3.4.

	Site L		Site M		Site N	
	Mean	St. Dev.	Mean	St. Dev.	Mean	St. Dev.
Altitude (m a.s.l.)	177.49^{a}	3.37	177.49^{a}	4.85	270.17^{b}	4.44
Soil depth (cm)	8.23^{a}	3.12	9.01^{a}	4.82	17.24^{b}	8.15
Soil pH	6.50^{a}	0.54	$6.31^{a,b}$	0.48	5.91^{b}	0.46
Soil % loss on ignition	46.23^{a}	16.36	42.78^{a}	11.99	35.96^{a}	15.56
Vegetation height (cm)	31.15^{a}	8.36	33.49^{a}	11.38	26.91^{a}	5.89
% Arctostaphylos uva-ursi	10.64^{a}	11.01	27.71^{b}	15.34	6.34^{a}	4.15
% Dryas octopetala	17.77^{a}	18.03	7.37^{b}	10.93	4.47^{b}	8.80
% Empetrum nigrum	0.04^{a}	0.13	0.03^{a}	0.12	0.10^{a}	0.20
% Juniperus communis	0.00^{a}	0.00	0.00^{a}	0.00	4.27^{b}	6.11
% Erica cinerea	3.17^{a}	2.95	7.00^{a}	7.60	9.80^{a}	8.41
% Calluna vulgaris	53.33^{a}	20.47	43.93^{a}	17.69	25.00^{b}	15.65
% shrubs	74.33^{a}	17.71	76.73^{a}	10.63	51.67^{b}	19.03
% forbs	23.07^{a}	11.12	26.33^{a}	11.33	18.93^{a}	9.18
% graminoids	43.33^{a}	16.44	$47.00^{a,b}$	15.74	61.33^{b}	17.85
% bryophytes	54.33^{a}	23.29	60.87^{a}	15.30	45.67^{a}	19.18
% bracken	1.63^{a}	1.61	2.53^{a}	2.42	0.17^{b}	0.52
% litter	3.90^{a}	2.78	8.07^{a}	5.35	17.80^{b}	9.14
% bare ground	0.47^{a}	0.58	1.87^{b}	1.13	2.07^{b}	1.82
% exposed rock	0.67^{a}	0.77	1.10^{a}	1.69	0.93^{a}	0.86
Species richness	40.13^{a}	4.82	36.07^{a}	4.15	37.73^{a}	5.36
Ellenberg L (light)	6.93^{a}	0.13	7.05^{b}	0.08	7.21^{c}	0.11
Ellenberg F (moisture)	5.32^{a}	0.15	5.50^{b}	0.19	5.74^{c}	0.35

Ellenberg indices. Ellenberg L (light) values are approximately 7: that of plants in well-lit places but also partial shade (Hill et al., 2004), and Ellenberg F (moisture) values are between 5 and 6: fresh soils of average dampness, moist site (Hill et al., 2004). Site L has the lowest mean Ellenberg L ($p < 0.001$) and F values ($p < 0.001$) inferring that the plots in Site L get the least amount of light and moisture of the three sites – values for site M are intermediate and highest for site N.

3.3.2. Analysis of the effects of cutting on vegetation

NMS analysis recommended a 3-dimensional solution. Stress levels stabilised after 42 iterations with a final stress level of 15.010 and final instability of <0.000. Monte Carlo test result was p = 0.0040. The three axes explained 81.9% of the variance in the data set; axis 1 explained 17.3%, axis 2 explained 46.3% and axis 3 explained 18.4% of the variance. The ordination plots (Figs. 3.5a and 3.5b - relevés and 3.6 - species) are shown displaying axes 1 and 2 as this plot is easier to interpret in relation to ecology. Figure 3.5a shows a separation of relevés from 2013 (closed symbols grouped to the right) and 2015 (open symbols to the left) along axis 1, including those taken in control plots. The spring cut plots pre-cutting were located mainly to the right, with three plots in the bottom left; these shifted down and to the left following cutting. The autumn cut plots shifted from right to left in an upward direction following cutting, and the uncut control plots also shifted from the lower right to the upper left. After cutting, spring, autumn and control plots are all negatively correlated with axis 1. Therefore they are associated with a decrease in vegetation height and an increase the % cover of bare rock and forbs and, to a lesser extent, in evenness (Table 3.2). Spring plots correlate positively most with axis 3 (Fig 3.5b, Table 3.2), and thus with a decrease in % shrub cover, and an increase in % cover of bare ground, light (Ellenberg L) and evenness.

The sites also show differences, sometimes also in response to the cutting dates. Site L 2013 pre-cutting relevés are nearly all clustered in the lower right quadrant of the ordination and shift to the left and spread out vertically in 2015, the majority remaining in the lower half of the ordination

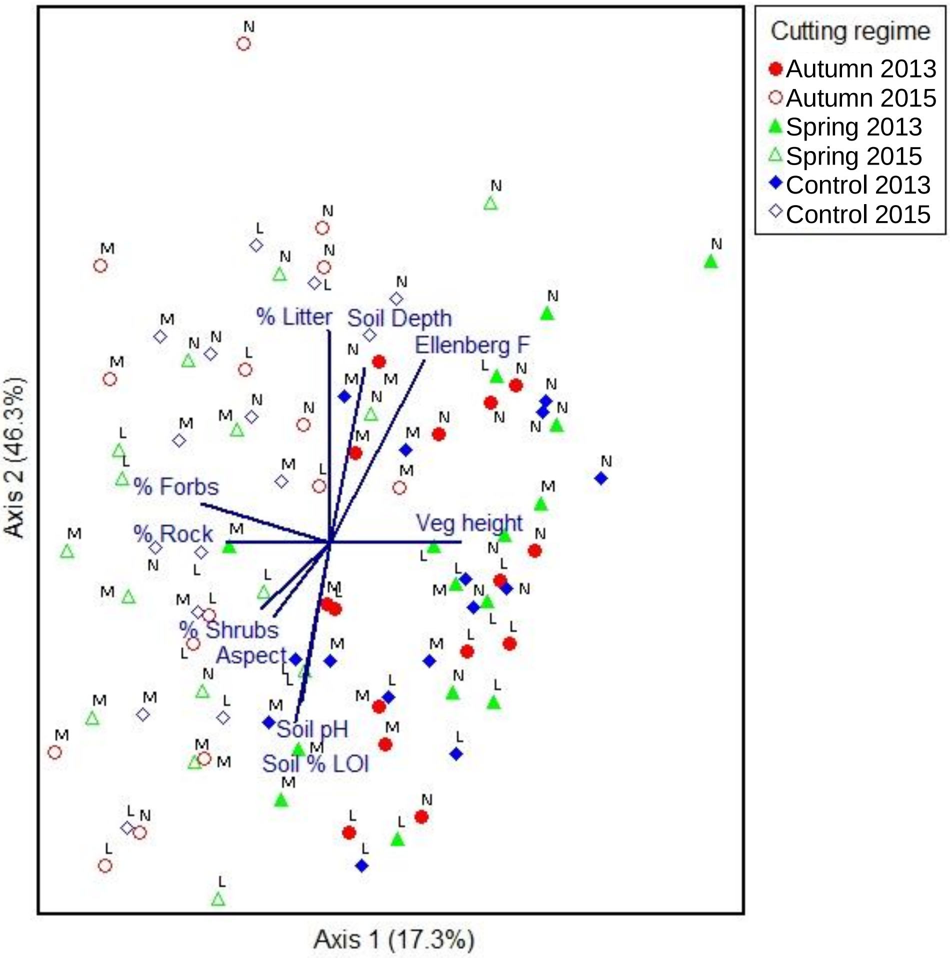


Figure 3.5a. NMS ordination for axis 1 vs. 3, coded for 2013 - pre-cutting (filled symbols) and 2015 - two years after cutting (open symbols) and the type cutting regime (Autumn cut: red circles; Spring cut: green triangles; Control: blue diamonds) with biplot of life form/environmental variables. Letters L, M and N represent the three sites (Fig 3.1). Vector length indicates the strength of correlation between variables and relevés > 0.19 (Table 3.2). Ellenberg F is a measure of moisture; Soil % LOI (loss-on-ignition) is a measure of organic matter.

with some in the upper left. Site M 2013 pre-cutting relevés are located at the bottom and centre of the plot, mostly on the right side, and the 2015 relevés separate further, according to date cut: autumn and control shift from right to left but spring mostly remain in the lower left. Site N 2013 relevés are located to the right and mostly towards the top of the plot, whereas 2015 relevés are mostly to the left and quite spread out but also located mainly towards the top of the ordination. Site N correlates positively with axis 2 (and with % litter, soil depth and Ellenberg F); while sites L and M are more negatively correlated with axis 2 (and therefore positively with % shrubs, aspect, soil pH and soil % LOI). Site M separates out along both axes 3 (Fig. 3.5b) and 1 while Site L separates out along axis 1: axis 1 is correlated

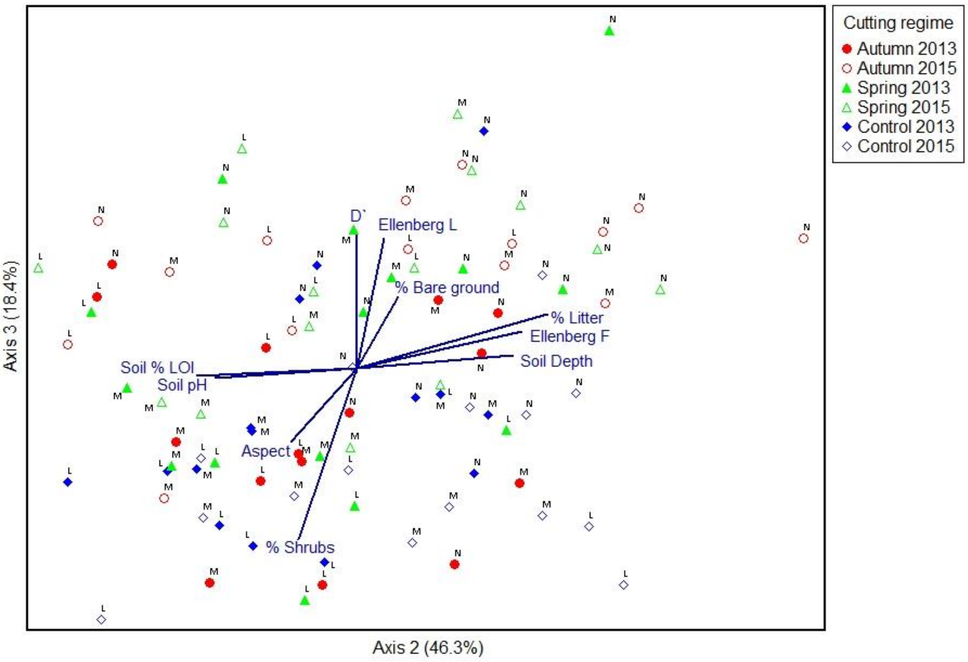


Figure 3.5b. NMS ordination for axis 2 vs 3, coded for 2013 - pre-cutting (filled symbols) and 2015 - two years after cutting (open symbols) and the type cutting regime (Autumn cut: red circles; Spring cut: green triangles; Control: blue diamonds) with biplot of life form/environmental variables. Letters L, M and N represent the three sites (Fig 3.1). Vector length indicates the strength of correlation between variables and relevés > 0.19 (Table 3.2). Ellenberg F is a measure of moisture; Soil % LOI (loss-on-ignition) is a measure of organic matter.

positively with vegetation height and negatively with % forbs and % bare rock, and axis 3 correlates negatively with % shrubs and positively with Simpson's evenness and the Ellenberg L index for light (Table 3.2).

Figure 3.6 shows the species associated with the separation of relevés on the NMS plots: this explains some of the differences along axis 2. Wet heath species (e.g. *Narthecium ossifragum, Trichophorum germanicum, Pedicularis sylvaticum*) are located in the top right of the plot; pasture species (*Trifolium repens, T. pratense, Dactylis glomerata*) are found at the bottom left; dry limestone heath/grassland species (e.g. *Briza media, Linum catharticum, Dryas octopetala, Sesleria caerulea, Listera ovata, Rubia peregrina*) are located centrally and top left, and finally species of dry acid soils (*Erica cinerea, Lathyrus linifolius*) are found between the dry limestone suite and wet heath suite in the top middle of the ordination. The pasture species and the dry limestone/grassland species, located mostly to the left of the ordination are associated with the relevés taken in 2015, two years after cutting. Numerous bryophyte species (e.g. *Frullania tamarisci, Racomitrium* *lanuginosum, Scapania aspera, Rhytidiadelphus* spp.) are located to the right-hand side of the plot, associated with vegetation height and the pre-cutting 2013 relevés. Site N is mostly associated with the wet heath/grassland species in addition to bryophyte species. Site M associates almost exclusively with dry limestone heath/grassland species and Site L associates with pasture species, bryophytes and with dry limestone heath/grassland species.

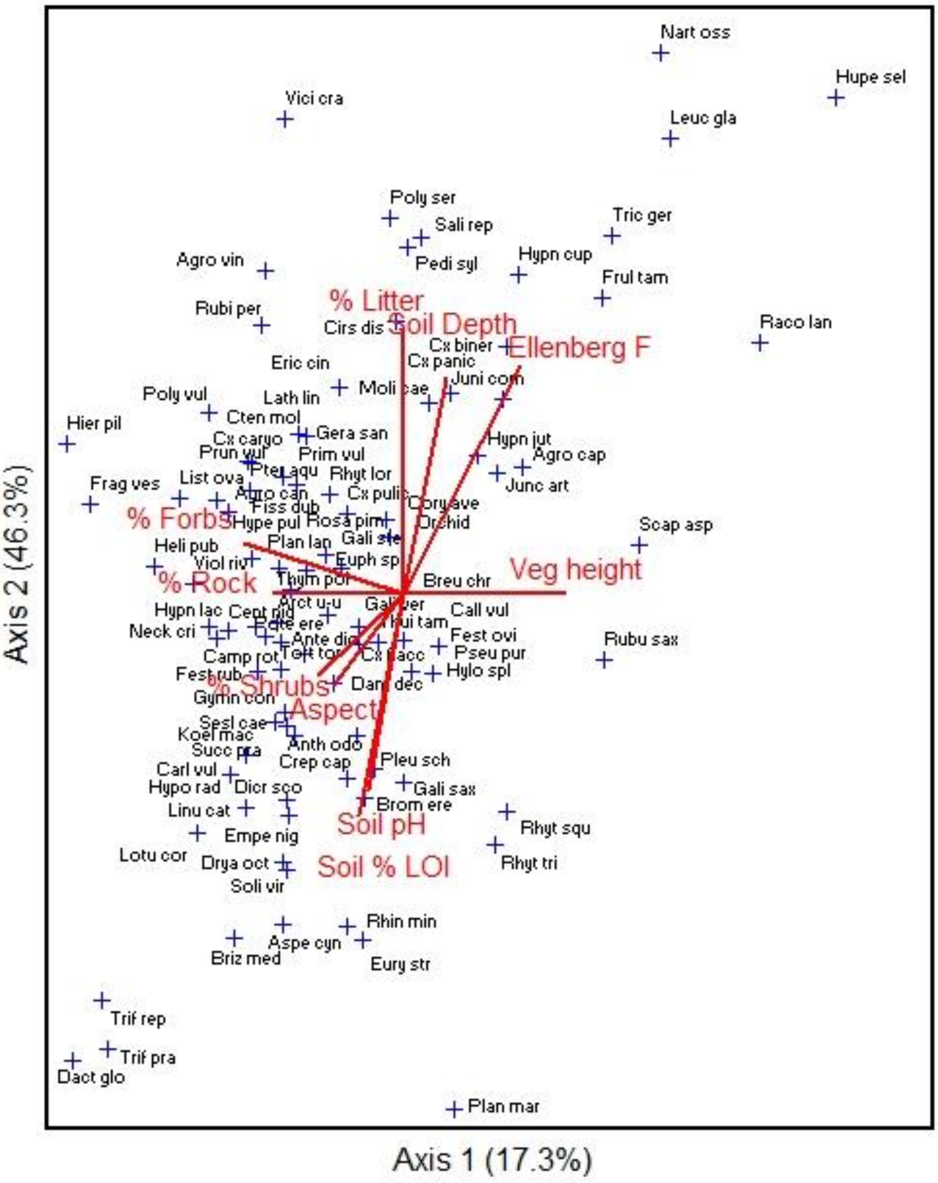


Figure 3.6. NMS ordination as in Fig. 5; species are plotted with biplot of life form/environmental variables. Vector length indicates the strength of correlation between variables and relevés (Table 2). Ellenberg F is a measure of moisture; Soil % LOI (loss-on-ignition) is a measure of organic matter.

Table 3.2. Pearson (r^2 - parametric) and Kendall (tau – non-parametric) correlation coefficients between each axis (1 to 3) of the NMS plot and environmental variables and life forms, r^2 and tau values >0.2 are shown in bold. The r value indicates whether the Pearson correlation is positive or negative.

Axis:		1			2			3	
	r	r^2	tau	r	r^2	tau	r	r^2	tau
% Shrubs	-0.404	0.163	-0.28	-0.393	0.154	-0.238	-0.668	**0.447**	**-0.484**
% Forbs	-0.55	**0.302**	**-0.383**	0.306	0.094	0.149	0.316	0.1	0.234
% Graminoids	0.157	0.025	0.096	-0.034	0.001	-0.003	-0.017	0	-0.009
% Bare ground	-0.321	0.103	-0.203	0.327	0.107	0.258	0.431	0.186	0.44
% Rock	-0.495	**0.245**	**-0.32**	-0.014	0	-0.054	0.352	0.124	0.377
% Litter	-0.063	0.004	-0.053	0.707	**0.5**	**0.529**	0.376	0.142	0.304
Vegetation height	0.553	**0.306**	**0.434**	0.054	0.003	0.047	-0.336	0.113	-0.253
Soil Depth	0.283	0.08	0.191	0.64	**0.409**	**0.532**	0.184	0.034	0.157
Soil pH	-0.256	0.065	-0.172	-0.609	**0.371**	**-0.463**	-0.158	0.025	-0.091
Soil % LOI	-0.288	0.083	-0.197	-0.648	**0.42**	**-0.43**	-0.141	0.02	-0.089
Slope	-0.035	0.001	0.033	-0.048	0.002	0.026	-0.122	0.015	-0.051
Aspect	-0.366	0.134	-0.296	-0.417	0.174	-0.251	-0.44	0.194	-0.277
Species richness	-0.06	0.004	-0.042	-0.2	0.04	-0.122	0.311	0.097	0.243
D` Simpson's evenness	-0.434	0.189	-0.273	0.028	0.001	0.041	0.59	**0.348**	**0.46**
Ellenberg L (light)	0.142	0.02	0.087	0.267	0.071	0.19	0.584	**0.341**	**0.423**
Ellenberg F (moisture)	0.472	**0.222**	**0.299**	0.655	**0.429**	**0.48**	0.31	0.096	0.205

Axis 2 has a strong positive correlation with a number of environmental variables such as Ellenberg F (moisture) r^2 = 0.429, soil depth r^2 = 0.409, % litter r^2 = 0.50, (Table 3.2), which are also shown as vectors on Figures 3.5 a, 3.5 b and 3.6, and species (Table 3.3): *Molinia caerulea* r^2 = 0.668, *E. cinerea* r^2 = 0.509, *Cirsium dissectum* r^2 = 0.367 and has a weaker positive correlation with *Pedicularis sylvatica* r^2 = 0.221, *Carex panicea* r^2 = 0.215 and *Polygala vulgaris* r^2 = 0.20. Axis 2 also has a negative correlation with soil pH r^2 = 0.371 and soil % LOI r^2 = 0.42, as well as *B. media* r^2 = 0.313, *D. octopetala* r^2 = 0.447 and *Succisa pratensis* r^2 = 0.226. Axis 1 correlates positively with vegetation height r^2 = 0.306 and Ellenberg F (moisture) r^2 = 0.222 and negatively correlates with % forbs r^2 = 0.302, % exposed rock r^2 = 0.245, *Arctostaphylos uva-ursi* r^2 = 0.348, *Festuca rubra* r^2 = 0.227, *Hypericum pulchrum* r^2 = 0.293, *Lotus corniculatus* r^2 = 0.202, *Potentilla erecta* r^2 = 0.477, *S. caerulea* r^2 = 0.238, *S. pratensis* r^2 = 0.214, and *Viola riviniana* r^2 = 0.314. Axis 3 has a strong negative correlation with % shrubs r^2 = 0.447 and *Calluna vulgaris* r^2 = 0.822, and correlates positively with Simpson's diversity (D') r^2 = 0.348, Ellenberg L (light) r^2 = 0.341 and *Carex pulicaris* r^2 = 0.203. Axis 3 is not shown on the

Table 3.3. Pearson (r^2 - parametric) and Kendall (tau – non-parametric) correlation coefficients between each axis (1 to 3) of the NMS plot and species for which r^2 and tau values are >0.2 (shown in bold) for at least one axis. The r value indicates whether the Pearson correlation is positive or negative.

Axis:		1			2			3	
	r	r^2	tau	r	r^2	tau	r	r^2	tau
Arctostaphylos uva-ursi	-0.59	**0.348**	**-0.417**	-0.106	0.011	-0.074	-0.107	0.012	-0.031
Briza media	-0.349	0.122	-0.263	-0.559	**0.313**	**-0.524**	-0.081	0.007	-0.133
Calluna vulgaris	0.004	0	0.018	-0.247	0.061	-0.18	-0.907	**0.822**	**-0.747**
Carex panicea	0.137	0.019	0.207	0.464	**0.215**	**0.329**	0.231	0.053	0.326
Carex pulicaris	-0.137	0.019	0.059	0.156	0.024	0.243	0.45	**0.203**	**0.416**
Cirsium dissectum	-0.023	0.001	0.124	0.605	**0.367**	**0.508**	0.23	0.053	0.219
Dryas octopetala	-0.38	0.145	-0.239	-0.668	**0.447**	**-0.561**	0.09	0.008	0.014
Erica cinerea	-0.282	0.079	-0.12	0.713	**0.509**	**0.579**	0.251	0.063	0.227
Festuca rubra	-0.476	**0.227**	**-0.371**	-0.203	0.041	-0.114	0.021	0	0.075
Hypericum pulchrum	-0.541	**0.293**	**-0.468**	0.102	0.01	-0.074	0.087	0.008	0.111
Lotus corniculatus	-0.449	**0.202**	**-0.414**	-0.414	0.172	-0.337	-0.145	0.021	-0.072
Molinia caerulea	0.135	0.018	0.112	0.817	**0.668**	**0.71**	0.256	0.065	0.192
Pedicularis sylvatica	0.008	0	0.179	0.47	**0.221**	**0.473**	0.238	0.057	0.288
Polygala serpyllifolia	-0.02	0	0.116	0.448	**0.2**	**0.317**	0.262	0.069	0.217
Potentilla erecta	-0.691	**0.477**	**-0.566**	-0.169	0.029	-0.182	-0.297	0.088	-0.22
Sesleria caerulea	-0.488	**0.238**	**-0.33**	-0.434	0.189	-0.357	0.118	0.014	0.096
Succisa pratensis	-0.463	**0.214**	**-0.276**	-0.475	**0.226**	**-0.365**	-0.141	0.02	-0.063
Viola riviniana	-0.56	**0.314**	**-0.427**	0.02	0	-0.127	-0.036	0.001	-0.081

plot however the vector for % shrubs is present and correlates with relevés from both Sites L and M in the bottom left corner of the plot.

The Pearson and Kendall correlations with axis 1 indicate differences between 2013 and 2015, where a negative correlation indicates a positive change since 2013 (Tables 3.2 and 3.3). Whereas vegetation height obviously dropped after the cutting and % exposed rock increased as a result, the % forbs also increased, as did the % cover especially of *Arctostaphylos uva-ursi, Festuca rubra, Hypericum pulchrum, Lotus corniculatus, Potentilla erecta, Sesleria caerulea* and *Viola riviniana* (Figs. 3.5a and b and 3.6).

PerManova analysis indicated that while there were no significant differences between relevés in 2013 (p = 0.9942; Appendix 3.1, Table 3.5 and

3.6), in 2015, even with significant differences between sites (p < 0.001), the cutting regime effect was evident, if not significant (p = 0.12, Table 3.4) and pairwise comparisons between the spring and control was nearly significant (p = 0.0632; Table 3.4), though not between autumn and control or autumn and spring.

Table 3.4. PerManova results of site and cutting regime effects on species composition in 2015 and pairwise comparison between plots assigned the cutting regimes.

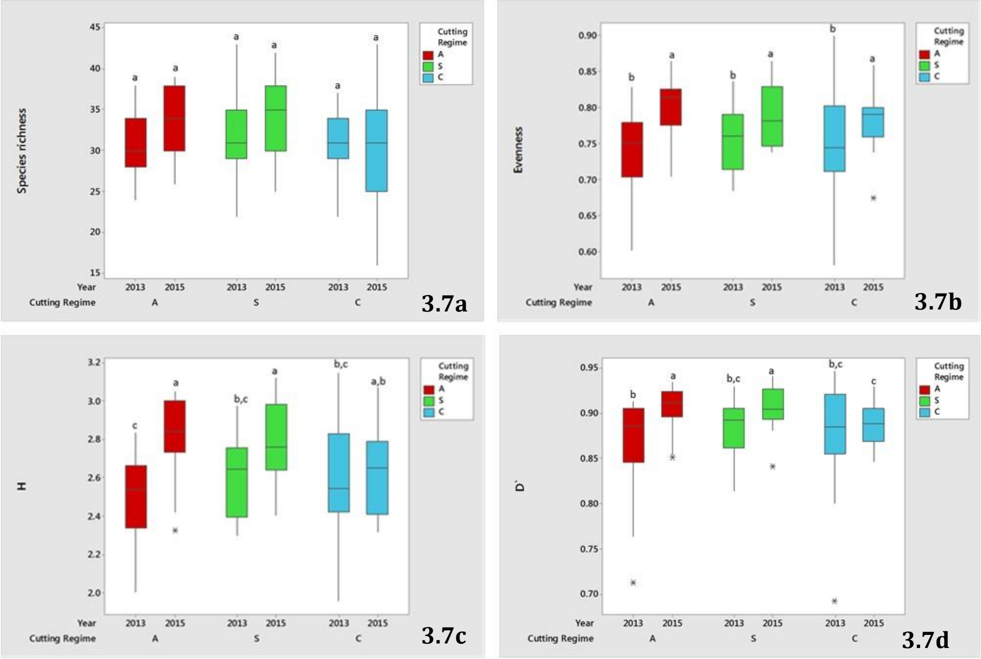
	df	SS	MS	F	p
Site	2	1.1913	0.5957	3.0630	**0.0002**
Cutting regime	2	0.5174	0.2587	1.3303	0.1200
Interaction	4	0.6137	0.1534	0.7889	0.8458
Residual	36	7.0010	0.1945		
Total	44	9.3234			

Pairwise comparisons for cutting regime

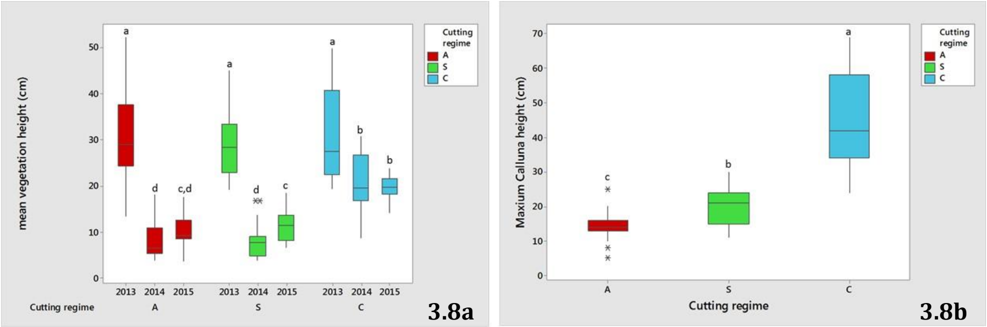
	t	p
Autumn vs Spring	0.8695	0.7110
Autumn vs Control	1.2483	0.1072
Spring vs Control	1.2846	0.0632

The boxplots in conjunction with GLM (Figs. 3.7a to c) and Kruskal-Wallis (Fig. 3.7d) analyses showed that Species richness (Fig. 3.7a) increased in both autumn (A) and spring (S) but not in the uncut control (C), however this was not statistically significant and species evenness (Fig. 3.7b) increased significantly for all regimes, including the control between 2013 and2015 (p < 0.05). Both Shannon diversity (H; Fig. 3.7c) and Simpson's diversity index (D'; Fig. 3.7d) increased between 2013 and 2015 for A (autumn) and S (spring) (p < 0.05) but not for C (control).

For mean vegetation height (Fig. 3.8a) all three years of sampling are shown as in this case, the inclusion of the middle year explains the data better. While the mean height decreased from 2013 to 2014 for the control, the cut plots showed a significantly greater decrease (p < 0.05). There was also a slight increase in the mean height between 2014 and 2015, which was significant only for the spring cut (p < 0.05). There was a significant difference in maximum *Calluna vulgaris* height in 2015 (Fig. 3.8b) between both cutting regimes (p < 0.001) and the control, with the autumn cut plots also being significantly shorter than those cut in spring (p < 0.01). It should be noted that mean vegetation height and maximum *Calluna* height are not the same measure – often the vegetation recorded for the mean height was a grass, forb or bracken – mean height was not reduced in the same way the *Calluna* height was.



Figures 3.7a to d. Boxplots for **(a)** species richness, **(b)** evenness and diversity indices **(c)** H (Shannon diversity) and **(d)** D' (the complement of Simpson's diversity) in years 2013 and 2015 for cutting regimes: autumn (A), spring (S) and control (C). Letters indicate significant differences between the groups' median value tested by GLM with Tukey posthoc test (the letter 'a' is assigned to the highest value, 'b' to the next highest where significantly different to 'a', and so on), except for **d)** which did not conform to assumptions of ANOVA and were tested by Kruskal-Wallis and pairwise Mann-Whitney tests. For all test results see Appendix 3.1, Tables 3.7 to 3.14.



Figures 3.8a & b. (a) Boxplot of mean vegetation height (cm) for all three years of sampling (2013, 2014 and 2015) for both cutting regimes: autumn (A), spring (S) and control (C) and **(b)** Boxplot of maximum *Calluna vulgaris* height (cm) in the final year of survey only (2015) for both cutting regimes: autumn (A), spring (S) and control (C). **(b)** did not conform to the assumptions of ANOVA thus were tested by Kruskal-Wallis and pairwise Mann-Whitney; letters indicate significant differences between the groups ('a' is assigned to the highest value, 'b' to the next highest where significantly different to 'a', and so on).

Of the species listed in Table 3.3, though there was a change in percent cover for many species from 2013 to those for 2015, this was significant for only a few species (Appendix 3.1, Tables 3.15 to 3.18). The decrease in % *Calluna vulgaris* in 2015 was significant for the autumn cut (A) ($p < 0.001$) but not for the spring cut (S) ($p = 0.2529$) and there was an increase in 2015 in the control (C) from 2013 ($p < 0.05$). There was also an increase in % *Arctostaphylos uva-ursi* between the two years for both cutting regimes and the control, but this was not statistically significant. The % *Erica cinerea* cover increased for A and S ($p < 0.05$), but also in C ($p < 0.05$) in 2015 compared to 2013. In addition % cover of *Festuca rubra*, *Hypericum pulchrum*, *Lotus corniculatus, Potentilla erecta* and *Viola riviniana* increased significantly for both cutting regimes and the control between 2013 and 2015 but there was no significant difference between A, S and C.

3.3.3. Patterns of re-growth: site-by-site

In terms of the species which have responded either negatively or positively by ≥ 2% mean cover from 2013 to 2015 (≥ 3% for forbs, Table 3.6) on a site-by site basis in terms of cutting regime we can see that there are some changes, however these were not statistically significant (PerManova results: Appendix 3.1, Tables 3.19 to 3.21). *Arctostaphylos uva-ursi* increased after both cutting treatments, but appeared to increase by a greater amount in the control in sites M and N (Table 3.5); *D. octopetala* increased notably in the cut plots especially in site L, where it also decreased in the control; it responded most to the spring cut in site N; the response is less evident in site M; *Calluna* increased in the control and decreased in the autumn and spring plots except for a small increase in site N spring plots; *Erica cinerea* increased for all cutting regimes and the control for all sites, as did *Pteridium aquilinum* which had a greater increase following spring cutting (except in site N where there was no change); *Thymus polytrichus* increased with spring and autumn cuts and decreased in the control except site N which had a

Table 3.5. Net increase (green)/decrease (red) from 2013 to 2015 in the mean % cover of shrub species and *Pteridium aquilinum* that responded by ± > 2 for over half of the treatments for sites L, M and N and cutting regimes (CR) A (autumn), S (spring) and C (control). ♀ denotes pollen production; ╫ denotes nectar production (Clapham et al., 1987).

Species/Site_CR	L_A	L_S	L_C	M_A	M_S	M_C	N_A	N_S	N_C
Arctostaphylos uva-ursi ♀ ╫	12.6	10.58	3.6	8.1	13.98	19.4	3.78	15.2	19.2
Calluna vulgaris ♀ ╫	-39.4	-34.2	6	-27.6	-7.8	22.6	-32.4	5.2	22.8
Dryas octopetala ♀ ╫	10.1	14.7	-5.1	8.6	6	0.9	4	10.3	4.5
Erica cinerea ♀ ╫	13	17.8	18.5	11.8	4.4	4.2	16.4	14	23.6
Thymus polytrichus ♀	3.1	2.4	-1.4	1.7	8.6	-0.1	3	7.3	1.9
Pteridium aquilinum	4.5	15.6	7.6	3.6	10.2	12	3.6	0	1.9

Table 3.6. Net increase (green)/decrease (red) from 2013 to 2015 in the mean % cover of forb species that responded by ± > 3 for over half of the treatments plus for sites L, M and N and cutting regimes (CR) A (autumn), S (spring) and C (control). ♀ denotes pollen production; ╫ denotes nectar production (Adams, 1955, Clapham et al., 1987, Masierowska, 2006, de Vere, 2007).

Species/Site_CR	L_A	L_S	L_C	M_A	M_S	M_C	N_A	N_S	N_C
Cirsium dissectum ♀╫	4.2	3.4	12	6.3	2.7	5.3	11.6	8.9	14.7
Geranium sanguineum ♀╫	5.9	4.5	7.2	7.6	5.3	5.8	4.8	7	7.7
Lotus corniculatus ♀╫	14.5	9.8	15.7	8.2	8.4	0.2	5.5	3.1	5.2
Potentilla erecta ♀╫	7.6	7.4	14.6	7.8	8.4	12	5.7	3.2	4.8
Succisa pratensis ♀╫	17.6	15.6	8	2	15.5	19.7	6.2	8.3	8.3
Viola riviniana ♀	1.3	3.2	3.4	6.9	4.7	3.9	1.2	-0.1	1.6

Table 3.7. Net increase (green)/decrease (red) from 2013 to 2015 in the mean % cover of grass, sedge and bryophyte species that responded by +/- > 2 for over half of the treatments for sites L, M and N and cutting regimes (CR) A (autumn), S (spring) and C (control). Grasses are at the top, sedges in the middle and bryophytes are at the bottom of the table.

Species/Site_CR	L_A	L_S	L_C	M_A	M_S	M_C	N_A	N_S	N_C
Festuca ovina	-2	15.2	-7	-0.6	-2.8	-6.2	-0.8	0.2	-11.2
Festuca rubra	7.8	3.4	2.1	5.2	4.4	3.2	2.2	3.8	6.6
Molinia caerulea	12.4	-1.8	4.6	1.2	-5.3	6.9	18.8	20.6	19.2
Sesleria caerulea	-0.9	8.1	-3.4	3.9	13.8	-1.3	7.5	7.2	3.1
Carex flacca	12.1	1.8	-1.8	9.7	8.6	-1.6	-1.6	6	2
Carex pulicaris	2.4	1	0	2.9	2.1	-0.6	5.8	5.6	7.8
Hylocomium splendens	-16.2	3	-6.2	0.8	-19.4	-9.2	-8	-6.9	-10.8
Pseudoscleropodium purum	-3.6	6.2	-2.6	-6.6	-10.2	-3.8	-7.2	-2	-3

small increase. Forb species shown (Table 3.6) all increased in mean % cover by ≥ 3% from 2013 to 2015, however species responded in a similar way in the cutting regimes compared to the control. The graminoids and bryophyte species listed (Table 3.7) responded either negatively or positively by ≥ 2%: *Festuca ovina* increased in the spring cut in sites L and N and decreased in all other cutting regimes and the control; *F. rubra* increased in all site and regimes, whether cut or not; *Molinia caerulea* decreased in the spring cut for both sites L and M, but not N, autumn cut and control increased for all sites; *Sesleria caerulea* increased in spring and autumn and decreased in the control in two of the three sites; *Carex flacca* decreased in control plots in sites L and M and autumn cut in site N, increasing for all other plots; *C. pulicaris* increased for all plots except the control in L where there was no change; the bryophytes *Hylocomium splendens* and *Pseudoscleropodium purum* decreased for both cutting regimes as well as in control plots except for spring cut in L where both species increased and autumn in site M where *H. splendens* showed a small increase. A full list of species and their responses to cutting regimes per site is presented in Appendix 3.1, Table 3.22.

Species that produce significant pollen and /or nectar are indicated (Tables 3.5 and 3.6) and, though *Calluna vulgaris*, a high pollen and nectar producer has reduced in cover under the two cutting regimes, other pollen and nectar producers increase, especially relative to the Control, such as *Dryas octopetala* and *Thymus polytrichus* (Table 3.5), though there is little observable pattern of change in the key forb % cover (Table 3.6).

3.3.4. Interviews with farmers

The three farmers on whose land the cutting trials were carried out all responded to the survey (Questionnaire in Appendix 4.2). The consensus was that it was a lack of grazing, or an insufficient grazing level, that had contributed to the heather (*Calluna vulgaris*) becoming so tall, and one farmer also said the climate was contributing to it (the ‘wet years’ came in the late 1960s). The main reason for this lack of grazing had been due to a problem of access but also a lack of water. Two of the farmers did not have easy access to their winterage pasture but this has recently been addressed and access tracks have been installed on both farms.

One farmer had issues with stock breaking out of the winterage – after feral goats knocked down the stone walls – and coming down to the green land but he claims this is no longer a problem as it is fenced off since 2015 and he can now access the land to provide supplementary feed in the form of nuts from February on. On this farm 15-20 cattle were put up on the 1st of October and brought down at the end of March since 2000; in 2017 it was also grazed for 2 weeks in May (Table 3.8). Prior to 2000 there were typically 15 cattle on the winterage and they were brought down in January as often water was scarce; in 2017 the farmer was hoping to install a water trough. These works were the recommendations of the Burren Programme. A second farmer has 12 cattle on the winterage from the 1st of October to the end of March, and is also planning to graze the winterage for 6 to 8 weeks at the end of May in 2018. He did not know about stock number prior to acquiring the land in 1998. The third farmer leased the land for two years following its purchase (1997 – 1999) during which time 26 cattle were grazed from 1st October to the end of January; since 2000 there have been 5 cattle and 4 or 5 ponies are kept on the farm all year round – they are mainly on the lower green fields in summer months and on the winterage between the months of October and March. This farmer has been practising light summer grazing since 2010 (previously he was in REPS and summer grazing was prohibited on winterage pastures), he has already installed a water trough and access tracks, however the gates are left open so the stock can roam from upland to green pasture outside of winter months.

Table 3.8. Summary of responses to the Farmer questionnaire. Questions refer to farming practice since ownership started

Site:	1	2	3
Date ownership started	1997	1998	Always in the family
Heather cut?	Not until 2014	No	No
Heather burnt?	No	No	No
Fertiliser application	No	No	No
Stock type	Cattle + horses	Cattle	Cattle
Stock number	5 cattle + 6 horses	12	15-20
Timing	1st Oct to end Mar	1st Oct to end Mar	1st Oct to end Mar
Recent/planned changes in grazing times	light summer grazing since 2010	6-8 weeks end of May 2018	2 weeks end of May 2017

There was no knowledge of any past burning or cutting having been carried out on these sites. However one farmer undertook cutting using a hedge cutter in the same year as the cutting trials for this study were being carried out (2014); care was taken not to interfere with the trial plots. There was also no knowledge of any fertiliser being used due to a lack of access.

In summary, the main reason for the predominance of tall *Calluna* at the three sites was an absence of grazing for some time which stemmed from a lack of access, meaning supplementary feed could not be provided, and water troughs could not be supplied when needed, in particular in early spring and summer. The stocking levels were not determined here as the areas in question were not stock-proofed until recently, however it is clear that the numbers of grazers are too few at present.

3.4 Discussion

3.4.1. Control of *Calluna vulgaris* and effects on other species of interest

While this study covers a very short timescale in terms of vegetation growth and recovery, the cutting had the desired effect of removing tall *Calluna vulgaris* – there was a significant decrease in *Calluna* height and % cover following cutting. In addition the cutting trials had a beneficial effect on species richness and evenness related to the removal of dominant *Calluna*. A similar study in northern Spain also showed that species richness, evenness and diversity increased following cutting over a monitoring period of two years (Calvo et al., 2005). The cover of *Arctostaphylos uva-ursi* was not adversely affected by the cutting, as in northern Spain where the vegetative recovery of *A. uva-ursi* after disturbance was observed to be very quick, following an initial period of increase of herbaceous species (del Barrio et al., 1999).

Calluna over 20 years of age has a poor capacity to regenerate following cutting (Mohamed and Gimingham, 1970, Calvo et al., 2005) but when in its building phase (6 – 15 years) can withstand cutting every third year (Kvamme et al., 2004). In this study it appears that even mature stands do regrow, however cutting *Calluna* in autumn may suppress the regrowth more than spring cutting. If the mature-degenerate stands of *Calluna* were cut (cuttings removed) and this was followed by grazing, for a longer period than has been practiced in recent decades, the stock would graze the palatable *Calluna* regrowth thereby maintaining it in its building phase, and possibly avoiding the need for further cutting in future years, or at least extending the period between cuts (Backshall, 2001). The areas of short *Calluna* are found on the stronger winterage pastures where Parr et al. (2009b) recommends late summer grazing as well as winter grazing, therefore it would appear that this grazing regime would also be beneficial to sites following the removal of mature *Calluna.* Grazing of heathland areas in summer months can control heather growth, maintaining it in a short sward (Backshall, 2001) and keeping it in its more productive and palatable phase (Mowforth and Sydes, 1989, Gimingham, 1995). *Calluna* can be grazed throughout the year, most importantly in winter when forage material may be sparse and edible green shoots are particularly high when *Calluna* is in its building phase (Gimingham, 1992); low intensity grazing can have the beneficial effect of perpetuating this vigorous phase (Backshall, 2001) thereby providing more forage material for stock. In some cases grazing in autumn and spring may damage the *Calluna* plants (Mowforth and Sydes, 1989), and stocking levels should be reduced during these times (Backshall, 2001). In Scottish populations *Arctostaphylos uva-ursi* has been seen to colonise gaps in the *Calluna* stand and also to do well following burning, as this provides more open areas into which it can spread (Gimingham, 1992); whether cutting will have the same effect on its growth remains to be seen.

Cutting time. Cutting of the vegetation showed a difference even after two years, although for many factors this was not statistically significant. The overall effects of cutting in early spring (February) was nearly significant, while cutting in autumn (October) showed less difference from the control. As expected, the cover and height of *Calluna* decreased significantly following cutting and this difference was more pronounced in the autumn plots. *Arctostaphylos* was not negatively affected by the cutting and in fact its cover increased in 2015 whether cut or not. Diversity indices (Shannon and Simpson) both showed a significant increase following cutting and species richness increased for cut plots (both spring and autumn cuts) but not in the control.

When carrying out cutting it is important to remove the vegetation cuttings as leaving the material can adversely affect the site by providing nutrients which would have been lost in the more typical management process of burning (Mowforth and Sydes, 1989). In lab trials cutting *Calluna* in summer (July/August) was more effective at dwarfing plants than winter clipping (December/January) (Grant and Hunter, 1966). In dry *Calluna* heath in the Czech Republic cutting plots of mature-degenerate phase *Calluna* promoted increased grass cover followed by a slow recovery of *Calluna* whereas burning encouraged germination of *Calluna* as well as vegetative regrowth (Sedláková and Chytrý, 1999). In this study *Molinia caerulea* was found to be kept in check with the spring cut, whereas there was an increase following the autumn cut. As *Molinia* is deciduous cutting in autumn would have removed the *Molina* litter and therefore increased light availability. *Molinia* dies off in winter, its leaves turn to leaf litter and tussocks form which can be hard to remove or utilise - it has no grazing value during this time - but the removal of litter, or intensive grazing of these tussocks in spring can aid in providing good summer grazing (Mowforth and Sydes, 1989). And summer grazing, particularly from mid-May to mid-July (Backshall, 2001), by cattle has proven to be effective at limiting the invasion of *Molinia* in the UK (Welch, 1984) and this practice has been considered in this area of the Burren with some of the farmers now putting stock out in e.g. May.

The cover of *Sesleria caerulea* and *Festuca rubra* increased following cutting but these species are slow-growing stress-tolerators, and when grazed periodically have not been problematic on heathlands elsewhere. *Sesleria* is another relict arctic-alpine species and as such can become dominant in places of summer drought and low nutrient status, but so long as winter grazing keeps it in check in the Burren, sward species diversity is maintained (O'Donovan and Jefferey, 1990). The increase here, particularly in spring cut plots, of *Pteridium aquilinum* can be a problem, as it is an invader on heathlands (Måren et al., 2008). Cutting twice yearly in June and July has been shown to be effective at controlling the density of *P. aquilinum* (Snow and Marrs, 1997) and trampling by cattle may also reduce its spread (Gimingham, 1992). In general grazing in spring and/or early summer may have the further benefit of reducing the threat of scrub encroachment, as the leaves and young shoots of woody plants are palatable to browsers but are largely inedible after midsummer due to lignin deposition (Crofts and Jefferson, 1999).

3.4.2. Changes in cover of species providing ecosystem services for insects

There was an increase in the percent cover of *Dryas octopetala* and *Thymus polytrichus* following cutting – this may have the added benefit of increasing the pollen and/or nectar resources for pollinators. The majority of forb species present increased in 2015 as compared with 2013 whether cut or not, as did *Erica cinerea* and *A. uva-ursi*; this has the wider benefit of ecosystem services by providing pollen and/or nectar to native pollinators in upland areas of the Burren. These changes in forb cover may not have been linked to management as they also responded positively in the control plots. It is possible that the increased growth is due to climatic variations: the summers of 2013 and 2014 were unusually warm and dry (Met Éireann, 2017) and may have led to the growth of many species being stunted due to drought conditions; in contrast 2015 was colder and wetter than usual (Met Éireann, 2017) – so an increased water availability could have provided the conditions for increased growth in vegetation specifically adapted to an oceanic habitat. In any event the increase in forb species and of *Calluna* in the control plots were not considered to be significant. The removal of the *Calluna* canopy exposed more bare rock and created bare ground and increased light availability which may facilitate colonisation by *A. uva-ursi* (Watt, 1947). The increased structural diversity and provision of open areas created by cutting patches of *Calluna* may contribute to habitat creation for invertebrates such as spiders and beetles in conjunction with a low-intensity grazing regime and these factors may also support bird communities, not only for the structure for nest creation but also insect-food availability for chicks (Rosa Garcia et al., 2013). Bare ground may also provide sites for seedling establishment (Gimingham, 1992).

3.5 Conclusions and recommendations

Cutting in spring appeared to be more effective but was not significantly different over the short time scale of this study. Thus in terms of controlling the heather and encouraging the key species *Dryas octopetala* and *Arctostaphylos uva-ursi* the time of year the vegetation is cut did not appear to be an important factor. It would, in any case, be recommended that all cutting take place between October and February outside of bird nesting season (1st March to 31st August). Additionally the removal of cuttings should be undertaken as this is an important factor in maintaining the species diversity in these low-nutrient systems.

The time of cutting did however affect potentially dominant species in different ways; a spring cut favoured *Pteridium aquilinum* (bracken) more than cutting in autumn, but the reverse was observed for *Molinia caerulea*. Therefore it is recommended that light spring/early summer grazing be practiced following cutting when *Molinia* has young leaves and shoots and is most palatable as this may help to keep it in check. The farmer who carried out his own cutting noted that while there was an improvement in grass quality the growth of bracken had also increased. However trampling by stock, in particular cattle, has also been seen to help keep bracken at bay (Gimingham, 1992), and as cattle are the main stock grazed in these uplands, they may be beneficial in reducing the growth of bracken. The increase in *Sesleria caerulea* following cutting may provide extra resources for grazers in early spring (February-March) when it begins to flower.

In terms of maintaining the *Arctostaphylos*-rich heaths, regular grazing seems to be the key factor, and with more stock than is currently practised, both throughout the winter months and with additional short periods of grazing in the summer. In order to facilitate the grazing access and water provisions are essential and if there are winterages with similar problems to those addressed in this study these should be factored into any management plans along with the cutting and grazing regimes. It should also be noted that specially-formulated supplementary feed in the form of nuts is often provided to out-wintering stock, however point source feeding should be avoided to prevent poaching of the ground and the provision of excess nutrients in the form of dung (BurrenLIFE Project, 2010). The last issues have already been provided for by farmers in the Burren Programme.

3.6 References

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Chapter 4. Experimental pollination studies of *Arctostaphylos uva-ursi* in low-altitude Atlantic heath, Western Ireland

4.1 Introduction

4.1.1. *Arctostaphylos uva-ursi* distribution and conservation importance

Arctostaphylos uva-ursi is an evergreen patch-forming procumbent shrub (Rose, 2006) with a circumpolar distribution; it mainly occurs within the coniferous forest zone of the Boreal-montane biome (Hill et al., 2004). In Britain and Ireland *A. uva-ursi* occurs on upland heaths, moors and rocky or gravelly ground, or ravines (Preston et al., 2002). In Britain it grows between 60m and 914m above sea level although typically the minimum altitude is 160m (Gimingham pers. comm. in Fitter and Peat, 1994). In Ireland it grows near the north and west coasts and is rather rare (Parnell and Curtis, 2012). Its most southerly location in Ireland is on the Burren limestones in Counties Clare and Galway (Preston et al., 2002). Like many northern-montane species at the southern end of their range, *A. uva-ursi* has a somewhat disjunct distribution in Ireland. While it would be expected to be restricted to hilltop populations and is mostly found on high ground above 160m in the western Burren, it also occurs on the low-lying limestone outcrops in the eastern the Burren, where it grows at ca. 30m above sea level (Webb and Scannell, 1983, Preston et al., 2002). *Arctostaphylos uva-ursi* is one of the key species in the Alpine and boreal heath community (Annex I habitat 4060) sub-type *Arctostaphylo-Dryadetum* which occurs in the Burren (NPWS, 2007), and a positive indicator species for the calcareous variant of (4030) European dry heath, also found in the Burren. These plant communities, which are also associated with *Empetrum nigrum,* are rare (Parr et al., 2009) and *Arctostaphylos*-rich heaths form an important part of the vegetation on high ground in the Burren (Ivimey-Cook and Proctor, 1966, Webb and Scannell, 1983, Proctor, 2013).

4.1.2. *Arctostaphylos uva-ursi* and climate change

The species' geographical range in Britain has slightly contracted in recent years, based on distribution data from between 1930-1960 and 1987-1999 (Hill et al., 2004). This trend is apparent in Ireland too; Irish records from the nineteenth-century suggest it was more abundant then than it is now (Webb and Scannell, 1983) as well as some more recent (1970s) records which were not re-found by the author (Chapter 2). With the ongoing effects of climate change this negative change might be accelerated further (JNCC, 2013). Species that occupy restricted or vulnerable habitats, for example those that are 'alpine' in affinity and therefore largely confined to mountain-tops, may be particularly vulnerable to climate change effects (Wyse Jackson, 2008, Coll et al., 2013). Indeed many plant species with arctic-alpine and/or montane affinities at the southern end of their distribution have been projected to shift their ranges upwards, from lower to higher altitudes due to temperature rises (Hodd and Sheehy Skeffington, 2011), and with the acceleration of climate change this upward and northward shift is predicted to continue which will result in arctic-alpine species being under threat, in particular those species with poor dispersal ability (Hodd et al., 2014). These are often long-lived slow-growing evergreen species, reproducing vegetatively (Grime, 1979, Hodd and Sheehy Skeffington, 2011), and many are stress tolerators, as indeed is *Arctostaphylos uva-ursi* (Hunt et al., 2004).

4.1.3. Growth strategies of *Arctostaphylos uva-ursi*

Arctostaphylos uva-ursi has a prostrate, spreading habit and adventitious root formation therefore it has a capacity for clonal vegetative spread (Salemaa and Sievanen, 2002). This is a growth strategy observed in woody plants growing in extreme habitats in order to be able to regenerate following damage or disturbance (Crawford, 2008). Anecdotal evidence of commercial growing of *A. uva-ursi* by transplanting has had limited success because its roots do not like disturbance (Indian Mirror, 2014, Missouri Botanical Garden, 2018). Its germination requirements are not fully understood, although scarification and stratification of seeds has increased germination success (USDA NRCS Northeast Plant Materials Program, 2006, Plants for a Future, 2012). Mycorrhizal associations may be an important factor affecting seedling establishment (Krpata et al., 2007, Liston and Harrington, 2012), but also may account for its root sensitivity to disturbance.

If the populations are clonal, resulting from purely vegetative reproduction, then by definition there is poor genetic diversity and this is particularly of concern where climate change and further habitat fragmentation may reduce the species' range and its ability to adapt either to the resultant environmental changes or to competition from species that benefit from the effects of climate change (Hodd and Sheehy Skeffington, 2011). This would include its potential susceptibility to disease, which, with low genetic diversity, might threaten the entire population (Callaghan et al., 1992).

4.1.4. Pollination and reproduction of *Arctostaphylos uva-ursi*

As a key and vulnerable species with fragmented populations in a rare and protected habitat type it is important to gain more knowledge of the reproductive biology of *A. uva-ursi,* in order to further the understanding of its conservation requirements (Yates and Ladd, 2005) and therefore the conservation of *Arctostaphylos*-rich heaths that are vulnerable in the Burren. At present there is no Biological Flora for *A. uva-ursi.* A number of studies have been undertaken on the morphology and architecture of *A. uva-ursi* (Remphrey et al., 1983a, Remphrey et al., 1983b, Remphrey and Steeves, 1984a, Remphrey and Steeves, 1984b), but little is known about its reproductive biology other than that it mostly flowers between May and July (Clapham et al., 1987), although in Irish populations flowering may occur in early April when few other flowers are open. It is also known to be pollinated by thrips in continental Europe (Garcia-Fayos and Goldarazena, 2008), by bumble-bees, or is self-pollinated (Knuth, 1909, Clapham et al., 1987). It produces only a small amount of pollen but also offers pollinators a nectar reward which is occasionally the more attractive reward as evidenced by small holes pierced at the base of the flower near the nectaries by 'nectar-robbing' insects (Garcia-Fayos and Goldarazena, 2008). In early-flowering *Arctostaphylos* spp. in California bumblebee pollination is known to occur, particularly when pollen sources are scarce; once more abundant sources of pollen became available these pollinators ceased visiting *Arctostaphylos* spp. flowers (Brum, 1975). *Arctostaphylos uva-ursi,* being an early flowering species would thus be expected to be visited by the common early emerging species of bumblebees such as *Bombus pratorum, B. terrestris, B. lucorum, B. pascuorum, B. jonellus* and *B. hortorum,* all of which have been seen to emerge as early as January or February in Ireland (Fitzpatrick et al., 2007) although in England the dates for spring queen emergence, perhaps more typically, range from mid-March (*B. pratorum* and *B. terrestris*) to late April (*B. hortorum*), depending on the maximum soil temperature (Prŷs-Jones and Corbet, 2014). The Burren, as a low intensity agricultural environment, is considered to be a prime landscape providing a refuge for pollinators within an Irish farming context (Santorum and Breen, 2005, Deenihan, 2011).

Given that the *A. uva-ursi* populations in the Burren region are at its southern-most lowland limit on the Atlantic seaboard, it is important to determine how reliant *A. uva-ursi* is on vegetative reproduction and whether it is self-compatible and thus whether sexual reproduction occurs in the absence of pollinators. With growing evidence for the decline of bumblebees across North America, Europe and also in Ireland, driven mainly by loss of habitat (Goulson et al., 2005, Fitzpatrick et al., 2007), it is of interest to determine to what extent it is dependent on these vectors for the maintenance of the population. It is important also to establish baseline data of bumblebee abundance and diversity on Alpine heath in these Burren habitats.

The questions that will be addressed in this paper are: Is sexual reproduction in *A. uva-ursi* taking place in some form, be it by zoophily or by self-fertilization? In other words, is it being pollinated to any extent by insects and if so, is this out-crossing a requirement for its fruit to set or can it produce fruit via self-pollination? Or, alternatively, is the species mostly reliant on vegetative reproduction at this limit of its range? An additional question concerns whether there is any difference in sexual reproduction success between upland and lowland sites for the species in the Burren.

4.1.5. Aims

In order to determine the requirements for fruit set, a pollination experiment was undertaken, along with observations of pollinator visitation (Reynolds and Fenster, 2008), with the following objectives:

- To examine the need for out-crossing to set seed. For this, selected inflorescences were bagged prior to bud opening in order to exclude visitors and to control the movement of pollen between these flowers (Stout, 2007).
- To quantify floral abundance and establish fruit and seed set as a measure of pollinator effectiveness (Reynolds and Fenster, 2008) and as a function of floral abundance.
- To document the phenology of the species from bud to fruit maturity.

4.2 Methodology

4.2.1. Site selection

Four sites were selected, based on the abundance of *Arctostaphylos uva-ursi* flowers, ease of access for regular visits and representativity of both lowland and upland sites. Two lowland sites, each at ca 30 m altitude: at Cregballymore (CM), Ballinderreen, Co. Galway [53.1715°N, 8.8861°W] and the Ardrahan grasslands SAC at Caherateige (CT), Ardrahan, Co. Galway [53.1695°N, 8.8279°W]; and two upland (> 100 m above sea level) sites: at Caherbullog (CB), Caher valley, Co. Clare [53.0890°N, 9.2455°W] and Carnsefin (CS), Black head, Co. Clare [53.1502°N, 9.2595°W] (Fig. 4.1).

Figure 4.1. Map of study area in the Burren, western Ireland, with two lowland sites: CM (Cregballymore), CT (Caherateige); and two upland sites (> 100m a.s.l.): CB (Caherbullog) and CS (Carnsefin). Map of Ireland inset.

4.2.2. Flowering patterns

Each site was visited fortnightly from mid-March to mid-September 2015 (and weekly during flowering period from April to May) in order to record the phenology of *A. uva-ursi.* On each visit counts were made of the total number of inflorescences, and the number of inflorescences in bud, flower and fruit within four 0.5m x 0.5m (0.25m^2) fixed quadrats – permanent markers were left in the ground for each quadrat and for the duration of the recording season (Fig. 4.2). Each quadrat was located on what was considered to be a different plant, as it was ensured that there was always a separation of 5 metres where *A. uva-ursi* was absent between sampled plants.

Prior to the opening of the first flower the inflorescence was taken to be in the budding phase, when the first flower opens on an inflorescence, that inflorescence was considered to be in the flowering phase and likewise when the first flower had wilted or the first fruit was beginning to develop the inflorescence was taken to be in the fruiting phase. Figures 4.3a to d illustrate the various phenophases discussed here. The counts for the two upland sites (n = 4 for each) were combined, as well as for the two lowland sites (n = 4 for each) and the mean values (n = 8) are presented for $0.25m^2$ along with the standard deviation. The data were not normally distributed therefore the non-parametric Mann-Whitney U test was performed to test for significant differences between the median values for each phenophase per location.

Figure 4.2. One of the sixteen 0.5 m x 0.5 m (fixed point) quadrats used for monitoring the phenology of *Arctostaphylos uva-ursi* from bud through flowering to fruit development in 2015. Note the permanent markers top left and bottom right.

Figures 4.3a to d. (a) *Arctostaphylos uva-ursi* in bud (photo taken on: 19/03/2015); (b) *A. uva-ursi* in full flower (photo taken on: 16/04/2013); (c) *A. uva-ursi* withered flowers and developing fruit (photo taken on: 01/05/2013); and (d) *A. uva-ursi* with ripe fruit (photo taken on: 18/08/2015).

4.2.3. Pollination study

Observations were made of pollinator visitors, undertaken on a weekly basis during the flowering periods of 2013, 2014, 2015 on days when the weather conditions were suitable for bumblebee activity i.e. in dry weather when the minimum temperature was above 12°C (Carvell, 2002), with little or no breeze (less than Beaufort force 3 – leaves in slight motion) (NBDC, 2009). Observation periods (5 periods of 30 mins on 3 dates in 2013, lowland only; 2 periods of 30 mins and 1 period of 20 mins on 2 dates in 2014, lowland only; and 9 periods of 30 mins on 8 dates in 2015, upland and lowland) took place between 9am and 6pm (Carvell, 2002). All pollinators were recorded, whether visiting flowers within the quadrats or flying past the observation station. The species of pollinator, in particular bumblebees, was identified and the number of flowers each individual visited was recorded. Other pollinator types were also noted where observed. No invertebrates were collected during this study.

4.2.4. Breeding systems and fruiting patterns study

Twenty inflorescences were bagged in March/April 2015 while still in bud (five at each of the four observation stations per site; not within the quadrats) with <1mm mesh nylon netting (Stout, 2007), in order to exclude bumblebee visitors (Fig. 4.4). Twenty additional paired open-pollinated (i.e. un-bagged) inflorescences were tagged to provide a comparison with the bagged ones; each of these was located as close as possible (<5cm) to its bagged pair on the same plant. The netting remained in place for the duration of flowering and was then removed once flowering had ceased, so as not to cause any damage to any potential fruit developing (Stout, 2007) and to keep conditions as similar as possible to un-bagged paired inflorescences. All fruit in the paired inflorescences were collected on the 22nd (lowland sites) and 28th (upland sites) of August 2015, by which time they were fully ripe and they were subsequently dissected and the number of seeds counted. The fruit set and seed set data were averaged for bagged vs un-bagged and upland vs lowland plants and compared. A pilot study was carried out in 2014 at a single site where twenty inflorescences were bagged

Figure 4.4. Bagged inflorescence of *Arctostaphylos uva-ursi*. A marked un-bagged inflorescence is to the left of the netting. All paired inflorescences were labelled as shown in the photo.

to exclude visitors; however these were not paired with open inflorescences and open-pollinated fruits were collected at random from the same plants as had the bagged inflorescences, in addition to the fruit from bagged inflorescences.

4.3 Results

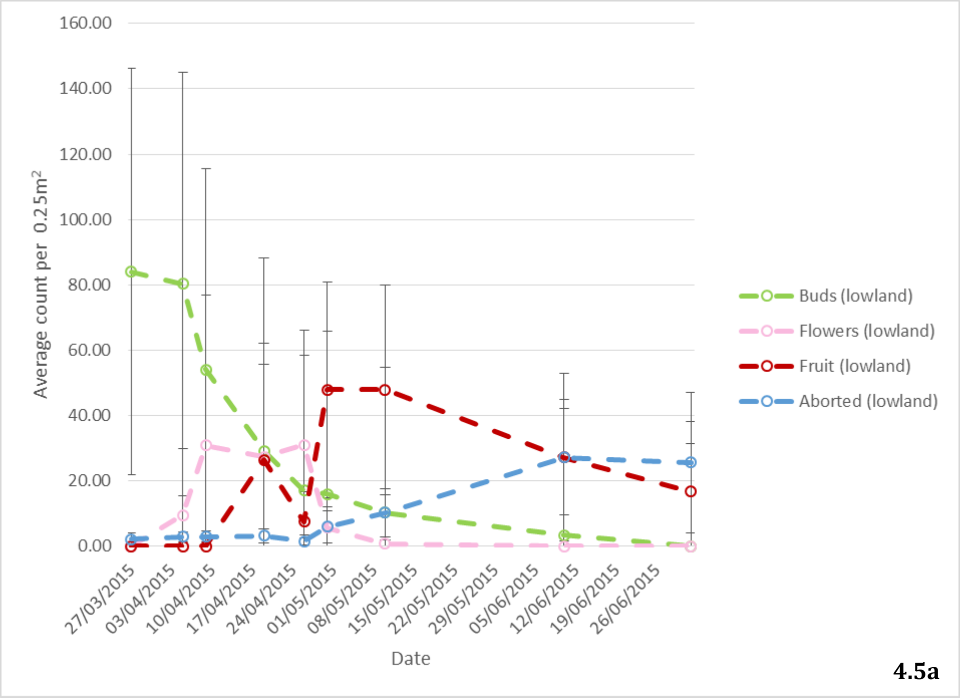
4.3.1. Flowering patterns

In 2015 flowering began on the 5th of April at lowland sites and on the 16th of April at upland sites. The last open flowers were recorded on the 10th of May at lowland sites and on the 26th of May at upland sites, so the flowering duration for lowland and upland sites was 35 and 40 days respectively. The first week and the last two weeks of flowering had a relatively small number of flowers and the middle three weeks were the main flowering period (Figs. 4.5a and b). Fruit formation was first observed on the 19th of April in the lowlands and on the 23rd of April in the uplands in 2015. The average number of developing fruit peaked from the 19th of April to the 10th of June in the lowlands and from the 1st of May to the 10th of June in the uplands (Figs. 4.5a and b; Table 4.1a). A similar trend can be seen with a peak in buds at the start, followed by a much smaller peak in flowering and then a small peak in fruit which is then equal to or surpassed by the peak in aborted fruit/inflorescences as the number of buds and flowers drops and subsequently the number of fruit also drops.

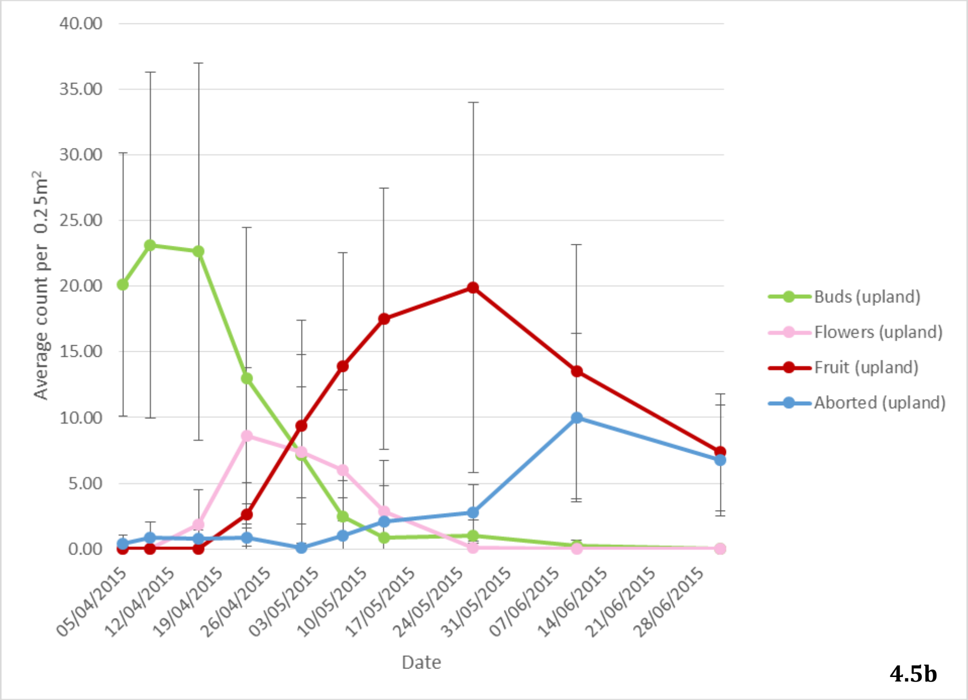
The total number of inflorescences was significantly higher at the lowland sites than at the upland sites (Mann-Whitney: lowland N = 68, Median = 46.5; upland N = 80, Median = 20.0; p < 0.001, where N is the number of quadrats counted), the total number of buds were also found to be significantly higher (M-W: lowland N = 68, Median = 11.5; upland N = 80, Median = 3.0; p < 0.001), as were the total number of aborted buds, fruit and inflorescences (MW: lowland N = 68, Median = 4.0; upland N = 80, Median = 1.0; p < 0.001). However the median numbers of flowers and fruit were not significantly different if one considers the counts for all weeks, this is because there are a large number of zeros in the data, but if the weeks where flowers were not present are removed from the data set and the main flowering weeks are tested i.e. weeks 2 to 6 for lowland sites and weeks 4 to 8 for upland sites, there are a significantly higher number of flowers in the lowland sites (MW: lowland N = 36, Median = 7.0; upland N = 40, Median = 3.0; $p = 0.0248$). Similarly if we remove the weeks where fruit are not present and isolate the fruiting weeks i.e. from week 4 for lowland sites and from week 5 for upland sites, there are a significantly higher number of fruit at lowland sites (MW: lowland N = 44, Median = 18.0; upland N = 56, Median = 11.5; $p = 0.0159$).

In the lowlands, over the time observed (27th March 2015 [week 1] – 2nd July 2015 [week 14]), the highest mean count per 0.25m^2 for each phenological stage, on the date recorded, was: inflorescences 93.13 ± 64.79; buds 84.0 ± 62.46; flowers 31.0 ± 27.58; fruit 47.88 ± 33.08; and aborted fruit/buds 27.25 ± 17.65 (Fig. 4.5a; Table 4.1a). In the uplands, during the observation period (5th April [week 2] – 1st July 2015 [week 14]), the highest mean count per 0.25m^2 for each phenological stage, on the date recorded, was: infl. 25.25 ± 12.71 ; buds 23.13 ± 13.19; flowers 8.63 ± 5.19; fruit 19.88 ± 14.1; and aborted fruit/buds = 10.0 ± 6.40 (Fig. 4.5b; Table 4.1a). The peak number of buds was significantly higher in the lowlands (MW: lowland N = 8, Median = 60.50; upland N = 8, Median = 19.00; $p = 0.0313$); there were no statistically significant differences for the other maximum counts at $p < 0.05$. The flowers are opening and forming fruit continuously, which explains why the number of fruit may exceed the maximum number of flowers at a given time.

There was a large amount of variation in the data collected at the different sites as shown by the standard deviation error bars (Figs. 4.5a and b, Table 4.1a, Appendix 4.1 Figs. 4.1a and b, and 4.2a and b). A large proportion of fruit was found to abort and in addition numerous entire inflorescences aborted from the peduncle (Figs. 4.7a and b).



4.5a



4.5b

Figures 4.5a & b. Mean count (n=8) in 2015 per 0.25m² for inflorescences in bud, flower and fruit, and aborted inflorescences/fruit for (a) lowland NB. Counts for one lowland site are missing for 26/04/2015 resulting in a dip in fruit numbers for that date; and (b) upland sites. Standard deviation from the mean is shown by vertical error bars. Actual recording dates are in Table 4.1a.

Table 4.1a. Mean number of inflorescences per quadrat ($0.25m^2$) noted for each observation date and their phenology for upland and lowland sites (n = 8; 4 per site, averaged for 2 sites each in lowland and upland regions). NB. Counts for one lowland site are missing for 26/04/2015*.

Date	Inflorescences		Buds		Flowers		Fruit		Aborted (buds/fruit)	
	Mean	St. Dev.	Mean	St. Dev.	Mean	St. Dev.	Mean	St. Dev.	Mean	St. Dev.
lowland										
27/03/2015	86.50	62.19	**84.00**	62.46	0.00	0.00	0.00	0.00	2.13	1.96
05/04/2015	**93.13**	64.79	80.38	61.31	9.50	20.38	0.00	0.00	2.88	1.62
09/04/2015	87.75	61.68	54.00	50.72	30.88	45.87	0.00	0.00	2.88	1.69
19/04/2015	86.25	58.88	29.25	24.13	27.38	28.44	26.38	35.64	3.25	2.17
26/04/2015	56.75	49.27	17.00	14.07	**31.00**	27.58	7.50*	9.12	1.50	1.12
30/04/2015	75.63	49.86	16.00	14.14	5.75	6.26	**47.88**	33.08	6.00	5.00
10/05/2015	69.25	44.44	10.25	13.48	0.75	1.09	**47.88**	32.10	10.25	7.41
10/06/2015	58.13	38.86	3.38	5.34	0.00	0.00	27.25	25.74	**27.25**	17.65
02/07/2015	42.38	31.47	0.00	0.00	0.00	0.00	16.75	21.48	25.63	21.43
upland										
05/04/2015	20.50	9.76	20.13	9.99	0.00	0.00	0.00	0.00	0.38	0.70
09/04/2015	24.00	12.93	**23.13**	13.19	0.00	0.00	0.00	0.00	0.88	1.17
16/04/2015	**25.25**	12.71	22.63	14.34	1.88	2.67	0.00	0.00	0.75	0.66
23/04/2015	25.00	12.45	13.00	11.45	**8.63**	5.19	2.63	2.39	0.88	1.05
01/05/2015	24.25	12.11	7.13	5.23	7.38	10.05	9.38	5.45	0.13	0.33
07/05/2015	23.50	11.27	2.50	1.41	6.00	6.12	13.88	8.71	1.00	1.12
13/05/2015	23.38	10.27	0.88	0.93	2.88	3.82	17.50	9.92	2.13	2.71
26/05/2015	23.75	12.49	1.00	1.22	0.13	0.33	**19.88**	14.09	2.75	2.17
10/06/2015	23.75	13.31	0.25	0.43	0.00	0.00	13.50	9.66	**10.00**	6.40
01/07/2015	14.13	7.69	0.00	0.00	0.00	0.00	7.38	4.44	6.75	4.24

Figure 4.7a & b. Close-up of aborted inflorescence (a) and aborted fruit (b).

The mean number of ripe fruits produced at the end of the recording season (i.e. 1st and 2nd July 2015, uplands and lowlands respectively) per 0.25m^2 (16.75 ± 21.48 lowland; 7.38 ± 4.44 upland; Figs. 4.5a and b, Tables 4.1a and b) was 19.94% (lowland) and 31.91% (upland) of the mean maximum amount of buds observed (84.0 ± 62.46 lowland; 23.13 ± 13.19 upland) and 57.00% (lowland) and 85.95% (uplands) of the mean amount of developing fruits observed at the peak (47.88 ± 33.08 lowland; 19.88 ± 14.09 upland). Fruit set as a percentage of the mean maximum number of flowers recorded is 54.03% in lowland sites (31.00 ± 7.50) and 85.52% in upland sites (8.63 ± 2.63) where floral abundance was very low on any given date but fruit remained on the plant and less of them aborted once formed, resulting in the numbers being higher than the maximum number of flowers recorded at any given time. Although the actual numbers of fruit found in the uplands was significantly less than in the lowlands, a greater proportion of the buds and flowers resulted in fruit set but this was not statistically significant.

Table 4.1b. Fruit set at the end of the recording season (1st & 2nd July 2015) as a percentage of the mean maximum number of buds and flowers recorded (as per Table 4.1a).

		Mean max no.	% fruit set
lowland	Buds	84.0 ± 62.46	19.94
	Flowers	31.0 ± 7.5	54.03
	Fruit	16.75 ± 21.48	-
upland	Buds	23.13 ± 13.19	31.91
	Flowers	8.63 ± 2.63	85.52
	Fruit	7.38 ± 4.44	-

4.3.2. Pollination study

Bumblebees are the main visitors to *Arctostaphylos uva-ursi.* There were four common species of bumblebee observed visiting the flowers: *Bombus terrestris* Buff-tailed bumblebee*, B. lucorum* White-tailed bumblebee, *B. pascuorum* Common carder bee and *B. pratorum* Early bumblebee (Tables 4.3a and b; Figs. 4.8a to f). There was also one butterfly visitor: *Cupido minimus* Small blue and there were two species of shield bug observed on the outside of the flowers although these were not likely to be genuine visitors and were in fact possible nectar-robbers (Table 4.3a; Figs. 4.9a to c and Fig. 4.10a). Ants (a brown ant species) were also found on one flower at an upland site, apparently after having eaten through the corolla at its base, possibly to get at the nectar (Fig. 4.10b). All pollinator visitors and non-visitors observed during this study were recorded. In 2015 the number of pollinators observed on any one day, taking into account both visitors and non-visitors, were lower than the numbers observed in 2013 and 2014 despite observation effort having increased in 2015 (Table 4.4). Approximately the same observation time was put in at lowland (330 minutes) and upland (300 minutes) sites; bumblebees were seen in the uplands but mainly appeared to be carried along by the breeze; on one date only (23rd April) in 2015 two individuals of *B. lucorum* visited flowers of *A. uva-ursi* – one bumblebee visited two flowers, and the other only visited one (Table 4.3b). The lowland sites had only 8 visitors in 2015 – one individual of *B. pratorum* visited 8 flowers (5th April), two individuals of *B. pratorum* visited 24 and 11 flowers, respectively (12th April), and again one individual of *B. pratorum* visited 4 flowers (19th April) and on the same date the butterfly *C. minimus* visited one flower, the shield bug *Palomena prasina* visited two flowers and two individuals of *Dolycoris baccarum* both visited one flower, but these shield bugs may have been robbing nectar.

Figures 4.8a to f. Bumblebee pollinators on *A. uva-ursi.* (a) *Bombus terrestris* Buff-tailed bumblebee queen; (b) *B. pratorum* Early bumblebee – side view and (c) top view; *B. lucorum* White-tailed bumblebee – (d) side view and (e) front view; and (f) *B. pascuorum* Common carder bee.

Figures 4.9a to c. Non-bumblebee visitors on *A. uva-ursi:* (a) *Cupido minimus* Small blue butterfly; (b) *Dolycoris baccarum* Hairy shield bug; and (c) *Palomena prasina* Green shield bug.

Figures 4.10a & b. (a) *Palomena prasina* Green shield bug appears to have been nectar-robbing – inset is a close up of a hole at the base of the corolla near the nectaries; and (b) exposed anthers and ovary after corolla was apparently eaten by ants (species unknown).

Table 4.3a. Records of observations of insect visitors to *Arctostaphylos uva-ursi* flowers in the study area and the number of flowers visited during each observation period of 20-30 minutes. Each record refers to a **single** individual of that species. Non-visitor species were also recorded (with zero inflorescences visited). Observation periods where no pollinators were seen are included in the table. In 2013 and 2014 observations were only carried out in the lowland site CM. Inflorescence (infl.) count is given.

Date	Site	Order	Family	Species	Obs. time (min)	Infl. no. per $0.25m^2$	No. infl. visited
19/04/2013	CM	Lepidoptera	Pieridae	*Gonepteryx rhamni*	30	not counted	0
19/04/2013		Hymenoptera	Apidae	*Bombus lucorum*			0
19/04/2013		Hymenoptera	Apidae	*B. pascuorum*			0
19/04/2013		Hymenoptera	Apidae	*B. terrestris*			0
19/04/2013		Lepidoptera	Pieridae	*G. rhamni*			0
19/04/2013		Lepidoptera	Nymphalidae	*Aglais io*			0
23/04/2013	CM	Hymenoptera	Apidae	*B. pascuorum*	30	158	5
23/04/2013		Hymenoptera	Apidae	*B. terrestris*			14
23/04/2013		Hymenoptera	Apidae	*B. pascuorum*			3
23/04/2013		Lepidoptera	Pieridae	*G. rhamni*			0
23/04/2013		Hymenoptera	Apidae	*B. lucorum*			13
23/04/2013		Hymenoptera	Apidae	*B. pratorum*			0
23/04/2013		Hymenoptera	Apidae	*B. pratorum*			0
23/04/2013	CM	Hymenoptera	Apidae	*B. pascuorum*	30	133	6
23/04/2013		Hymenoptera	Apidae	*B. pascuorum*			2
23/04/2013		Hymenoptera	Apidae	*B. terrestris*			11
23/04/2013		Hymenoptera	Apidae	*B. lucorum*			0
01/05/2013	CM	Hymenoptera	Apidae	*B. lucorum*	20	123	2
01/05/2013		Lepidoptera	Nymphalidae	*A. io*			0
01/05/2013		Hymenoptera	Apidae	*B. pascuorum*			8
01/05/2013		Hymenoptera	Apidae	*B. terrestris*			3
01/05/2013		Hymenoptera	Apidae	*B. pascuorum*			0
01/05/2013		Hymenoptera	Apidae	*B. lucorum*			0
14/04/2014	CM	Hymenoptera	Apidae	*B. terrestris*	30	98	2
14/04/2014		Hymenoptera	Apidae	*B. pratorum*			1
14/04/2014		Hymenoptera	Apidae	*B. pascuorum*			1
14/04/2014		Hymenoptera	Apidae	*B. lucorum*			0
14/04/2014		Hymenoptera	Apidae	*B. terrestris*			0
14/04/2014		Hymenoptera	Apidae	*B. terrestris*			0
14/04/2014		Hymenoptera	Apidae	*B. lapidarius*			0
14/04/2014	CM	Hymenoptera	Apidae	*B. pratorum*	30	24	10
14/04/2014		Hymenoptera	Apidae	*B. pratorum*			1
14/04/2014		Hymenoptera	Apidae	*B. pratorum*			21
23/04/2014	CM	Hymenoptera	Apidae	*B. terrestris*	20	147	2
23/04/2014		Hymenoptera	Apidae	*B. pascuorum*			3
23/04/2014		Hymenoptera	Apidae	*B. lucorum*			4
23/04/2014		Hymenoptera	Apidae	*B. lucorum*			4
23/04/2014		Hymenoptera	Apidae	*B. pascuorum*			3
23/04/2014		Hymenoptera	Apidae	*B. lucorum*			15
23/04/2014		Hymenoptera	Apidae	*B. pascuorum*			2
23/04/2014		Hymenoptera	Apidae	*B. lucorum*			5
23/04/2014		Hymenoptera	Apidae	*B. pratorum*			4
23/04/2014		Hymenoptera	Apidae	*B. lucorum*			0
23/04/2014		Hymenoptera	Apidae	*B. pascuorum*			0
23/04/2014		Hymenoptera	Apidae	*B. lucorum*			0
23/04/2014		Hymenoptera	Apidae	*B. pratorum*			0

Table 4.3b. Records of observations of insect visitors to *Arctostaphylos uva-ursi* flowers in the study area and the number of flowers visited during each observation period of 30 minutes. Each record refers to a single individual of that species. Non-visitor species were also recorded (with zero inflorescences visited). Observation periods where no pollinators were seen are included in the table. In 2015 observations were undertaken at all four phenology study sites: lowland sites CM and CT; upland sites CS and CB. Inflorescence (infl.) count is given for the highest count of the four quadrats per site (see methodology) and this is where observations took place.

Date	Site	Order	Family	Species	Obs. time (mins)	Infl. no. per $0.25m^2$	No. infl. visited
05/04/2015	CM	Hymenoptera	Apidae	*B. pratorum*	30	63	8
05/04/2015		Hymenoptera	Apidae	*B. lucorum*			0
05/04/2015		Hymenoptera	Apidae	*B. pascuorum*			0
05/04/2015		Hymenoptera	Apidae	*B. lapidarius*			0
05/04/2015	CT	No visitor			30	2	0
09/04/2015	CT	No visitor			30	7	0
12/04/2015	CM	Hymenoptera	Apidae	*B. pratorum*	30	144	24
12/04/2015		Hymenoptera	Apidae	*B. pratorum*			11
12/04/2015		Hymenoptera	Apidae	*B. lucorum*			0
16/04/2015	CB	No visitor			30	8	0
16/04/2015	CS	No visitor			30	2	0
19/04/2015	CT	No visitor			30	93	0
19/04/2015	CM	Hymenoptera	Apidae	*B. pratorum*	30	49	4
19/04/2015		Lepidoptera	Lycaenidae	*Cupido minimus*			1
19/04/2015		Hemiptera	Pentatomidae	*Dolycoris baccarum*			1
19/04/2015		Hemiptera	Pentatomidae	*D. baccarum*			1
19/04/2015		Hemiptera	Pentatomidae	*Palomena prasina*			2
23/04/2015	CS	Hymenoptera	Apidae	*B. lucorum*	30	14	2
23/04/2015		Hymenoptera	Apidae	*B. lucorum*			1
23/04/2015	CB	No visitor			30	16	0
26/04/2015	CT	No visitor			30	77	0
30/04/2015	CT	No visitor			30	20	0
30/04/2015	CM	No visitor			30	7	0
01/05/2015	CB	No visitor			30	4	0
01/05/2015	CS	No visitor			30	29	0
07/05/2015	CB	No visitor			30	2	0
07/05/2015	CS	Hymenoptera	Formicidae	Ants (sp. unknown)	30	17	1
10/05/2015	CT	No visitor			30	3	0
10/05/2015	CM	No visitor			30	2	0
13/05/2015	CS	No visitor			30	11	0
26/05/2015	CS	No visitor			30	1	0

Table 4.4. Summary of observation effort and numbers of insect visitors to *Arctostaphylos uva-ursi* in 2013, 2014 and 2015. The total number of pollinators observed includes individuals that did not visit any flowers.

Year	Total observation effort (mins)	Total no. observation periods	No. obs periods with visitors	No. obs periods with no visitors	Total no. of visitors	Total no. of pollinators observed
2013	110	4	3	1	10	23
2014	80	3	3	0	15	23
2015	630	21	5	16	11	15
2015 lowland	330	11	3	7	8	12
2015 upland	300	10	2	8	3	3

4.3.3. Breeding systems and fruiting patterns study

Ripe fruit were produced on both the open pollinated and pollinator-excluded bagged inflorescences suggesting that self-pollination is occurring in *A. uva-ursi* populations in the Burren. However this would require further testing, since tiny invertebrates such as thrips may have gained access to some bagged inflorescence and may have acted as pollen vectors, as they do elsewhere (Garcia-Fayos and Goldarazena, 2008). Nonetheless, the total number of fruit collected was greater from the open pollinated: 12/20 compared to the bagged pairs: 9/20 (Tables 4.5a and b): of the 20 paired inflorescences at each site, only 3 bagged and 2 open inflorescences retained fruit at CM, 2 bagged and 1 open retained fruit at CB, 2 bagged and 2 open retained fruit at CT and 2 bagged and 7 open inflorescences retained ripe fruit at CS. The average number of seeds per fruit was 6.17 ± 0.98 for bagged fruit and 6.40 ± 1.14 for open fruit (Table 4.5a and b) and from the pilot study (Appendix 4.2, Table 4.1) 6.53 ± 1.42 (bagged) and 6.70 ± 1.30 (open). The total number of: fruit-bearing inflorescences were 9 out of 80 (bagged) and 12 out of 80 (open), 11.25% and 15% respectively; fruit collected was 15 (bagged) and 24 (open); seeds collected was 93 (bagged) and 153 (open). The differences between bagged and open totals and between upland and lowland were not statistically significant (Mann-Whitney test: seeds p = 1.000; fruit p = 0.4359), despite the fact that many more fruit had reached maturity at one upland site (CS) in the open inflorescences than for any of the other inflorescences in the study (Table 4.5b).

Table 4.5a. Fruit and seed set for inflorescences with visitor-excluding mesh bags (bagged) and paired unbagged open pollinated (open) inflorescences at two sites in the study area in 2015. Sites CM and CT are in the lowland east Burren (Fig. 4.1).

site	bagged (20 per site)	no. of fruit collected per inflorescence	no. of seeds per fruit	open (20 per site)	no. of fruit collected per inflorescence	no. of seeds per fruit
CM	1	0		1	0	
Lowland	2	0		2	3	6; 6; 6
	3	0		3	0	
	4	0		4	0	
	5	0		5	0	
	6	0		6	0	
	7	0		7	1	5
	8	0		8	0	
	9	1	5	9	0	
	10	1	5	10	0	
	11	0		11	0	
	12	0		12	0	
	13	0		13	0	
	14	1	6	14	0	
	15	0		15	0	
	16	0		16	0	
	17	0		17	0	
	18	0		18	0	
	19	0		19	0	
	20	0		20	0	
CT	1	0		1	0	
Lowland	2	0		2	0	
	3	0		3	0	
	4	0		4	0	
	5	0		5	0	
	6	0		6	0	
	7	0		7	0	
	8	0		8	2	6; 7
	9	0		9	0	
	10	1	7	10	0	
	11	3	7; 7; 6	11	0	
	12	0		12	0	
	13	0		13	0	
	14	0		14	0	
	15	0		15	1	7
	16	0		16	0	
	17	0		17	0	
	18	0		18	0	
	19	0		19	0	
	20	0		20	0	
No. fruit & seeds collected (lowland CM & CT)		**7**	**43**		**7**	**43**

Table 4.5b. Fruit and seed set for inflorescences with visitor-excluding mesh bags (bagged) and paired unbagged open pollinated (open) inflorescences at two sites in the study area in 2015. Sites CB and CS are in the upland west Burren (Fig.4.1).

site	bagged (20 per site)	no. of fruit collected per inflorescence	no. of seeds per fruit	open (20 per site)	no. of fruit collected per inflorescence	no. of seeds per fruit
CB Upland	1	0		1	0	
	2	0		2	0	
	3	0		3	0	
	4	0		4	0	
	5	0		5	0	
	6	3	7; 6; 6	6	0	
	7	0		7	3	7; 8; 8
	8	0		8	0	
	9	0		9	0	
	10	0		10	0	
	11	1	7	11	0	
	12	0		12	0	
	13	0		13	0	
	14	0		14	0	
	15	0		15	0	
	16	0		16	0	
	17	0		17	0	
	18	0		18	0	
	19	0		19	0	
	20	0		20	0	
CS Upland	1	0		1	0	
	2	0		2	0	
	3	0		3	0	
	4	0		4	0	
	5	0		5	0	
	6	0		6	4	6; 5; 6; 7
	7	0		7	2	7; 6
	8	0		8	0	
	9	0		9	2	5; 7
	10	1	7	10	1	6
	11	0		11	0	
	12	0		12	0	
	13	0		13	1	8
	14	0		14	0	
	15	0		15	0	
	16	0		16	3	6; 6; 6
	17	3	6; 5; 6	17	0	
	18	0		18	1	6
	19	0		19	0	
	20	0		20	0	
No. fruit & seeds collected (upland CB & CS)		**8**	**50**		**17**	**110**
Total fruit count		**15**			**24**	
Total no. inflorescences with fruit (out of 80)		**9**			**12**	
Mean no. fruit per infl.		**0.19**			**0.30**	
St. Dev.		**0.62**			**0.82**	
Total seed count			**93**			**153**
Mean no. seeds per fruit			**6.17**			**6.40**
St. Dev.			**0.98**			**1.14**

4.4 Discussion

4.4.1. Flowering patterns

At the lowland sites flowering occurred approximately 10 days earlier in 2015 than at the upland sites – this may be linked to differences in temperature as it is on average 1° C cooler in summer months in the uplands (Chapter 2) at approx. 160 m above sea level than it is in the lowlands (approx. 35 m a.s.l.). The average temperature for March 2015 was 6.65°C in the lowland sites and 5.58°C in the upland sites; in April 2015 it was 9.97°C (lowlands) 8.57°C (uplands); in May 2015 it was 11.13°C (lowlands) and 9.31°C (uplands) and in June 2015 it was 14.32°C (lowlands) and 11.93°C (uplands). Lowland sites tended to have a greater density of inflorescences and therefore greater floral abundance than the upland sites. However while the numbers of fruit set was lower in the uplands, the relative success rate was in fact greater in the uplands than the lowlands: 31.91% compared to 19.94%. *Arctostaphylos glauca* (Californian species) was found to produce greater numbers of fruit per inflorescence on the north-facing side of the shrub compared to the south-facing side (Brum, 1975) – this may be likened to the difference in temperature between those sites, related to aspect.

4.4.2. Pollination study

The number of pollinators observed was quite small, possibly related to the early flowering time of *Arctostaphylos uva-ursi* when the numbers of bumblebees are relatively low and the main bumblebees on the wing would be recently emerged overwintered queens, worker bees emerge later in late spring/early summer (NBDC, 2009, Deenihan, 2011, Prŷs-Jones and Corbet, 2014). In the latter half of the flowering period of *A. uva-ursi* when other more abundant floral resources typically become available pollinators may choose those species preferentially over *Arctostaphylos;* this has been observed with *A. uva-ursi* populations in Banff National Park, Alberta, Canada (Mosquin, 1971), and also occurs in similar species of *Arctostaphylos* in California (Brum, 1975). In 2015 when observations were carried out in both upland and lowland sites, of the 15 pollinators recorded, 12 individual visitors to *A. uva-ursi* were observed at the lowland sites, and only 3 at the upland sites. As observed for flowering times and abundance, the lower temperatures as well as the more exposed nature of the upland sites may combine to reduce the number of passing pollinators. In a brief study in April 2018, the relative low breeze and warm sun at the Caherbullog (CB) upland site seemed to induce more bumblebees to visit patches of *A. uva-ursi* than when the sun disappeared or the breeze became stronger. The warm, still air may also help the bees smell the flowers, as they seemed to fly directly to sometimes quite hidden inflorescences (M. Sheehy Skeffington pers. comm. and Appendix 4.3).

4.4.3. Breeding systems and fruiting patterns study

Despite the low number of pollinators, particularly in the uplands, the rate of fruit set was relatively high, even where larger pollinators were excluded by bagging the inflorescences. This suggests that pollination success is not reliant on bumblebees and that another vector must be at play and/or that there is a degree of self-pollination occurring. It is possible that thrips and/or ants may play an important role in pollen transfer, particularly in the relative absence of bumblebees, as observed in Spanish populations of *Arctostaphylos uva-ursi* (Garcia-Fayos and Goldarazena, 2008). Thrips pollination by *Ceratothrips* (*Taeniothrips*) *ericae* has also been documented in *Erica tetralix* populations in the Botanical Gardens, Copenhagen (Hagerup and Hagerup, 1953), and in *Calluna vulgaris* in arctic regions (Hagerup 1950, cited in Hagerup and Hagerup, 1953), but curiously they were not found in the flowers of other Ericaceous plants, namely *A. uva-ursi,* by these authors (Hagerup and Hagerup, 1953).

If out-crossing is facilitated by thrips it would be by the females, as unusually, they are winged and move between flowers while the males are rare and wingless and tend to remain within a single flower for the duration of their life cycle (Hagerup and Hagerup, 1953, Proctor and Yeo, 1973, Garcia-Fayos and Goldarazena, 2008). In eastern Spain seven species of thrips including *Ceratothrips ericae* and *Haplothrips setiger* (these two species accounted for 95% of individuals found) were found inside the flowers of *A. uva-ursi* and through a thrips-exclusion experiment were found to contribute significantly to its pollination success: 13% of thrips-excluded inflorescences bore fruit while 30% of thrips-only inflorescences were fruit bearing compared with 60% of open-pollinated (Garcia-Fayos and Goldarazena, 2008). At the Burren study sites thrips were not observed inside *A. uva-ursi* flowers, even during a specific investigation of flowers for thrips in April 2018 (Appendix 4) although the species *C. ericae* is known to occur in Ireland (O'Connor, 2008), the emergence time is not known.

The percentage of inflorescences bearing fruit was not significantly different between treatments: 11.25% for pollinator-excluded compared to 15% of for open-pollinated inflorescences. It may be important to bear in mind however that the exclusion bags were of 1mm mesh size and therefore ants were able to gain access to the flowers and if thrips were present they would probably have gained access also as thrips-exclusion bags require a mesh size of 250 µm (Garcia-Fayos and Goldarazena, 2008).

While the percentage of inflorescences bearing fruit was similar between treatments, there was a greater number of fruit collected from open pollinated inflorescences than from pollinator excluded ones, suggesting that fruit set is higher when flowers are out-crossed; and the number of fruit per inflorescences was also higher but these were not statistically significant. There was no significant difference in the mean seed set of open pollinated and pollinator-excluded flowers.

At lowland sites fruit set was the same for open pollinated and pollinator excluded inflorescences, however at upland sites the rate of fruit set was greater for open pollinated inflorescences compared to their pollinator excluded pairs although this was not statistically significant.

4.5 Conclusions

Though the scope of this study was limited, there were some interesting findings: *Arctostaphylos uva-ursi* flowers are being pollinated in the Burren populations, in particular those in the lowlands are being visited by bumblebees. Fruit set, however seems to be also occurring via self-pollination. Although more pollinators were observed in the lowlands, and flowers were more abundant, the relative numbers of fruit reaching maturity was greater in the uplands. In fact the proportion of fruit set to buds in the upland sites was nearly twice that of the lowland sites. Self-pollination may be in part facilitated by thrips, increasing the rate of fruit set, but so far this has not been demonstrated. As outcrossing is occurring it is likely that populations are not solely clonal but curiously seedlings were not seen throughout the study area, nor was any frugivorous activity, both of which presumably do occur. As even the very rare transfer of genetic material through outcrossing is sufficient to maintain genetic diversity (Proctor and Yeo, 1973), the presence of effective pollinators may play an important role in the potential for long-term genetic survival of the *Arctostaphylos* populations in the Burren.

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Chapter 5. General discussion

5.1 Introduction

Heathlands are an important habitat type, both in terms of nature conservation (Fagúndez, 2013) and as cultural landscapes (Krzywinski et al., 2009): they are living evidence of a landscape formed by humans through the removal of woodlands and subsequently maintained by traditional farming practices (Gimingham, 1972, Webb, 1986, Kvamme et al., 2004). Heathlands were previously extensive across Western Europe but currently only a small proportion remains (Webb, 1998) and where they do occur they tend to be highly fragmented and largely under threat from various factors: change of land-use, eutrophication, pollution and climate change (Fagúndez, 2013). In order to conserve some of the remaining intact heathlands of conservation value within EU member states, seven different heathland types (and numerous sub-types) are included on the list of Annex I habitats (European Commission, 2013) in the EU Habitats Directive (Council Directive 92/43/EEC). Two of these are important in the context of this thesis: European dry heaths (4030) and Alpine and Boreal heaths (4060), both of which have two distinct varieties within Ireland. Those relevant to this study are calcareous dry heaths and the Burren alpine heaths, as sub-communities of EU habitats 4030 and 4060 respectively (NPWS, 2013a, NPWS, 2013b, Wilson and Fernández, 2013, Perrin et al., 2014).

5.2 The rarity and vulnerability of the Burren *Arctostaphylos* – rich heaths

The heath communities described in this study are quite rare in Ireland and the distribution of *Arctostaphylos uva-ursi*, one of the key species, seems to be decreasing within Ireland. Historical records suggest a greater abundance of the species on a local and country-wide scale (Webb and Scannell, 1983, Webb et al., 1996), and as an arctic-montane species it is at the southern edge of its range in Ireland and therefore especially vulnerable. Another key species, *Empetrum nigrum* is more widespread throughout Ireland (Webb et al., 1996), and in the Burren particularly on higher ground (Webb and Scannell, 1983), however it is not found in the Burren lowland heaths. Therefore the lowland heaths described here, in particular, are rare in the Buren and therefore especially so nationally and as such are important in terms of conservation.

5.2.1. The *Arctostaphylos* - heath communities

The lowland heaths are distinctive from the upland communities; the *Arctostaphylos – Juniperus* heaths are defined by a high cover of prostrate *Juniperus communis* together with *Arctostaphylos uva-ursi* and calcareous grassland species on rocky pastures. This community is unusual in that although it has a lower presence of D*ryas octopetala*, it may still be defined as alpine heath (4060) due to the predominance of the dwarf shrubs *Juniperus* and *Arctostaphylos* (Perrin et al., 2013), and it also has affinities to *Festuco – Brometalia* dry calcareous grasslands (6210).

There are two upland communities that are quite dissimilar to each other. The *Calluna – Arctostaphylos* heaths are more acidic and found on deeper somewhat peaty soils above 170m altitude; they have relatively tall vegetation and were the target of the restorative cutting trials in chapter 3, and related most to the calcareous dry heaths (4030) classification but also had elements of the Burren alpine heaths (4060). The second upland plant community identified, the *Dryas – Empetrum* heaths are found on shallower mineral-rich calcareous soils with short vegetation between 140m and 310m altitude, these have affinities with calcareous dry heaths (4030), Burren alpine heaths (4060) and elements of *Festuco – Brometalia* (6210).

Finally, the *Arctostaphylos – Sesleria* community, located both the uplands and lowlands and somewhat more widespread within the region, was found in rocky pastures with shallow calcareous soils and numerous grassland species together with dominant *Arctostaphylos, Dryas* and *Calluna;* it has affinities to both the *Festuco – Brometalia* (6210) and the calcareous dry heaths (4030).

Overall the lowland *Arctostaphylos – Juniperus* heaths appear to be the rarest community type of the four described here. They are in danger of being overlooked and generally these *Arctostaphylos* – rich heaths are vulnerable to threats by and large arising from a lack of grazing.

5.2.2. The *Arctostaphylos* – heaths in the Burren's Special Areas of Conservation (SACs)

The SAC (Special Area of Conservation) site synopsis for Moneen Mountain (000054) describes the *Arctostaphylos* (Bearberry) heath as 'well-developed in the north of the site'; and at the East Burren Complex (001926) it is said to occur on the 'western shores of Lough Bunny, at one of its few inland lowland locations'; several attempts were made to locate these areas of heath but they were not found. At the Castletaylor Complex (000242), while *Arctostaphylos* heath was found at Caranavoodaun it was only of sufficient size for two relevés (2m x 2m), and at the Attyslaney woods (Coillte LIFE woodland restoration site) the heath habitat size was also very small (two relevés). There is no indication in the SAC site synopses of the extent of this heath when the sites were designated, so it is difficult to determine if a recent decline in extent has occurred or not. While at the other lowland sites Lough Fingall Complex (000606) and Ardrahan Grasslands (002244) the areas of heath were seen to be fairly extensive, but at both sites they appeared to be under threat by encroaching scrub (primarily *Corylus avellana*) and *Molinia caerulea*, respectively and some clearance of rocky land. Within the Black Head – Poulsallagh Complex (000020) there are areas of 'well developed limestone heath… with *Arctostaphylos…* to the north and north east of the site on higher ground'; this heath also occurs on the hills between Black Head and Cappanawalla to the east, and Feenagh, above the Caher valley to the south of the site; mostly occurring above 160m.

While the heaths were present at this last site it would appear that these SAC site descriptions may not have been updated or backed up by ground-truthing in some time and it is possible that some of the habitats they were designated for may have declined in extent or in quality since that time. The extent of *Arctostaphylos uva-ursi* is known to be declining (Webb and Scannell, 1983, Webb et al., 1996) and it appears this decline may even be occurring in the designated sites mentioned above but this is not conclusive and needs verifying. In the case of the upland sites under-grazing may be a local problem (Chapter 3), but elsewhere it is not clear why a decline in the plant community might have occurred, if it did.

5.3 Threats to the Burren *Arctostaphylos* – rich heaths

The main threats to the Burren limestone heathlands and grasslands are under-grazing, overgrazing, and scrub encroachment; land reclamation and fertilizer addition are lesser threats (Bohnsack and Carrucan, 1999). One of the foremost conservation issues for these vulnerable heath habitats in the Burren region is that of maintaining them in good condition through management. Where they have been poorly managed, generally due to under-grazing, there have been significant levels of encroachment by more vigorous species to the point where there is a pressing need for the management of these sites to be addressed. Other threats include that of climate change, which is predicted to impact notably on arctic-montane species in oceanic heathlands (Fagúndez, 2013).

5.3.1. Scrub encroachment and grazing

The greatest visible threat to the rare *Arctostaphylos* - rich heaths is that of encroachment resulting from under-grazing. This is of concern particularly in light of the findings regarding the possible decline in the distribution and extent of these heaths within SAC designated sites. This habitat loss as well as the loss of habitat condition appears to be occurring in lowland areas for the most part but low shrub encroachment is also a threat at some upland sites. Dunford (2002) notes that many of the Burren's species-rich grasslands and limestone pavements have been replaced by species-poor habitats as a result of changes in the levels of land use - land abandonment and the intensification of land use. The prevention of such processes are paramount to the conservation of these important habitats.

In contrast to the present-day situation, in the mid-nineteenth century, when Ireland's population was at its peak, there was so little growth of woody species in the Burren that there was a widespread 'fuel famine' when people collected hazel branches, heath, dried fern and brambles to use for cooking (Dunford, 2002). Sods of heathy soil or peat were also cut to use for fuel and left to dry in stone structures called 'turf tiles' (Dunford, 2001). In a number of upland areas where *Arctostaphylos* heaths are present today these stone structures remain, posing the question as to what impact the cutting of turves may have had on the species and related habitats in terms of limiting or expanding its range? Since this time, and following the drastic decline of the human population (by over 60%) as well as a decrease in livestock numbers in the region, scrub (in particular *Corylus*) has been on the increase (Kirby, 1981 cited in Keane, 1990). In the Burren the scrub threat from *Corylus*, on skeletal soils, is well documented; *Prunus spinosa* and *Crataegus monogyna* are more problematic on deeper soils (Dunford and Feehan, 2001). *Corylus* (and *P. spinosa*) was found to be more of an issue at lower altitudes and the threat from *Calluna* was much greater at higher altitudes, on deeper soils and where grazing pressure was lower (Parr et al., 2009). It is reasonable to assume that while *Corylus* was on the increase in the past century, so were other species such as *Calluna vulgaris*, especially in the Burren uplands. And in lowland heathlands in Britain the absence of grazing has resulted in increased scrub, bracken and *Molinia*, and has led to dwarf shrubs becoming tall and degenerate (Bullock and Pakeman, 1997). Here in the Burren the *Arctostaphylos* - heaths are under a similar threat.

Part of this research has focused on the cutting of tall mature-degenerate *Calluna vulgaris* as a restorative measure for the *Arctostaphylos* heaths. Besides *Corylus* and *Calluna* there are other threat species to consider: *Molinia caerulea* and *Pteridium aquilinum* (bracken). At present bracken did not appear to be a big problem on the heaths studied, although there was an increase in its cover following cutting in spring in this study, and as a known invader of heathlands (Måren et al., 2008), it is one to keep an eye on. Parr et al. (2009) found low levels of bracken throughout their survey sites and anecdotal evidence suggests that it may have increased following cutting of *Calluna*. *Molinia* was widespread in many of the heathland sites surveyed as part of this research and measures for its control, as well as the control of bracken, are discussed below.

Besides management issues climate change is another big concern for these rare heaths, it is predicted to have a greater effect on species with an arctic-montane distribution than other groups of species, and the effects will be most noticeable in species at the edge of their range (Coll et al., 2013). Thus it was important to establish the level of vulnerability of *Arctostaphylos uva-ursi,* one of the key species in these habitats, in terms of its reproduction strategies, pollination, fruit set and phenology.

5.3.2. Potential impacts of climate change

Western Ireland experiences an oceanic climate meaning that it has mild temperatures throughout the year with high levels of cloud cover, humidity and rainfall, and high wind speeds are common (Hodd and Sheehy Skeffington, 2011). Climate change is predicted to affect Ireland in the following ways: temperature rises of approximately 3-4°C by the end of the century, resulting in lower incidences of frost particularly in oceanic upland areas, wetter winters and drier summers (Hodd and Sheehy Skeffington, 2011, Coll et al., 2013). Climate change has already been the cause of changes in the phenology of species and shifts in the geographic range of species upwards and northwards (Walther, 2003).

Boreal-montane and arctic-montane species and species with disjunct distributions were found to be among those most at risk from the potential effects of climate change in Ireland (Coll et al., 2013) as they tend to be stress tolerators and poor competitors (Hunt et al., 2004). Many species with these attributes tend to be restricted to the uplands and have a poor dispersal ability, or reproduce vegetatively (Hodd and Sheehy Skeffington, 2011). It is unlikely that they will be able to colonise suitable new areas given the rate at which climate change is predicted to occur (Coll et al., 2013). The loss of species is under greater threat where genetic diversity is low, for example in populations of rare species, clonal species are particularly vulnerable to disturbances (Callaghan et al., 1992).

The effects of climate change also has knock-on effects in terms of plant-pollinator interactions. Warmer temperatures in spring have resulted in the early emergence of insects (Willmer, 2012). In many plant species bud burst and flowering times are also occurring earlier but others are more affected by photoperiod than temperature (Walther, 2003), and some plants may not flower in time to avail of pollination services; early flowering species were found to be the most affected by warming (Fitter and Fitter, 2002) and of these woody species were affected less than non-woody species (Post and Stenseth, 1999 cited in Walther, 2003). The shift in species geographic ranges is a phenomenon observed in insect species as well as plants, the insects have a quicker response time and any shift in range may prove to be more deleterious to plant pollination success than phenological mismatches (Willmer, 2012). The range of alpine and boreal heath habitats in Ireland is predicted to undergo shifts, with a potential gain of climate space in the northern part of the Island but much of the Burren region is predicted to undergo losses (Coll et al., 2016).

The range of *Arctostaphylos* in Ireland, as in Britain, has been observed to possibly be contracting (Webb and Scannell, 1983, Webb et al., 1996, Hill et al., 2004), this is worrying and might be due to climate effects: the potentially expanding range of species with southern distributions (Walther, 2003), and competition by more vigorous species, that respond positively to warmer temperatures may also be a factor in its displacement. *Juniperus communis*, particularly dwarf juniper, the prostrate subspecies *nana* (Syn. *alpina*) has been observed to be shifting upwards on mountainous regions of central Spain (Crawford, 2008), and this may also be a concern for the lowland populations in western Ireland. On the other hand the distribution of *Empetrum nigrum* is more frequent throughout Ireland, mostly found in the uplands but also on lowland bogs (Webb et al., 1996), thus it appears to be better adapted to a wider range of habitat conditions than *Arctostaphylos. Empetrum* is wind-pollinated (Bell and Tallis, 1973) and therefore not dependent on insects, thus it may be less at threat from changes in phenological patterns resulting from climate change, and its fruits have been observed in the Burren populations during this study. *Dryas octopetala* is an arctic-montane species (Elkington, 1971) restricted to the rocky limestone regions of Ireland, in particular the Burren, and some outlying areas for example in Fermanagh (Webb et al., 1996). Although for much of its geographical range it is found on high mountains, in the Burren, and west Scotland, it grows at sea-level (Elkington, 1971). Throughout most of the Burren it is abundant (Webb and Scannell, 1983), flowering profusely in late April or May and flowers are visited mainly by bees and Diptera, and to a lesser extent beetles and Lepidoptera (Elkington, 1971). Maximum summer temperatures are likely to be a limiting factor in the distribution of *Dryas* (Dahl, 1951 cited in Elkington, 1971) and therefore its range may shift northwards and upwards as a result of potential climate change (Walther, 2003).

5.4 Restorative measures under consideration to meet conservation objectives

In terms of climate change it is difficult to pinpoint remedial action but monitoring of these habitats and some of their species would be an important action to implement. It would also be beneficial to determine the genetic diversity of the Irish *Arctostaphylos uva-ursi* populations, and perhaps a number of other arctic-alpine or montane species as these are predicted to be most under threat in relation to climate change.

The more immediate actions that can be taken to restore these vulnerable habitats relate to management and largely to the control of species that are currently problematic or may become a problem in the future. The main species of concern, namely *Arctostaphylos, Dryas* and *Empetrum,* are all low-growing prostrate dwarf shrubs (Clapham et al., 1987) and therefore they are vulnerable to being out-competed for resources such as light by taller more vigorous species such as *Calluna vulgaris, Molinia caerulea* and *Corylus avellana.*

5.4.1. Control of problem species

At present, in the uplands, the main species in terms of its encroachment is *Calluna vulgaris* and its control was the main focus of chapter 3. Given the short time-scale of this study - the final year of survey was only 23 months and 19 months respectively after the cutting had been carried out - it yielded limited results in terms of regrowth. Nevertheless species richness and diversity increased in the cut plots, regardless of the cutting season, but not in the control plots. *Calluna* cover decreased in both cutting regimes as expected though the other species did not show an obvious trend. Overall *Arctostaphylos* had a higher cover in 2015 than in 2013, as did several species of forbs and the cover of exposed rock, but this could not be pinpointed to the cutting as this trend was observed in the control plots as well. Therefore it may have been influenced somewhat by weather conditions, since 2013 and 2014 were warmer and drier than usual and may have reduced the level of growth due to drought whereas 2015 was cooler and wetter than average (Met Éireann, 2017) and may have provided the conditions preferred by species adapted to this oceanic climate thereby enabling them to undergo increased growth.

However as mentioned above there are other potentially invasive species to consider here mainly *Pteridium aquilinum* (bracken) and *Molinia caerulea*. Bracken was not seen to be a big problem at present but it does have the potential to become dominant and it is desirable to prevent this from occurring by keep its growth in check. There did appear to be a decrease in bracken cover following autumn cutting but the levels were very low (<5% cover) throughout all plots. Trampling and grazing of the young shoots of bracken in summer or autumn by cattle or ponies may prevent its dominance by maintaining it in the juvenile stage (Gimingham, 1992, Crofts and Jefferson, 1999). But where an infestation does occur cutting has been effective; annual cuts in July over 6-8 years, or twice a year in June and July over a shorter period (Gimingham, 1992, Snow and Marrs, 1997).

Grasses can become dominant on heathlands both due to reduced grazing pressure and due to overgrazing (Gimingham, 1992). In the case of *Molinia* cutting in spring knocked back its growth while cutting in autumn had the opposite effect. This could be because the autumn cut would have removed the *Molina* litter, since it is a deciduous species and therefore increased light availability and subsequently its growth the following season also increased. *Molinia* growth can be addressed by light grazing between May and July when its fresh shoots are quite palatable, by cattle, ponies or horses; after this time it begins to die off and lose its nutritional value and digestibility (Welch, 1984, Backshall, 2001). Its grazing, particularly by cattle, has been shown to increase botanical diversity (Martin et al, 2013 cited in Glaves, 2015).

5.4.2. Reproduction and pollination of *Arctostaphylos uva-ursi*

Arctostaphylos uva-ursi offers pollen and nectar rewards to potential pollinators and is also self-fertile (Clapham et al., 1987, Knuth, 1909), however it reproduces poorly from seed, mainly undergoing vegetative reproduction (Remphrey et al., 1983b, Salemaa and Sievanen, 2002). It flowers from April to June in Burren populations; this is a little earlier than Britain where the flowering period is May to July (Clapham et al., 1987).

Presently in the Burren there are insects visiting the *Arctostaphylos* flowers, and the primary visitors are bumblebees, albeit at a low level but even this level of pollen transfer should ensure some genetic variability within the populations for the time being (Proctor and Yeo, 1973). Thrips were shown to play an important role in pollination in Spain (Garcia-Fayos and Goldarazena, 2008) but they were not observed in the *Arctostaphylos* flowers in the Burren (M Sheehy Skeffington pers. comm.). Higher numbers of insect visitors were observed on the flowers of lowland plants which also tended to have greater amounts of flowers; thus possibly upland populations are more clonal than lowland ones. Despite having lower number of flowers the rate of fruit set was somewhat higher at one upland site. Even in lowland sites pollinator numbers were quite low, and wild pollinators such as bumblebees are known to be declining largely due to habitat loss (Goulson et al., 2005, Fitzpatrick et al., 2007). The Burren is considered to be a refuge for pollinators given the low intensity farming methods employed in the region (Santorum and Breen, 2005, Deenihan, 2011) but even here, and particularly in the lowland areas where there is a greater number of residential dwellings and roads, there may be a need to conserve pollinators, and therefore increase the chances of out-crossing in rare species such as *Arctostaphylos uva-ursi.*

Seedlings were not observed in the field in this study, seed viability may be a factor, as may the presence or absence of the required soil mycorrhizae in terms of seedling establishment (Liston and Harrington, 2012), a phenomenon which occurs in orchid populations (Duffy et al., 2009).

5.5 Conclusions and future work

The rare heaths this research has focused on have been described floristically and related to their corresponding EU Annex I habitats: the most widespread type is found throughout both the Burren uplands and lowlands, the *Arctostaphylos – Sesleria* community with affinities to the calcareous variant of European dry heaths (4030) and as it is especially rich in calcareous grassland species, it also relates to the *Festuco – Brometalia* dry calcareous grasslands (6210). There were also two distinct upland communities, the *Calluna – Arctostaphylos* heaths occurring on deeper more acidic peaty soils corresponds most to the calcareous dry heaths (4030), and the *Dryas – Empetrum* heaths has elements of alpine heaths (4060), dry heaths (4030) and *Festuco – Brometalia* (6210).

The lowland *Arctostaphylos – Juniperus* heaths are the community with the closest affinity to alpine heaths (4060), despite their relatively low cover of *Dryas octopetala,* because of the presence of *Juniperus* and *Arctostaphylos*; the community is therefore distinct and possibly unique to the Burren. They are the rarest of the heaths detailed in this study and seem to be also the most vulnerable of the heaths described here, in spite of their location within SAC designated areas. They are situated in the Burren lowlands and yet apparently they are managed as winterage pastures, a practice which is mainly used in upland areas. This low level of grazing is insufficient to prevent the invasion of problem species, as evidenced by the condition of many of the sites, where *Corylus avellana* and *Molinia caerulea* are the main species of concern. This is of concern and needs to be addressed with some urgency before any loss of species occurs and in order to prevent further habitat degradation. At present some of the farmers with land in the aforementioned SACs are participating in the Burren Programme: two in the Ardrahan grasslands, one in Lough Fingall, having joined this year and last year, and numerous farmers in the East Burren complex, some recently enlisted while others are participants since the BurrenLIFE pilot phase in 2005), currently none of the Castletaylor SAC farmers have signed up (B. Dunford pers. comm.); and whether or not the heathland areas are included is not clear. If not, it would be recommended that these areas are targeted for inclusion in the Programme and that the *Corylus* and *Molinia* issues are tackled through a longer grazing period with summer grazing and/or scrub removal.

The *Calluna* cutting trials were somewhat inconclusive over the time-scale of this study in terms of recommending when to cut regarding the regrowth of *Dryas* and *Arctostaphylos*. However, cutting in early spring resulted in a greater difference to the control than cutting in autumn; depending on whether *Molinia* or *Pteridium* is present in the site, a spring or autumn cut may be more favourable to control each species respectively.

The pollination studies confirmed that *Arctostaphylos uva-ursi* is very likely being out-crossed and the primary visitors are bumblebees. Fruit set was higher in open-pollinated flowers than in pollinator-excluded ones suggesting that there is some genetic diversity in the populations where out-crossing is taking place. However, the lack of observed seedlings at any site raises the question as to whether these out-crossed fruits formed actually produce mature plants. This is another matter for investigation and further suggestions for future research follow.

Additional more thorough investigations are required in terms of mapping of the distribution and extent of *Arctostaphylos uva-ursi* and the related heath habitats. The relevé data base for this study forms a basis for monitoring the long-term presence of the alpine heath species, but detailed mapping of smaller more vulnerable sites would help determine possible future decline of these plant communities. Re-surveys could include methods for determining the health of the habitats and monitoring the level of potential threats. Follow-up vegetation sampling is required at sites where cutting took place in order to identify the changes in species cover and composition over a longer timescale than was possible given the limitations of this study. While the management of these upland sites is being addressed by the farmers and managers in the Burren Programme it is important to flag any sites that are not in this farming for conservation programme and are therefore in danger of deteriorating if not managed properly, namely the aforementioned lowland SAC sites.

Further pollination studies could be undertaken, in particular to determine conclusively whether thrips are present and functioning as pollinators of *Arctostaphylos* throughout the flowering season in the Burren, in combination with follow-up pollinator exclusion experiments using thrip-excluding mesh in addition to the 1mm mesh bags used in the study here. An investigation into whether the lack of *Arctostaphylos* seedlings in the field is due to the seeds not being viable or to a lack of the mycorrhizal species associated with *Arctostaphylos* would be an interesting follow-on research project, this should be carried out in conjunction with seed viability testing and germination trials. It would also be interesting to undertake genetic sampling of the species, both of Irish populations and world-wide, especially in order to determine the genetic diversity and origins of the relict populations.

The prime habitats of the Burren are maintained through the low intensity traditional farming methods that are practiced here. In some areas where farmers were restricted with grazing times or stock numbers, whether this was due to a lack of access, water supply or due to limitations relating to the prescriptions of REPS (Rural Agricultural Protection Scheme), scrub encroachment resulted. Previous research has focused on the upland areas of the Burren, and this study focused the cutting trials in the uplands areas of overgrown *Calluna,* however scrub encroachment is currently also of concern in the eastern lowland areas and this study has found lowland the *Arctostaphylos* – heaths to be under threat from *Corylus* and *Molinia.* It is essential that these rare and vulnerable habitats be maintained, particularly in site where their coverage is fairly extensive, and in order to do so spring or early summer grazing is recommended, a practice that is already underway in some winterage pastures within the Burren Programme. It would also be beneficial to develop a ‘habitat health’ scoring system for these heaths, as is currently used in the Burren Programme for species-rich grasslands, together with monitoring following any changes in management, such as changes in grazing patterns and/or cutting of scrub species.

5.6 References

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Chapter 6. Supplementary Annex.

***Arctostaphylos* heath community ecology in the Burren, Western Ireland. Sarah Ann Hanrahan and Micheline Sheehy Skeffington. Published in *Ecological Questions* Volume 21/2015.**

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Arctostaphylos heath community ecology in the Burren, Western Ireland

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Abstract. *Arctostaphylo-Dryasetum* is a rare sub-type of Alpine and Boreal Heath which is known to occur only in Ireland on the limestone karst Burren, in County Clare. Relevés were taken across the Burren region and three groups were distinguished: *Empetrum nigrum* group; *Erica cinerea* group, *Juniperus communis* group. Altitude and soil conditions were found to be the main ecological factors responsible for the variation in the data set, especially pH, and the organic and mineral content. Winter grazing appears to maintain this habitat. In some areas *Calluna vulgaris* has encroached on the rarer plant species cutting trials are underway in an attempt to restore the habitat to good conservation status.

Key words: Alpine heath, *Arctostaphylos uva-ursi*, *Empetrum nigrum*, environmental variables, plant community.

1. Introduction

Alpine and Boreal heaths (EU Habitats Directive code: 4060) are a rare and protected habitat type in Europe and their management is a priority. There are two main subtypes of Alpine heath in Ireland: one is a community occurring at 350–400m on acidic slopes, dominated by *Calluna vulgaris* and characterised by dwarf shrubs, largely restricted to uplands in western counties Kerry, Galway (Connemara), Mayo and Donegal.

The other, the subject of this study, is the *Arctostaphylo-Dryadetum* where the presence of *Dryas octopetala* distinguishes it from other variants of this plant community and is only known to occur in Ireland in the limestone karst Burren, County Clare (NPWS, 2013). There it occurs on higher ground and in the 'low Burren' of south-east Galway and north Clare. *Arctostaphylos*-rich heaths form an important part of the vegetation on high ground in the Burren (Ivimey-Cook & Proctor, 1964; Webb & Scannell, 1983; Proctor, 2013) and are often associated with *Empetrum nigrum* (Parr et al., 2009). The objective of this study is to compare alpine heath plant communities associated with *A. uva-ursi* in the upland and lowland areas within the Burren region.

2. Study area: The Burren

From the Gaelic: *Boireann* meaning 'rocky place', the Burren is a region of karst landscape covering approximately 250km^2 of counties Clare and Galway on Ireland's mid-western seaboard. To the west the 'high Burren' is composed of terraced hills of 300–330m altitude and to the east the 'low Burren' limestone plains are just 20–30m in altitude. The Burren is internationally acclaimed for its unique assemblages of flora: the only place in the world where Arctic-Alpine and Mediterranean species grow side-by-side (Webb & Scannell, 1983).

The area has an oceanic climate, characterised by mild winters with few frosts, cool moist summers, high rainfall throughout the year and frequent strong winds (Webb & Scannell, 1983).This last factor is conducive to the presence of sclerophyllous species.

Figure 1. Example of lowland heath community with *Arctostaphylos uva-ursi* and exposed limestone

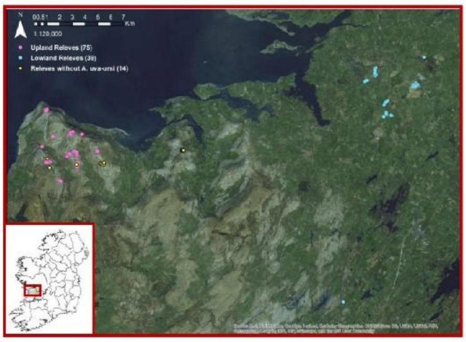

Figure 2. enlarged aerial photo of study area with relevé sites marked. Pink dots: upland; blue dots: lowland. NB the extent of exposed limestone throughout the region; (inset) map of Ireland showing Study Area

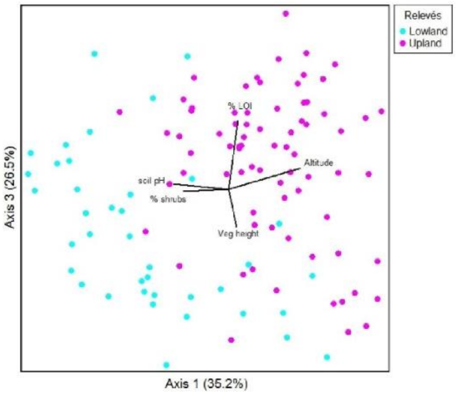

Figure 3. Non-metric Multidimensional Scaling plot of relevés summarised in Table 1. Vectors show variables most correlated with the data; LOI = Loss-on-ignition (organic matter)

Figure 4. Winter grazing in the Burren uplands

3. Methodology

Sample sites in the Burren were selected for the presence of *A. uva-ursi* and/or *E. nigrum* (Parr et al., 2009). In total 114 relevés were taken from 2m x 2m quadrats during 2013 and 2014 field seasons; 39 in the 'low Burren', and 75 in the 'high Burren', see Figure 2. Although this habitat is more widespread above 200m OD (Ordnance Datum) it is also present at 30m OD in the low east Burren The quadrats were located within pastures grazed during winter months. Environmental variables such as slope, aspect, altitude were recorded and soils were collected for analysis of pH and organic content. Data were analysed using TWINSPAN (Two Way Indicator Species Analysis) and Non-metric scaling (NMS) ordination plots (McCune & Mefford, 2006). Although issues have been highlighted with TWINSPAN (Perrin et al., 2006) it was nevertheless used for this preliminary anaylsis, as it has been used for many other vegetation studies in the Burren (Parr et al., 2009).

4. Preliminary Results

Calluna vulgaris, Dryas octopetala and *Arctostaphylos uva-ursi* are dominant across all relevés, however plant communities can be placed in three distinct groups as shown in Table 1: Upland relevés are placed in Groups

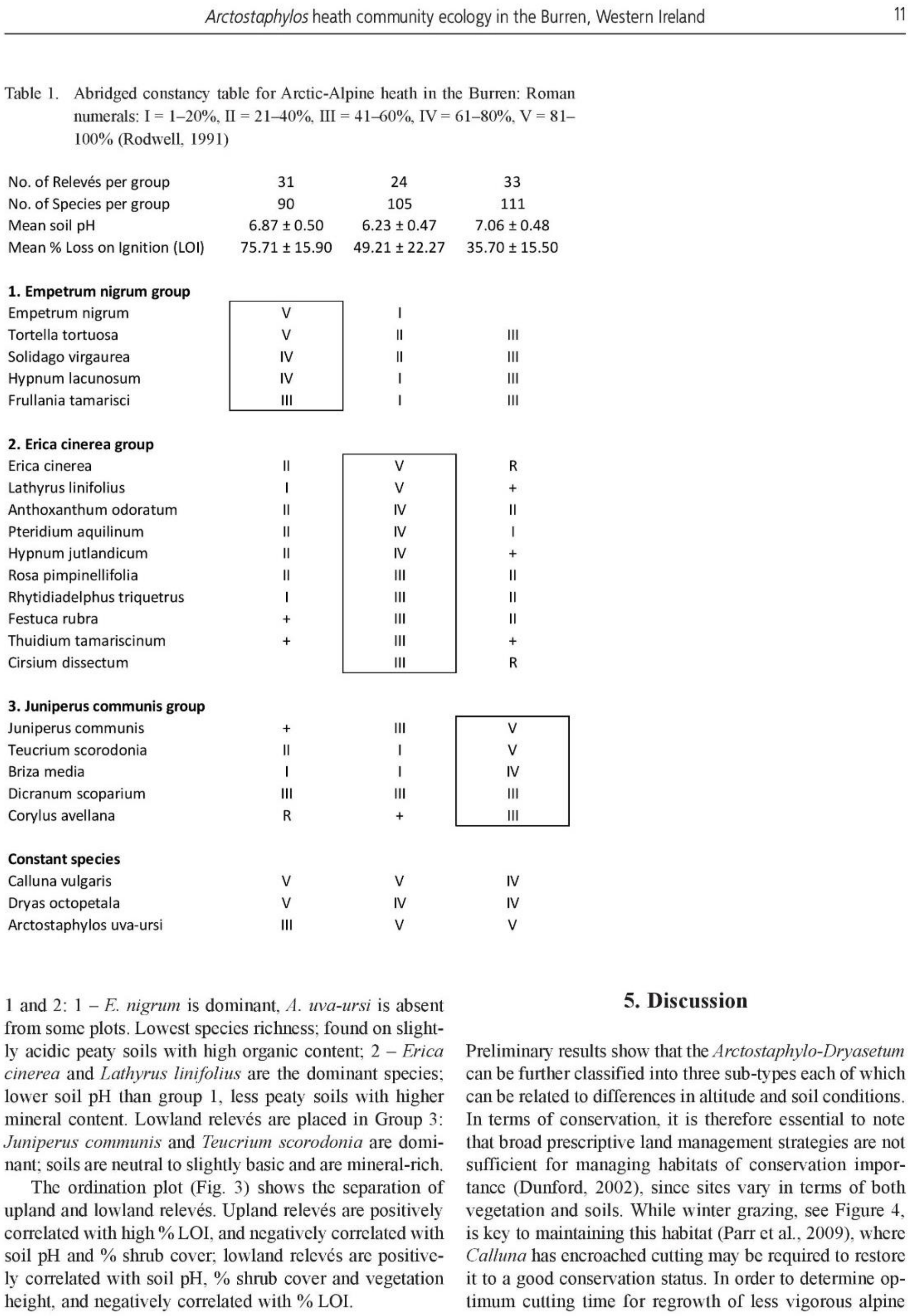

Table 1. Abridged constancy table for Arctic-Alpine heath in the Burren: Roman numerals: I = 1–20%, II = 21–40%, III = 41–60%, IV = 61–80%, V = 81–100% (Rodwell, 1991)

No. of Relevés per group	31	24	33
No. of Species per group	90	105	111
Mean soil pH	6.87 ± 0.50	6.23 ± 0.47	7.06 ± 0.48
Mean % Loss on Ignition (LOI)	75.71 ± 15.90	49.21 ± 22.27	35.70 ± 15.50
1. Empetrum nigrum group			
Empetrum nigrum	V	I	
Tortella tortuosa	V	II	III
Solidago virgaurea	IV	II	III
Hypnum lacunosum	IV	I	III
Frullania tamarisci	III	I	III
2. Erica cinerea group			
Erica cinerea	II	V	R
Lathyrus linifolius	I	V	+
Anthoxanthum odoratum	II	IV	II
Pteridium aquilinum	II	IV	I
Hypnum jutlandicum	II	IV	+
Rosa pimpinellifolia	II	III	II
Rhytidiadelphus triquetrus	I	III	II
Festuca rubra	+	III	II
Thuidium tamariscinum	+	III	+
Cirsium dissectum		III	R
3. Juniperus communis group			
Juniperus communis	+	III	V
Teucrium scorodonia	II	I	V
Briza media	I	I	IV
Dicranum scoparium	III	III	III
Corylus avellana	R	+	III
Constant species			
Calluna vulgaris	V	V	IV
Dryas octopetala	V	IV	IV
Arctostaphylos uva-ursi	III	V	V

1 and 2: 1 – *E. nigrum* is dominant, *A. uva-ursi* is absent from some plots. Lowest species richness; found on slightly acidic peaty soils with high organic content; 2 – *Erica cinerea* and *Lathyrus linifolius* are the dominant species; lower soil pH than group 1, less peaty soils with higher mineral content. Lowland relevés are placed in Group 3: *Juniperus communis* and *Teucrium scorodonia* are dominant; soils are neutral to slightly basic and are mineral-rich.

The ordination plot (Fig. 3) shows the separation of upland and lowland relevés. Upland relevés are positively correlated with high % LOI, and negatively correlated with soil pH and % shrub cover; lowland relevés are positively correlated with soil pH, % shrub cover and vegetation height, and negatively correlated with % LOI.

5. Discussion

Preliminary results show that the *Arctostaphylo-Dryasetum* can be further classified into three sub-types each of which can be related to differences in altitude and soil conditions. In terms of conservation, it is therefore essential to note that broad prescriptive land management strategies are not sufficient for managing habitats of conservation importance (Dunford, 2002), since sites vary in terms of both vegetation and soils. While winter grazing, see Figure 4, is key to maintaining this habitat (Parr et al., 2009), where *Calluna* has encroached cutting may be required to restore it to a good conservation status. In order to determine optimum cutting time for regrowth of less vigorous alpine heath species experimental cutting trials are underway in selected sites in the Burren uplands.

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Appendix 2.1. Statistical test results – vegetation study

Table 2.1. Kruskal-Wallis test results for environmental variables between for the four Vegetation groups described. Significant differences occur where p < 0.05.

Factor	H-test	df	p-value
soil pH	20.36	3	**> 0.0001**
soil loi	40.83	3	**> 0.0001**
altitude	51.21	3	**> 0.0001**
mean veg height	30.13	3	**> 0.0001**
mean soil depth	22.09	3	**> 0.0001**
S species richness	28.6	3	**> 0.0001**
E evenness	26.82	3	**> 0.0001**
H	30.93	3	**> 0.0001**
D'	26.78	3	**> 0.0001**
Ellenberg L	18.38	3	**> 0.0001**
Ellenberg F	18.06	3	**> 0.0001**
% bare ground	15.83	3	**0.001**
% exposed rock	12.8	3	**0.005**
% litter	6.8	3	0.078
% faeces	7.53	3	0.057
% bryos	1.72	3	0.632
% shrubs	14.38	3	**0.002**
% gramnoids	13.29	3	**0.004**
% forbs	4.68	3	0.196
% lichen	7.11	3	0.068
% bracken	17.32	3	**0.001**

Table 2.2. Posthoc pairwise Mann-Whitney U test results for variables from Table 1 where p < 0.05. Abbreviations: veg h (mean vegetation height); soil d (mean soil depth); S (species richness); E (evenness); H (Simpson diversity); D’ (Shannon diversity); Ellen L (Ellenberg L: light); Ellen F (Ellenberg F: moisture); brgrd (% bare ground); rock (% exposed rock); gramn (% graminoids); fern (% bracken). Significant differences occur between groups where p < 0.05.

	soil pH_1	soil pH_2	soil pH_3	soil pH_4
soil pH_1				
soil pH_2	0.975			
soil pH_3	**0.0003**	**0.0002**		
soil pH_4	0.0608	**0.0313**	**0.0033**	

	soil loi_1	soil loi_2	soil loi_3	soil loi_4
soil loi_1				
soil loi_2	**0.0014**			
soil loi_3	**0.0054**	0.3646		
soil loi_4	**0.0055**	**> 0.0001**	**> 0.0001**	

	altitude_1	altitude_2	altitude_3	altitude_4
altitude_1				
altitude_2	0.2052			
altitude_3	**0.0121**	**> 0.0001**		
altitude_4	**> 0.0001**	**> 0.0001**	0.1000	

	veg h_1	veg h_2	veg h_3	veg h_4
veg h_1				
veg h_2	0.3677			
veg h_3	**> 0.0001**	**0.0003**		
veg h_4	0.0745	**0.0067**	**> 0.0001**	

	Soil d_1	Soil d_2	Soil d_3	Soil d_4

Soil d_1				
Soil d_2	0.6597			
Soil d_3	**> 0.0001**	**0.0001**		
Soil d_4	0.271	0.6307	**0.0002**	
	S_1	S_2	S_3	S_4
S_1				
S_2	**> 0.0001**			
S_3	**0.0005**	0.1138		
S_4	**0.0001**	**0.0326**	0.7081	
	E_1	E_2	E_3	E_4
E_1				
E_2	**0.0234**			
E_3	0.4751	0.1641		
E_4	**> 0.0001**	0.0565	**0.0002**	
	H_1	H_2	H_3	H_4
H_1				
H_2	**0.0004**			
H_3	0.0546	0.0717		
H_4	**> 0.0001**	0.4986	**0.0017**	
	D'_1	D'_2	D'_3	D'_4
D'_1				
D'_2	**0.0053**			
D'_3	0.1502	0.2097		
D'_4	**>0.0001**	0.1038	**0.0015**	
	Ellen L_1	Ellen L_2	Ellen L_3	Ellen L_4
Ellen L_1				
Ellen L_2	**0.0043**			
Ellen L_3	**0.0191**	0.6909		
Ellen L_4	**0.0001**	0.1847	0.1305	
	Ellen F_1	Ellen F_2	Ellen F_3	Ellen F_4
Ellen F_1				
Ellen F_2	0.8144			
Ellen F_3	**0.002**	**0.0001**		
Ellen F_4	0.095	**0.0114**	**0.0239**	
	brgrd_1	brgrd_2	brgrd_3	brgrd_4
brgrd_1				
brgrd_2	0.6799			
brgrd_3	0.3575	0.2227		
brgrd_4	**0.0017**	**0.0006**	0.0792	
	rock_1	rock_2	rock_3	rock_4
rock_1				
rock_2	0.6886			
rock_3	**0.0068**	**0.0156**		
rock_4	0.8499	0.5555	**0.0001**	
	shrubs_1	shrubs_2	shrubs_3	shrubs_4
shrubs_1				
shrubs_2	0.4559			
shrubs_3	0.1767	0.5325		
shrubs_4	**0.0002**	**0.0146**	0.1226	
	gramn_1	gramn_2	gramn_3	gramn_4
gramn_1				
gramn_2	**0.013**			
gramn_3	**0.0095**	0.1586		
gramn_4	0.1771	0.0651	**0.007**	
	fern_1	fern_2	fern_3	fern_4
fern_1				
fern_2	**0.0482**			

fern_3	0.6467	**0.0098**	
fern_4	**0.002**	0.4338	**0.0002**

Appendix 2.2. List of species: full names and abbreviations

Full list of plant species with abbreviated names for NMS ordination plots.

Full Species name	**Abbreviated species name**
Agrostis canina	Agro can
Agrostis capilaris	Agro cap
Agrostis stolonifera	Agro sto
Agrostis vinealis	Agro vin
Antennaria dioica	Ante dio
Anthoxanthum odoratum	Anth odo
Arctostaphylos uva-ursi	Arct u-u
Arrhenatherum elatius	Arrh ela
Asperula cynanchica	Aspe cyn
Asplenium ruta-muraria	Aspl r-m
Asplenium scolopendrium	Aspl sco
Barbula convoluta	Barb con
Brachypodium sylvaticum	Brac syl
Breutelia chrysocoma	Breu chr
Briza media	Briz med
Bryum sp.	Bryum sp
Calliergonella cuspidata	Calli cus
Calluna vulgaris	Call vul
Calypogeia fissa	Caly fis
Calypogeia muelleriana	Caly mue
Campanula rotundifolia	Camp rot
Campylium protensum	Camp pro
Campylopus introflexus	Camp int
Carex binervis	Cx biner
Carex caryophyllea	Cx caryo
Carex flacca	Cx flacc
Carex hostiana	Cx hosti
Carex nigra	Cx nigra
Carex panicea	Cx panic
Carex pulicaris	Cx pulica
Carex sp.	Cx sp
Carlina vulgaris	Carl vul
Centaurea nigra	Cent nig
Cephalozia bicuspidata	Ceph bic
Cirsium dissectum	Cirs dis
Cladonia sp.	Cladonia
Corylus avellana	Cory ave
Crepis capillaris	Crep cap
Crepis sp.	Crep sp
Ctenidium molluscum	Cten mol

Cynosurus cristatus	Cyno cri
Dactylorhiza maculata	Dact mac
Dactylorhiza sp.	Dact sp
Dactylis glomerata	Dact glo
Danthonia decumbens	Dant dec
Dicranella schreberiana	Dicr sch
Dicranum scoparium	Dicr sco
Didymodon insulanus	Didy ins
Dryas octopetala	Drya oct
Empetrum nigrum	Empe nig
Encalypta streptocarpa	Enca str
Epipactis atrorubens	Epip atr
Erica cinerea	Eric cin
Euphrasia sp.	Euph sp
Eurhynchium praelongum	Eurh pra
Eurhynchium striatum	Eurh str
Festuca ovina	Fest ovi
Festuca rubra	Fest rub
Fissidens adianthoides	Fiss adi
Fissidens dubius	Fiss dub
Fissidens taxifolius	Fiss tax
Fragaria vesca	Frag ves
Fraxinus excelsior	Frax exc
Frullania dilitata	Frul dil
Frullania tamarisci	Frul tam
Galium saxatilis	Gali sax
Galium sterneri	Gali ste
Galium verum	Gali ver
Gentiana verna	Gent ver
Geranium robertianum	Gera rob
Geranium sanguineum	Gera san
Grimmia pulvinata	Grim pul
Gymnadenia borealis	Gymn bor
Gymnadenia conopsea	Gymn con
Hedera helix	Hede hel
Helictotrichon pubescens	Heli pub
Hieracium sp.	Hier sp
Holcus lanatus	Holc lan
Homalothecium lutescens	Homa lut
Homalothecium sericeum	Homa ser
Huperzia selago	Hupe sel
Hylocomium splendens	Hylo spl
Hypericum pulchrum	Hype pul
Hypnum cupressiforme	Hypn cup
Hypnum jutlandicum	Hypn jut
Hypnum lacunosum	Hypn lac

Hypochaeris radicata	Hypo rad
Juncus articulatus	Junc art
Juniperus communis	Juni com
Koeleria macrantha	Koel cri
Lathyrus linifolius	Lath lin
Lathyrus pratensis	Lath pra
Leiocolea turbinata	Leio tur
Lejeunea lamacerina	Leje lam
Lejeunea patens	Leje pat
Leontodon autumnalis	Leon aut
Leontodon hispidus	Leon his
Leontodon saxatilis	Leon sax
Leontodon sp.	Leon sp
Leucanthemum vulgare	Leuc vul
Leucobryum glaucum	Leuc gla
Linum catharticum	Linu cat
Loeskeobryum brevirostre	Loes bre
Lonicera periclymenum	Loni per
Lophocolea bidentata	Loph bid
Lotus corniculatus	Lotu cor
Luzula multiflora ssp congesta	Luzu m-c
Luzula multiflora ssp multiflora	Luzu m-m
Melampyrum pratense	Mela pra
Molinia caerulea	Moli cae
Neckera crispa	Neck cri
Neottia ovata	Neot ova
Nostoc sp.	Nost sp
Ophrys insectifera	Ophr ins
Orchid sp.	Orchid
Orchis mascula	Orch mas
Oxyrrhynchium hians	Oxyr hia
Pedicularis sp.	Pedi sp
Pedicularis sylvatica	Pedi syl
Pilosella officinarum	Pilo off
Pinguicula vulgaris	Ping vul
Plagiochila asplenioides	Plag asp
Plantago lanceolata	Plan lan
Plantago maritima	Plan mar
Pleurozium schreberi	Pleu sch
Polygala serpyllifolia	Poly ser
Polygala vulgaris	Poly vul
Potentilla erecta	Pote ere
Potentilla sterilis	Pote ste
Primula vulgaris	Prim vul
Prunella vulgaris	Prun vul
Prunus spinosa	Prun spi

Pseudoscleropodium purum	Pseu pur
Pteridium aquilinum	Pter aqu
Racomitrium lanuginosum	Raco lan
Rhinanthus minor	Rhin min
Rhytidiadelphus loreus	Rhyt lor
Rhytidiadelphus squarrosus	Rhyt squ
Rhytidiadelphus triquetrus	Rhyt tri
Rosa pimpinellifolia	Rosa pim
Rubia peregrina	Rubi per
Rubus fruticosus agg.	Rubu fru
Rubus saxatilis	Rubu sax
Salix repens	Sali rep
Sanguisorba minor	Sang min
Scapania aspera	Scap asp
Senecio jacobaea	Sene jac
Sesleria caerulea	Sesl cae
Solidago virgaurea	Soli vir
Sorbus aria	Sorb ari
Succisa pratensis	Succ pra
Taraxacum officinale	Tara off
Teucrium scorodonia	Teuc sco
Thuidium tamariscinum	Thui tam
Thymus polytrichus	Thym pol
Tortella tortuosa	Tort tor
Trichophorum cespitosum	Tric ces
Trichostomum crispulum	Tric cri
Trifolium pratense	Trif pra
Trifolium repens	Trif rep
Ulex europaeus	Ulex eur
Viburnum opulus	Vibu opu
Vicia cracca	Vici cra
Vicia sepium	Vici sep
Viola riviniana	Viol riv

Appendix 2.3. Mean monthly temperature data

Table 2.1. Difference between mean upland and lowland temperatures for all dataloggers (n) (a positive value indicates higher temperature in the lowlands and a negative value indicates a higher temperature in the uplands) and Kruskal-Wallis test results; p < 0.05 are significant.

Date	Total n	Difference of means	Kruskal-Wallis test		
			H	df	p
Aug-13	5	1.62 °C	3.00	1	0.083
Sep-13	5	1.47 °C	3.00	1	0.083
Oct-13	5	0.65 °C	3.00	1	0.083
Nov-13	5	0.15 °C	0.33	1	0.564
Dec-13	5	0.39 °C	1.33	1	0.248
Jan-14	5	0.51 °C	3.00	1	0.083
Feb-14	5	0.89 °C	3.00	1	0.083
Mar-14	5	1.20 °C	3.00	1	0.083
Apr-14	5	1.88 °C	3.00	1	0.083
May-14	4	0.34 °C	0.60	1	0.439
Jun-14	4	0.84 °C	2.40	1	0.121
Jul-14	4	1.87 °C	2.40	1	0.121
Aug-14	8	1.81 °C	5.00	1	**0.025**
Sep-14	8	1.35 °C	5.00	1	**0.025**
Oct-14	9	0.58 °C	4.86	1	**0.027**
Nov-14	9	-0.13 °C	0.06	1	0.806
Dec-14	9	-0.03 °C	0.54	1	0.462
Jan-15	9	0.37 °C	2.16	1	0.142
Feb-15	9	0.60 °C	4.86	1	**0.027**
Mar-15	9	1.07 °C	6.00	1	**0.014**
Apr-15	9	1.40 °C	6.00	1	**0.014**
May-15	10	1.81 °C	6.82	1	**0.009**
Jun-15	10	2.39 °C	6.82	1	**0.009**
Jul-15	11	1.54 °C	7.50	1	**0.006**
Aug-15	11	1.09 °C	6.53	1	**0.011**
Sep-15	11	0.88 °C	3.33	1	0.068
Oct-15	11	0.43 °C	2.70	1	0.100

Appendix 3.1. Statistical test results – *Calluna vulgaris* cutting trials

Table 3.1. One-way ANOVA test results for site characteristics in 2013 before cutting for factors that were normally distributed. Significant differences occur where p < 0.05.

Source	DF	Adj SS	Adj MS	F-Value	P-Value
Altitude (m a.s.l.)					
Site	2	88124.1	44062.1	2423.49	**0.000**
Error	42	763.6	18.2		
Total	44	88887.7			
Soil pH					
Site	2	2.697	1.3487	5.53	**0.007**
Error	42	10.247	0.244		
Total	44	12.944			
Vegetation height (cm)					
Site	2	333.9	166.94	2.14	0.130
Error	42	3278.1	78.05		
Total	44	3612			
% *Calluna vulgaris*					
Site	2	0.7849	0.39243	9.39	**0.000**
Error	42	1.7547	0.04178		
Total	44	2.5396			
% *Erica cinerea*					
Site	2	0.1347	0.06734	2.92	0.065
Error	42	0.9686	0.02306		
Total	44	1.1033			
% shrubs					
Site	2	0.6685	0.33425	9.97	**0.000**
Error	42	1.4086	0.03354		
Total	44	2.0771			
% forbs					
Site	2	0.06663	0.03332	1.96	0.153
Error	42	0.71237	0.01696		
Total	44	0.779			
% graminoids					
Site	2	0.2953	0.14766	4.69	**0.015**
Error	42	1.3229	0.0315		
Total	44	1.6182			
% bryophytes					
Site	2	0.1951	0.09757	2.26	0.117
Error	42	1.8106	0.04311		
Total	44	2.0057			
% litter					
Site	2	0.4139	0.20695	19.37	**0.000**
Error	42	0.4486	0.01068		
Total	44	0.8625			
% bare ground					
Site	2	0.06991	0.034957	13.33	**0.000**
Error	42	0.11014	0.002622		
Total	44	0.18005			
Species richness					
Site	2	86.18	43.09	2.47	0.097

Error	42	732.8	17.45		
Total	44	818.98			
Ellenberg L (light)					
Site	2	0.6134	0.3067	26.26	**0.000**
Error	42	0.4906	0.01168		
Total	44	1.104			

Table 3.2. Grouping information using Tukey post hoc and 95% confidence for factors in Table 1 where $p < 0.05$. Means that do not share a letter are significantly different. The letter 'A' is assigned to the greatest mean value, 'B' to the next greatest where it is significantly different from 'A', and so on.

	Site	N	Mean	Grouping
Altitude (m a.s.l.)	L	15	175.149	B
	M	15	177.49	B
	N	15	270.172	A
Soil pH	L	15	6.49867	A
	M	15	6.31	A B
	N	15	5.91133	B
% *Calluna vulgaris*	L	15	0.822208	A
	M	15	0.718619	A
	N	15	0.50501	B
% shrubs	L	15	1.05787	A
	M	15	1.07532	A
	N	15	0.80848	B
% graminoids	L	15	0.720406	B
	M	15	0.753723	A B
	N	15	0.906474	A
% litter	L	15	0.188053	B
	M	15	0.273962	B
	N	15	0.420361	A
% bare ground	L	15	0.048365	B
	M	15	0.128292	A
	N	15	0.135234	A
Ellenberg L (light)	L	15	6.9276	C
	M	15	7.04691	B
	N	15	7.21235	A

Table 3.3. Kruskal-Wallis test results for site characteristics in 2013 before cutting, for factors that did not have normal distributions. Significant differences occur where $p < 0.05$.

Factor	H-test	df	p-value
Soil depth (cm)	15.03	2	**0.001**
Soil % loss on ignition	3.4	2	0.183
% Arctostaphylos uva-ursi	13.54	2	**0.001**
% Dryas octopetala	7.43	2	**0.024**
% Empetrum nigrum	1.18	2	0.554
% Juniperus communis	21.65	2	**0.000**
% bracken	15.63	2	**0.000**
% exposed rock	0.71	2	0.700
Ellenberg F (moisture)	17.15	2	**0.000**

Table 3.4. Posthoc pairwise Mann-Whitney U test results for factors from Table 3 where p < 0.05. [Soil Dpt: soil depth; Arcto: *Arctostaphylos uva*-ursi; Dryas: *Dryas octopetala*; Bracken: *Pteridium aquilinum*; Rock: exposed rock; F: Ellenberg F (moisture); L, M and N relate to the sites]. Letters indicate significant differences between sites; medians that do not share a letter are significantly different. The letter 'a' is assigned to the greatest median value, 'b' to the next greatest where it is significantly different from 'a', and so on.

	Soil Dpt_L	Soil Dpt_M	Soil Dpt_N		Grouping
Soil Dpt_L	***			Soil Dpt_L	a
Soil Dpt_M	0.901	***		Soil Dpt_M	a
Soil Dpt_N	**0.0005**	**0.0016**	***	Soil Dpt_N	b
	Arcto_L	Arcto_M	Arcto_N		
Arcto_L	***			Arcto_L	a
Arcto_M	0.0065	***		Arcto_M	b
Arcto_N	0.5461	0.0005	***	Arcto_N	a
	Dryas_L	Dryas_M	Dryas_N		
Dryas_L	***			Dryas_L	a
Dryas_M	0.0597	***		Dryas_M	b
Dryas_N	**0.0092**	0.5192	***	Dryas_N	b
	Bracken_L	Bracken_M	Bracken_N		
Bracken_L	***			Bracken_L	a
Bracken_M	0.3646	***		Bracken_M	a
Bracken_N	**0.0004**	**0.0006**	***	Bracken_N	b
	Rock_L	Rock_M	Rock_N		
Rock_L	***			Rock_L	a
Rock_M	0.8237	***		Rock_M	a
Rock_N	0.4237	0.5516	***	Rock_N	a
	F_L	F_M	F_N		
F_L	***			F_L	a
F_M	**0.009**	***		F_M	b
F_N	**0.0002**	**0.038**	***	F_N	c

Table 3.5. PerManova results of year and cutting regime effects on species composition with a pairwise comparison for cutting regime.

	df	SS	MS	F	p
Year	1	1.6442	1.6442	8.1515	**0.0002**
Cutting regime	2	0.42313	0.21156	1.0489	0.3904
Interaction	2	0.24719	0.1236	0.61277	0.949
Residual	84	16.943	0.2017		
Total	89	19.257			

Pairwise comparisons for cutting regime

	t	p
Autumn vs Spring	0.7158	0.9414
Autumn vs Control	1.0266	0.3914
Spring vs Control	1.2609	0.0762

Table 3.6. PerManova results of site and cutting regime effects on species composition in 2013 and pairwise comparison between plots assigned the cutting regimes.

	df	SS	MS	F	p
Site	2	1.0567	0.5283	2.9955	**0.0002**
Cutting regime	2	0.1498	0.0749	0.4246	0.9942
Interaction	4	0.6883	0.1721	0.9756	0.5220
Residual	36	6.3496	0.1764		
Total	44	8.2443			

Pairwise comparisons for cutting regime

	t	p
Autumn vs Spring	0.3728	1.0000
Autumn vs Control	0.6443	0.9578
Spring vs Control	0.8793	0.6722

Table 3.7. GLM test results for changes in vegetation patterns before and after cutting and between cutting regimes. Site was set as a random factor, cutting regime and year were fixed factors. Factors that were not normally distributed were tested by Kruskal-Wallis (Table 3.9). Significant differences occur where $p < 0.05$.

	DF	Adj SS	Adj MS	F-Value	P-Value
Vegetation height					
Site	2	281.2	140.62	3.07	0.052
Cutting regime	2	332.3	166.16	3.63	**0.031**
Year	1	6243.3	6243.34	136.22	**0.000**
Cutting regime*Year	2	475	237.51	5.18	**0.008**
Error	82	3758.4	45.83		
% shrubs					
Site	2	0.8425	0.421267	14.39	**0.000**
Cutting regime	2	0.6432	0.321621	10.99	**0.000**
Year	1	0.0039	0.003944	0.13	0.715
Cutting regime*Year	2	0.5381	0.269051	9.19	**0.000**
Error	82	2.4008	0.029278		
% forbs					
Site	2	0.0911	0.04554	1.67	0.195
Cutting regime	2	0.0473	0.02365	0.87	0.424
Year	1	4.9418	4.94178	180.96	**0.000**
Cutting regime*Year	2	0.0969	0.04844	1.77	0.176
Error	82	2.2393	0.02731		
% graminoids					
Site	2	0.0151	0.007552	0.21	0.810
Cutting regime	2	0.0138	0.006907	0.19	0.825
Year	1	0.1084	0.10835	3.03	0.085
Cutting regime*Year	2	0.1002	0.050105	1.4	0.252
Error	82	2.9283	0.035711		
% bryophytes					
Site	2	0.3146	0.157279	4.57	**0.013**
Cutting regime	2	0.0092	0.00459	0.13	0.875
Year	1	0.321	0.321041	9.33	**0.003**
Cutting regime*Year	2	0.0022	0.001104	0.03	0.968
Error	82	2.8221	0.034415		
% litter					
Site	2	0.5541	0.27702	16.17	**0.000**
Cutting regime	2	0.0739	0.03693	2.16	0.122

Year	1	0.5424	0.54241	31.66	**0.000**
Cutting regime*Year	2	0.0223	0.01117	0.65	0.524
Error	82	1.4048	0.01713		
% bare ground					
Site	2	0.0593	0.029661	3.26	**0.043**
Cutting regime	2	0.1178	0.058915	6.48	**0.002**
Year	1	0.3842	0.384145	42.25	**0.000**
Cutting regime*Year	2	0.1469	0.073432	8.08	**0.001**
Error	82	0.7455	0.009091		
% exposed rock					
Site	2	0.006	0.003013	0.2	0.817
Cutting regime	2	0.2115	0.10575	7.1	**0.001**
Year	1	0.6092	0.60922	40.93	**0.000**
Cutting regime*Year	2	0.1656	0.082793	5.56	**0.005**
Error	82	1.2206	0.014885		
Species richness					
Site	2	141.16	70.58	3	0.055
Cutting regime	2	114.76	57.38	2.44	0.094
Year	1	32.4	32.4	1.38	0.244
Cutting regime*Year	2	97.87	48.93	2.08	0.132
Error	82	1931.8	23.56		
Evenness					
Site	2	0.0131	0.006539	3.1	0.050
Cutting regime	2	0.0016	0.000819	0.39	0.679
Year	1	0.1324	0.132403	62.84	**0.000**
Cutting regime*Year	2	0.0069	0.003445	1.64	0.201
Error	82	0.1728	0.002107		
H					
Site	2	0.3982	0.19908	5.15	**0.008**
Cutting regime	2	0.1364	0.0682	1.76	0.178
Year	1	1.8749	1.87489	48.46	**0.000**
Cutting regime*Year	2	0.3192	0.1596	4.13	**0.020**
Error	82	3.1723	0.03869		

Table 3.8. Grouping information using Tukey post hoc and 95% confidence for factors in Table 3.7 where $p < 0.05$ for Cutting regime, Year or the interaction term Cutting regime*Year. Means that do not share a letter are significantly different. The letter 'A' is assigned to the greatest mean value, 'B' to the next greatest where it is significantly different from 'A', and so on.

	Cutting regime*Year	N	Mean	Grouping		
Vegetation height	Autumn 2013	15	31.8133	A		
	Autumn 2015	15	10.2			C
	Spring 2013	15	29.5667	A		
	Spring 2015	15	11.7467			C
	Control 2013	15	30.1667	A		
	Control 2015	15	19.6267		B	
% shrubs	Autumn 2013	15	1.0167		B	
	Autumn 2015	15	0.84134		B	
	Spring 2013	15	0.91996		B	
	Spring 2015	15	0.93162		B	
	Control 2013	15	1.00501		B	
	Control 2015	15	1.20844	A		
% forbs	Autumn 2013	15	0.49535		B	
	Autumn 2015	15	1.00431	A		
	Spring 2013	15	0.45735		B	

	Spring 2015	15	0.97823	A		
	Control 2013	15	0.50583		B	
	Control 2015	15	0.88194	A		
% bryophytes	Autumn 2013	15	0.817445	A		
	Autumn 2015	15	0.685175	A		
	Spring 2013	15	0.830122	A		
	Spring 2015	15	0.721974	A		
	Control 2013	15	0.822921	A		
	Control 2015	15	0.704987	A		
% litter	Autumn 2013	15	0.332784		B	
	Autumn 2015	15	0.477997	A		
	Spring 2013	15	0.275558		B	
	Spring 2015	15	0.473443	A		
	Control 2013	15	0.274033		B	
	Control 2015	15	0.396729	A	B	
% bare ground	Autumn 2013	15	0.109001		B	
	Autumn 2015	15	0.283201	A		
	Spring 2013	15	0.093452		B	
	Spring 2015	15	0.293832	A		
	Control 2013	15	0.109439		B	
	Control 2015	15	0.126851		B	
% exposed rock	Autumn 2013	15	0.067353		B	
	Autumn 2015	15	0.249869	A		
	Spring 2013	15	0.073729		B	
	Spring 2015	15	0.333203	A		
	Control 2013	15	0.059995		B	
	Control 2015	15	0.111652		B	
Evenness	Autumn 2013	15	0.717267		B	
	Autumn 2015	15	0.816067	A		
	Spring 2013	15	0.7394		B	
	Spring 2015	15	0.814733	A		
	Control 2013	15	0.743		B	
	Control 2015	15	0.799	A		
H	Autumn 2013	15	2.45333			C
	Autumn 2015	15	2.8666	A		
	Spring 2013	15	2.55267		B	C
	Spring 2015	15	2.8772	A		
	Control 2013	15	2.55587		B	C
	Control 2015	15	2.68407	A	B	

Table 3.9. Kruskal-Wallis test results for species richness and D' Shannon diversity vs cutting regime. Where $p < 0.05$ the test is significant.

Factor	H	df	p
Species richness	8.9900	5	0.1100
D'	34.0700	5	**0.0000**

Table 3.10. Pairwise Mann-Whitney U test results for factors from Table 3.9 where $p < 0.05$. [D’: Shannon diversity; A, S and C represent the cutting regimes: Autumn, Spring and the uncut Control]. Letters indicate significant differences between sites; medians that do not share a letter are significantly different. The letter ‘a’ is assigned to the greatest median value, b to the next greatest where it is significantly different from ‘b’, and so on.

	D`_A-2013	D`_A-2015	D`_S-2013	D`_S-2015	D`_C-2013	D`_C-2015		Grouping		
D`_A-2013	***						D`_A-2013		b	
D`_A-2015	**0.0001**	***					D`_A-2015	a		
D`_S-2013	0.5474	**0.0007**	***				D`_S-2013		b	c
D`_S-2015	**0.0000**	0.5069	**0.0004**	***			D`_S-2015	a		
D`_C-2013	0.3837	**0.0028**	0.6482	**0.0021**	***		D`_C-2013		b	c
D`_C-2015	**0.0161**	**0.0344**	0.0564	**0.0107**	0.1844	***	D`_C-2015			c

Table 3.11. GLM results for vegetation height (2013, 2014 and 2015) with site as a random factor and cutting regime as a fixed factor. Where $p < 0.05$ the test is significant.

	DF	Adj SS	Adj MS	F-Value	P-Value
Vegetation height 2013					
Site	2	333.88	166.94	2.8	0.174
Cutting regime	2	40.6	20.3	0.34	0.73
Site*Cutting regime	4	238.63	59.66	0.72	0.586
Error	36	2998.88	83.3		
Total	44	3611.98			
Vegetation height 2014					
Site	2	156.3	78.14	1.78	0.281
Cutting regime	2	1475.4	737.72	16.76	**0.011**
Site*Cutting regime	4	176.1	44.01	2.25	0.082
Error	36	702.8	19.52		
Total	44	2510.6			
Vegetation height 2015					
Site	2	41.41	20.705	6.43	0.056
Cutting regime	2	766.74	383.372	119.13	**0**
Site*Cutting regime	4	12.87	3.218	0.28	0.889
Error	36	413.98	11.5		
Total	44	1235.01			

Table 3.12. Grouping information using Tukey post hoc and 95% confidence for factors in Table 3.11 where p < 0.05. Means that do not share a letter are significantly different. The letter 'A' is assigned to the greatest mean value, 'B' to the next greatest where it is significantly different from 'A', and so on.

Cutting regime	N	Mean	Grouping	
Vegetation height 2014				
C	15	20.4133	A	
S	15	8.2933		B
A	15	8.24		B
Vegetation height 2015				
C	15	19.6267	A	
S	15	11.7467		B
A	15	10.2		B

Table 3.13. Kruskal-Wallis test results for maximum *Calluna* height in 2015 vs cutting regime. Where p < 0.05 the test is significant.

Factor	H	df	p
Calluna height	31.36	2	**0.000**

Table 3.14. Pairwise Mann-Whitney U test results for maximum *Calluna* height in 2015; [A, S and C represent the cutting regimes: Autumn, Spring and the uncut Control]. Letters indicate significant differences between sites; medians that do not share a letter are significantly different. The letter 'a' is assigned to the greatest median value, 'b' to the next greatest where it is significantly different from 'a', and so on.

	Calluna Ht_A	Calluna Ht_S	Calluna Ht_C		Grouping		
Calluna Ht_A	***			Calluna Ht_A			c
Calluna Ht_S	0.0093	***		Calluna Ht_S		b	
Calluna Ht_C	0.0000	0.0000	***	Calluna Ht_C	a		

Table 3.15. GLM test results for changes in species % cover before and after cutting and between cutting regimes. Site was set as a random factor, cutting regime and year were fixed factors. Species that were not normally distributed were tested by Kruskal-Wallis (Table 3.17). Significant differences occur where p < 0.05.

Source	DF	Adj SS	Adj MS	F-Value	P-Value
% Calluna vulgaris					
Site	2	0.8299	0.41497	12.32	**0.00**
Treatment	2	1.3951	0.69755	20.72	**0.00**
Year	1	0.3413	0.34128	10.14	**0.00**
Treatment*Year	2	1.3813	0.69065	20.51	**0.00**
Error	82	2.7612	0.03367		
% Erica cinerea					
Site	2	0.41476	0.207382	5.1	**0.01**
Treatment	2	0.01258	0.006288	0.15	0.86
Year	1	0.89521	0.895206	22.01	**0.00**
Treatment*Year	2	0.00681	0.003407	0.08	0.92
Error	82	3.33458	0.040666		

Table 3.16. Grouping information using Tukey post hoc and 95% confidence for species in Table 3.15 where $p < 0.05$ for Cutting regime, Year or the interaction term Cutting regime*Year. Means that do not share a letter are significantly different. The letter 'A' is assigned to the greatest mean value, 'B' to the next greatest where it is significantly different from 'A', and so on.

	Cutting regime*Year	N	Mean	Grouping		
% Calluna vulgaris	Autumn 2013	15	0.731765	A	B	
	Autumn 2015	15	0.30995			
	Spring 2013	15	0.610594		B	C
	Spring 2015	15	0.478049			C
	Control 2013	15	0.703478	A	B	
	Control 2015	15	0.888361	A		
% Erica cinerea	Autumn 2013	15	0.214362		B	
	Autumn 2015	15	0.413536	A	B	
	Spring 2013	15	0.209628		B	
	Spring 2015	15	0.38793	A	B	
	Control 2013	15	0.21726		B	
	Control 2015	15	0.438185	A		

Table 3.17. Kruskal-Wallis test results for species indicated as important by the Pearson and Kendell correlations vs cutting regime. *Calluna vulgaris and Erica cinerea* were also tested here in order to compare with the other species tested. Where $p < 0.05$ test is significant.

Species name	H	df	p
Arctostaphylos uva-ursi	7.0900	5	0.214
Briza media	1.4100	5	0.924
Calluna vulgaris	42.1800	5	**0.000**
Carex panicea	2.7600	5	0.737
Carex pulicaris	3.6500	5	0.600
Cirsium dissectum	6.4500	5	0.265
Dryas octopetala	4.4600	5	0.485
Empetrum nigrum	1.8700	5	0.866
Erica cinerea	17.1200	5	**0.004**
Festuca rubra	17.9100	5	**0.003**
Hypericum pulchrum	30.8900	5	**0.000**
Lotus corniculatus	12.0600	5	**0.034**
Molinia caerulea	3.8000	5	0.578
Pedicularis sylvatica	3.3500	5	0.646
Polygala serpyllifolia	3.9000	5	0.564
Potentilla erecta	30.8600	5	**0.000**
Sesleria caerulea	9.0100	5	0.109
Succisa pratensis	8.1200	5	0.150
Viola riviniana	11.2700	5	**0.046**

Table 3.18. Posthoc pairwise Mann-Whitney U test results for factors from Table 3.17 where p < 0.05. Letters indicate significant differences between sites; medians that do not share a letter are significantly different. [Call: *Calluna vulgaris*; Eric: *Erica cinerea;* Fest: *Festuca rubra*; Hype: *Hypericum pulchrum*; Lotu: *Lotus corniculatus*; Pote: *Potentilla erecta*; Viol: *Viola riviniana.* A, S and C represent the cutting regimes: Autumn, Spring and the uncut Control]. The letter 'a' is assigned to the greatest median value, 'b' to the next greatest where it is significantly different from 'a', and so on.

	Call_A-2013	Call_A-2015	Call_S-2013	Call_S-2015	Call_C-2013	Call_C-2015	Grouping
Call_A-2013	***						b
Call_A-2015	**0.0001**	***					d
Call_S-2013	0.1837	**0.001**	***				b c
Call_S-2015	**0.0026**	**0.0034**	0.2529	***			c
Call_C-2013	0.8676	**0.0002**	0.2363	**0.0034**	***		b
Call_C-2015	**0.0433**	**0.0000**	**0.0065**	**0.0000**	**0.0166**	***	a
	Eric_A-2013	Eric_A-2015	Eric_S-2013	Eric_S-2015	Eric_C-2013	Eric_C-2015	
Eric_A-2013	**						b
Eric_A-2015	**0.0244**	**					a
Eric_S-2013	0.7383	**0.0147**	**				b
Eric_S-2015	**0.0244**	0.6313	**0.0076**	**			a
Eric_C-2013	0.9667	**0.0302**	0.95	**0.0371**	**		b
Eric_C-2015	**0.0206**	0.6756	**0.0146**	0.3161	**0.0218**	**	a
	Fest_A-2013	Fest_A-2015	Fest_S-2013	Fest_S-2015	Fest_C-2013	Fest_C-2015	
Fest_A-2013	***						b
Fest_A-2015	**0.0318**	***					a
Fest_S-2013	1.0000	**0.0284**	***				b
Fest_S-2015	**0.0019**	0.9666	**0.0025**	***			a
Fest_C-2013	0.3395	0.1597	0.3510	**0.0308**	***		a b
Fest_C-2015	**0.0113**	0.8165	**0.0106**	0.7862	0.0789	***	a
	Hype_A-2013	Hype_A-2015	Hype_S-2013	Hype_S-2015	Hype_C-2013	Hype_C-2015	
Hype_A-2013	***						b
Hype_A-2015	**0.0003**	***					a
Hype_S-2013	0.3569	**0**	***				b
Hype_S-2015	**0.005**	0.7854	**0.0027**	***			a
Hype_C-2013	0.9003	**0.0001**	0.2858	**0.0308**	***		b
Hype_C-2015	**0.0124**	0.8828	**0.0041**	0.7862	**0.0089**	***	a
	Lotu_A-2013	Lotu_A-2015	Lotu_S-2013	Lotu_S-2015	Lotu_C-2013	Lotu_C-2015	
Lotu_A-2013	***						b
Lotu_A-2015	**0.0115**	***					a
Lotu_S-2013	0.2585	**0.003**	***				b
Lotu_S-2015	0.1117	0.8186	**0.0336**	***			a
Lotu_C-2013	0.6426	0.0796	0.1894	0.2676	***		a b
Lotu_C-2015	0.2082	0.6013	0.0835	1	0.3782	***	a b
	Pote_A-2013	Pote_A-2015	Pote_S-2013	Pote_S-2015	Pote_C-2013	Pote_C-2015	
Pote_A-2013	***						b
Pote_A-2015	**0.0018**	***					a
Pote_S-2013	0.9333	**0.004**	***				b
Pote_S-2015	**0.0077**	0.9668	**0.0073**	***			a
Pote_C-2013	0.3899	0.0175	0.3146	**0.0274**	***		b
Pote_C-2015	**0.0002**	0.0674	**0.0003**	**0.0482**	**0.0007**	***	a

	Viol_A-2013	Viol_A-2015	Viol_S-2013	Viol_S-2015	Viol_C-2013	Viol_C-2015	
Viol_A-2013	***						b c
Viol_A-2015	**0.0289**	***					a
Viol_S-2013	0.6369	**0.0281**	***				c
Viol_S-2015	0.0874	0.721	0.1103	***			a b c
Viol_C-2013	0.0777	0.1344	0.096	0.4209	***		a b c
Viol_C-2015	**0.0252**	0.8832	**0.0327**	0.7061	0.1751	***	a b

Table 3.19. PerManova results for comparison of cutting regime effects for Site L.

	df	SS	MS	F	p
Cutting regime	2	0.444	0.222	1.1274	0.2854
Residual	12	2.363	0.19692		
Total	14	2.807			

	t	p
Autumn vs Spring	0.85342	0.7104
Autumn vs Control	1.1682	0.157
Spring vs Control	1.1061	0.2466

Table 3.20. PerManova results for comparison of cutting regime effects for Site M.

	df	SS	MS	F	p
Cutting regime	2	0.4491	0.22455	1.1019	0.36
Residual	12	2.4454	0.20379		
Total	14	2.8945			

	t	p
Autumn vs Spring	1.0661	0.3432
Autumn vs Control	1.0427	0.399
Spring vs Control	1.0383	0.3954

Table 3.21. PerManova results for comparison of cutting regime effects for Site N.

	df	SS	MS	F	p
Cutting regime	2	0.24247	0.12124	0.65548	0.8764
Residual	12	2.2195	0.18496		
Total	14	2.462			

	t	p
Autumn vs Spring	0.66535	0.9462
Autumn vs Control	0.85366	0.6866
Spring vs Control	0.89445	0.6364

Table 3.22. Net increase/decrease from 2013 to 2015 in the mean % cover of all recorded species for sites L, M and N and cutting regimes (CR) A (autumn), S (spring) and C (control). Full species names are given in Appendix 2.2.

		Site L			Site M			Site N		
Species	**life form**	A	S	C	A	S	C	A	S	C
Arct u-u	shrub	12.6	10.58	3.6	8.1	13.98	19.4	3.78	15.2	19.2
Call vul	shrub	-39.4	-34.2	6	-27.6	-7.8	22.6	-32.4	5.2	22.8
Cory ave	shrub	0	-0.3	0.4	0	0.2	0	0	0	0
Drya oct	shrub	10.1	14.7	-5.1	8.6	6	0.9	4	10.3	4.5
Empe nig	shrub	-0.02	-0.1	0	0	0	0	0.5	0.9	0.3
Eric cin	shrub	13	17.8	18.5	11.8	4.4	4.2	16.4	14	23.6
Juni com	shrub	0	0	0	0	0	0	0.2	9.2	11.78
Rosa pim	shrub	0	4.2	0.6	0.6	-1.3	-1.8	3.2	2.3	1.1
Rubu sax	shrub	0	0	0	0	-0.1	0	0	0	0
Sali rep	shrub	-0.1	0	3.4	0	0	0	0.1	0.9	1.2
Pter aqu	pteridophyte	4.5	15.6	7.6	3.6	10.2	12	3.6	0	1.9
Thym pol	dwarf shrub	3.1	2.4	-1.4	1.7	8.6	-0.1	3	7.3	1.9
Ante dio	forb	0.9	1.1	1.4	0.7	1.1	0.1	2.7	0.7	1.4
Aspe cyn	forb	0	-0.1	0	0.1	0.1	0.1	0.1	0	0
Camp rot	forb	1.2	0.7	0.9	0.1	0.4	0.5	1	0.3	0.7
Carl vul	forb	0.1	0	0	0	0	0	0	0.2	0
Cent nig	forb	2	1.1	1.4	1.6	0.9	3.2	0	0.2	0.1
Cirs dis	forb	4.2	3.4	12	6.3	2.7	5.3	11.6	8.9	14.7
Crep cap	forb	0	0	-0.1	0	0	0	0	0	0
Euph sp	forb	1.4	0	0.2	0.4	0.8	0.1	0.6	1.7	0.4
Frag ves	forb	0	2.9	0	0	0	0	0	0	0
Gali sax	forb	0	0	0	0	0	-0.1	0	0	0
Gali ste	forb	0	0.1	0	0	0.1	0	0.1	0.2	0.1
Gali ver	forb	1.4	0.4	0	0.8	0	-0.1	0	0.3	0.2
Gera san	forb	5.9	4.5	7.2	7.6	5.3	5.8	4.8	7	7.7
Gymn con	forb	0.7	0	0	0	0	0.2	0	0	0
Hier pil	forb	0	0.1	0	0	0	0	0	0	0
Hupe sel	forb	0	0	0	0	0	0	0	0	0
Hype pul	forb	0.6	2.3	0.1	3	3.8	2.2	2	1.8	4.9
Hypo rad	forb	1.1	0	0	0	0.3	0	0.9	0.1	0
Lath lin	forb	2.6	0.9	1	4.9	1.3	2.3	4.4	2.6	3.8
Linu cat	forb	0.3	0	0.1	0.2	0.1	0	0.4	0.1	0.1
List ova	forb	0	0	0.6	0	0.1	0	0	0	1
Lotu cor	forb	14.5	9.8	15.7	8.2	8.4	0.2	5.5	3.1	5.2
Nart oss	forb	0	0	0	0	0	0	0	1	0
Orchid	forb	0.2	0.3	0.2	0	-0.2	0.3	0	0	0.5
Pedi syl	forb	1.3	0.4	2	0.2	1.2	0	3	2	1.5
Plan lan	forb	0.2	0.1	0.4	1	0.5	0.8	1.1	1.9	1.3
Plan mar	forb	0	0	-0.1	0	0	0	0	0	0
Poly vul	forb	0.3	0	0.2	1.3	0.2	0.1	0.4	0	0.4
Pote ere	forb	7.6	7.4	14.6	7.8	8.4	12	5.7	3.2	4.8
Prim vul	forb	0	0.1	0	0	0.5	0.1	0	0	0.7
Prun vul	forb	0.1	0	0.2	0.1	1.6	0.1	0.2	0	0
Rhin min	forb	0	0	0	0	0	0	0	0	0
Rubi per	forb	0	0	0	0	0	0.1	0	0	0
Soli vir	forb	1.2	-0.2	-0.5	-0.1	0.2	0.3	2.5	0.1	-0.1

Succ pra	forb	17.6	15.6	8	2	15.5	19.7	6.2	8.3	8.3
Trif pra	forb	0	-0.1	1.4	0	0	0	0	0	0
Trif rep	forb	0.6	0	-0.2	0.4	0	0.2	0	0	0
Vici cra	forb	0	0	0.4	0	0	0	0	0	0
Viol riv	forb	1.3	3.2	3.4	6.9	4.7	3.9	1.2	-0.1	1.6
Agro can	grass	1.3	2.1	1.1	6.7	0.9	1.2	2	1.1	0.3
Agro cap	grass	-0.6	-5.5	-0.8	0.5	-0.7	-0.1	1	1.7	-0.2
Agro vin	grass	0	0	1.5	-0.2	0	0	2.8	2.8	2.6
Anth odo	grass	0.5	-0.9	0.6	0.9	-0.4	-2	1.5	1.1	0.4
Briz med	grass	0.4	0	0.2	0.9	0.3	0.4	0.2	0.1	0
Brom ere	grass	0	0.1	0	0	0	0	0	0	0
Dact glo	grass	0.1	0	0.4	0	0	0	0	0	0
Dant dec	grass	-0.5	0.2	0.1	0.2	-0.1	-0.2	0.2	0.4	0.6
Fest ovi	grass	-2	15.2	-7	-0.6	-2.8	-6.2	-0.8	0.2	-11.2
Fest rub	grass	7.8	3.4	2.1	5.2	4.4	3.2	2.2	3.8	6.6
Heli pub	grass	0	0.9	0	0	0	0	0	0	0
Koel mac	grass	0.9	0.7	-0.4	2.4	0.4	0.1	0.3	1.8	0
Moli cae	grass	12.4	-1.8	4.6	1.2	-5.3	6.9	18.8	20.6	19.2
Sesl cae	grass	-0.9	8.1	-3.4	3.9	13.8	-1.3	7.5	7.2	3.1
Cx biner	sedge	0.2	-0.1	-0.1	0.4	0	0	0.1	0.8	-0.1
Cx caryo	sedge	0	0	0	0	0	0	0.1	0.2	0
Cx flacc	sedge	12.1	1.8	-1.8	9.7	8.6	-1.6	-1.6	6	2
Cx panic	sedge	0.3	4.3	20	1.7	-1.9	-0.9	3.6	1	3.6
Cx pulica	sedge	2.4	1	0	2.9	2.1	-0.6	5.8	5.6	7.8
Tric ger	sedge	0	0	0	1.2	0	0	1.1	5.2	1.7
Junc art	rush	0	0	0	0	0	0	0	0	0
Breu chr	bryophyte	-2.4	-4.6	0.6	-6.9	3.6	-0.5	-0.6	-0.7	0.4
Cten mol	bryophyte	1.2	1.6	2.2	-3.1	1.5	-0.2	6	0.3	0.4
Dicr sco	bryophyte	0.7	-0.5	0.6	0.6	-0.4	0	0.7	0.1	0.8
Eury str	bryophyte	0	-0.2	0	-0.1	-3.7	0	0	0	0
Fiss dub	bryophyte	0.8	0.1	-0.2	1.5	0.1	-0.1	-0.1	0.2	0.2
Frul tam	bryophyte	-0.1	-0.1	0	-0.1	0	-0.2	2.2	2.5	0
Hylo spl	bryophyte	-16.2	3	-6.2	0.8	-19.4	-9.2	-8	-6.9	-10.8
Hypn cup	bryophyte	0	0	0.1	0	0	0	-0.1	0	0
Hypn jut	bryophyte	-1.3	0.5	-0.6	0.5	-0.2	0.8	-2.4	1.5	-2
Hypn lac	bryophyte	0.7	0	0.1	-0.1	0.5	0	0.3	0.1	0.4
Leuc gla	bryophyte	0	0	0	0	0	0	0	4	0
Neck cri	bryophyte	0	-0.1	0	0.4	-0.3	-0.2	0.2	0.8	1.2
Pleu sch	bryophyte	-0.2	-0.3	-4.2	1	0.6	1.6	-0.2	0	0.7
Poly ser	bryophyte	0.4	0	0.7	-0.1	0.1	-0.1	4.3	1.6	0.5
Pseu pur	bryophyte	-3.6	6.2	-2.6	-6.6	-10.2	-3.8	-7.2	-2	-3
Raco lan	bryophyte	-0.6	-0.2	0.1	0	0.6	0	0.4	-6.6	-0.4
Rhyt lor	bryophyte	-0.2	-1.6	-0.9	0.2	0.1	3.2	0.1	0.1	0
Rhyt squ	bryophyte	-0.6	0	-4.2	-0.5	-1	0.1	-0.8	-0.6	-0.7
Rhyt tri	bryophyte	-1.5	-0.7	-4.5	-0.1	-2.1	-0.5	0	0	0
Scap asp	bryophyte	-0.1	0	0	0	-0.1	0	0	-0.1	0
Thui tam	bryophyte	-0.2	-0.2	3.1	2.2	-1	1.3	-0.5	-0.2	0.3
Tort tor	bryophyte	1.1	1.2	0.1	0.2	0.6	-0.1	0	1.9	0.5

Appendix 3.2. Farmer questionnaire

Farmer Questionnaire for research into the management of Alpine heath in the Burren by Sarah Hanrahan.

I have been doing research in conjunction with the Burren LIFE project and Brendan Dunford and Sharon Parr. This research is for my PhD and also will inform management recommendations for limestone heath in the Burren uplands, specifically focusing on a rare type of low-growing alpine heath with bearberry and crowberry. In some areas the ling heather has become overgrown, over-crowding the alpine heath plants and is no longer palatable for grazers. My study has involved cutting trial plots to see if this cutting will benefit the growth of the rarer alpine heath species, as well as improve the grazing quality of the vegetation. In order to inform my research I have a few questions relating to the management of your upland areas where I have carried out botanical research.

This questionnaire is only for my research and will be kept confidential

Farmer no: ______

These questions apply specifically to the parcel of land where the study plots were located (see map)

Land area:_______

1) How far back do you know the land use for this land? Please give the nearest year or decade

2) Can you say when the heather became about as tall or as dominant as it is now? (have you any photos of it?)
   Please give an idea at least of the decade

3) What factors do you think led it to become overgrown? (If more than 1 factor, please put in order of importance)

4) Was the heather ever cut or burnt? If so, when/how often?
   a. List the years or decade(s) when cut:

   b. List the years or decade(s) when burnt:

5) Is this the same as was practised
   a. Before 1970? If not, how was it different?

b. Before 2000? If not, how was it different?

6) Have you ever added basic slag (Phosphorus), potash (Potassium), lime or any other fertiliser? If so, what type, when/how often?

Fertiliser	Basic slag	Potash	Lime	other
When added				
How often				

7) Is this the same as was practised
   a. Before 1970? If not, how was it different?

   b. Before 2000? If not, how was it different?

8) Do you manage this plot of land as a winterage?

9) If so, which grazing animals do you put on the winterage?
   a. ☐ Cattle ☐ Sheep ☐ Horses/ponies ☐ Goats ☐ Other (please specify)

   b. are there feral goats there?

10) How many stock do you keep on the winterage and for which months of the year?
Cattle ___ JFMAMJJASOND Sheep ___ JFMAMJJASOND Horses/ponies ___ JFMAMJJASOND Goats ___ JFMAMJJASOND Other ___ JFMAMJJASOND

11) Do the animals have access to other land or are they contained in the area in question when grazing the area?

12) Is this the same as was practised

a. Before 1970? If not, how was it different? Please give estimate for each where you remember

Animals	Cattle	Sheep	Horses/ponies	Goats	
Numbers					
Timing					

b. Before 2000? If not, how was it different? Please give estimate for each where you remember

Animals	Cattle	Sheep	Horses/ponies	Goats	
Numbers					
Timing					

13) Have you any further comments or observations to add regarding the history of land-use on your land with regards to the dominance of heather? This can also refer to areas of your land not studied for this research –please specify if so.

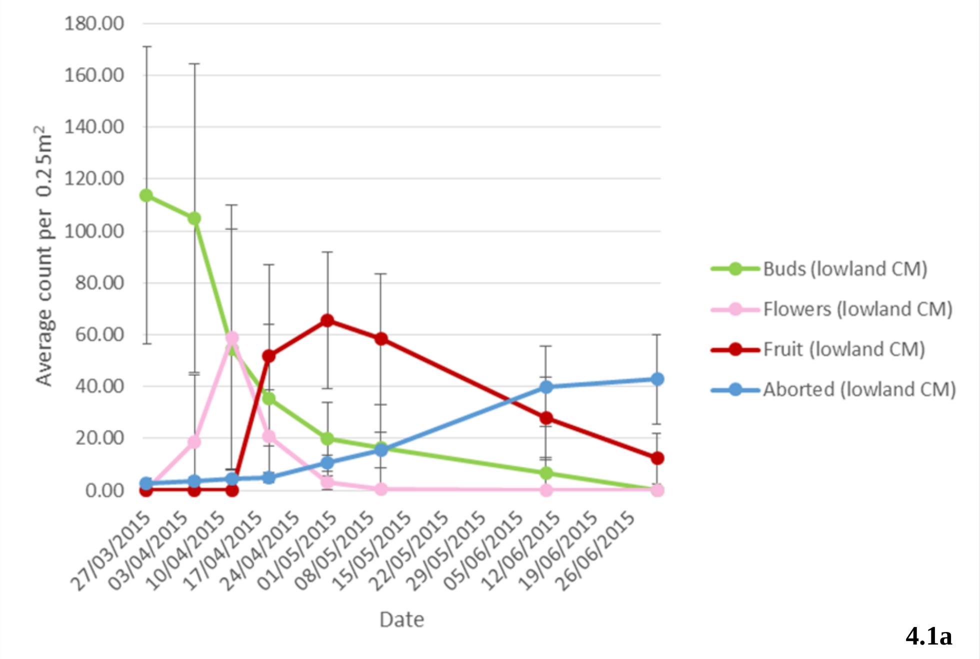
14) In relation to heather-dominated winterages have you any other comments or observations regarding
   a. barriers to farming e.g. use for grazing, timing of grazing?

   b. recommendations for future agri-environment schemes

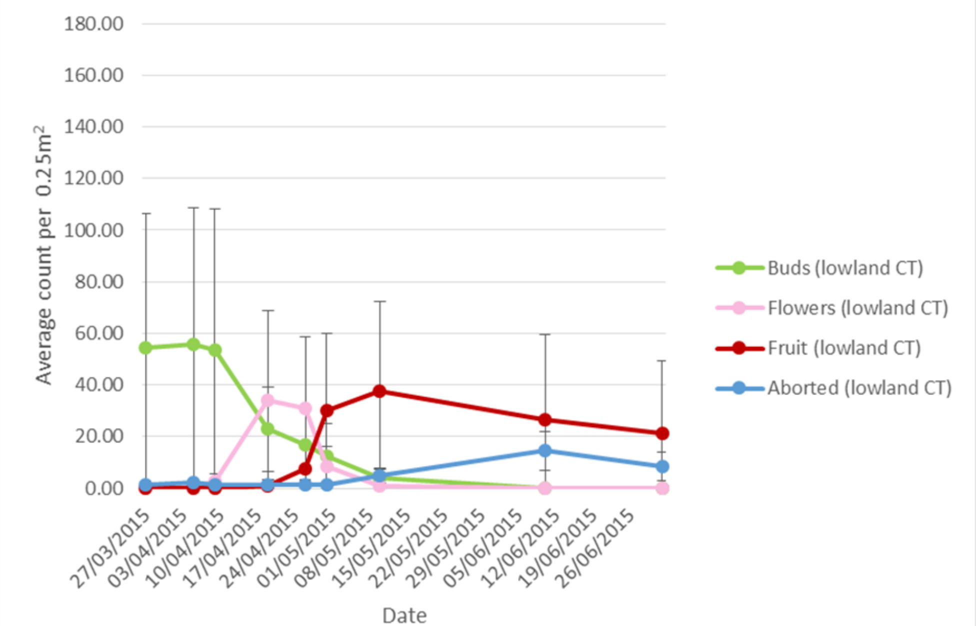
15) Do you know of any other farmers whose land has heather encroachment issues?

Many thanks for taking the time to participate in this survey. Your input is valuable to my research.

Appendix 4.1. Phenology results for individual sites

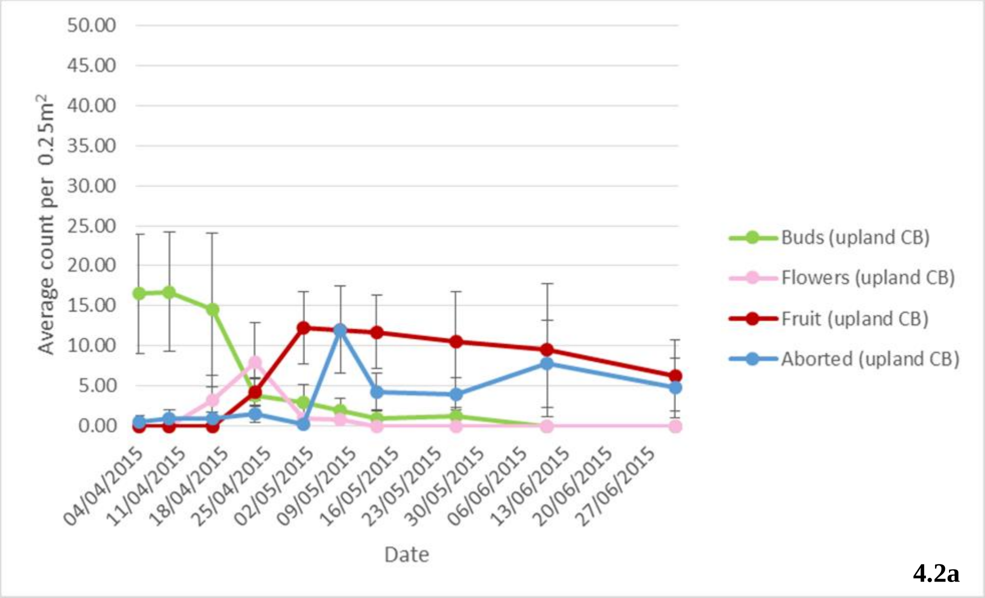


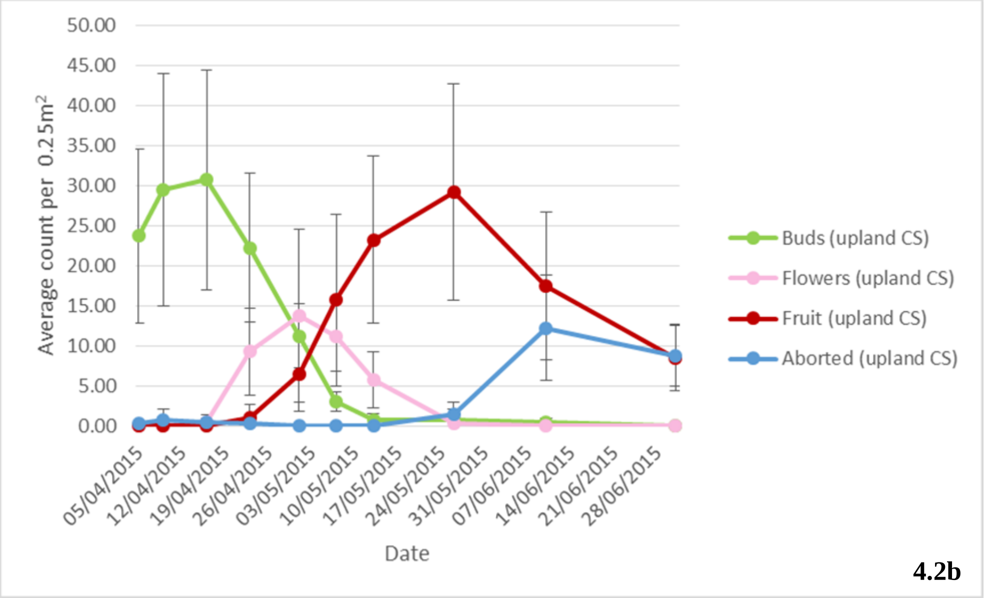
4.1a



4.1b

Figures 4.1a & b. Mean count (n=4) in 2015 per 0.25m² for inflorescences in bud, flower and fruit, and aborted inflorescences/fruit for lowland sites CM and CT. Standard deviation from the mean is shown by vertical error bars.





Figures 4.2a & b Mean count (n=4) in 2015 per $0.25m^2$ for inflorescences in bud, flower and fruit, and aborted inflorescences/fruit for upland sites CB and CS. Standard deviation from the mean is shown by vertical error bars.

Appendix 4.2. Fruit and seed set – pilot study

Table 4.1. Fruit and seed set for inflorescences with visitor-excluding mesh bags (bagged) and unbagged open pollinated (open) inflorescences at one pilot study site (CB) in 2014 (Chapter 4; Fig. 4.1). In the pilot study only the bagged inflorescences were tagged and these did not have an open pollinated pair therefore fruit was collected at random from open pollinated inflorescences on the same plant. The number of fruit per inflorescence was not noted in this case.

Pilot study site	bagged /open	no. of fruit collected per inflorescence	no. of seeds per fruit	Pilot study site	bagged /open	no. of fruit collected	no. of seeds per fruit
Bag 1	bagged	0		1	open	16	7
Bag 2	bagged	0			open		9
Bag 3	bagged	2	8		open		6
	bagged		7		open		9
Bag 4	bagged	3	10		open		8
	bagged		7		open		6
	bagged		8		open		7
Bag 5	bagged	1	8		open		8
Bag 6	bagged	0			open		7
Bag 7	bagged	4	5		open		8
	bagged		5		open		6
	bagged		5		open		5
	bagged		6		open		8
Bag 8	bagged	0			open		8
Bag 9	bagged	3	7		open		9
	bagged		6		open		7
	bagged		5	2	open	7	8
Bag 10	bagged	0			open		9
Bag 11	bagged	0			open		7
Bag 12	bagged	0			open		8
Bag 13	bagged	0			open		7
Bag 14	bagged	1	6		open		7
Bag 15	bagged	0			open		9
Bag 16	bagged	0		3	open	20	5
Bag 17	bagged	1	6		open		7
Bag 18	bagged	0			open		5
Bag 19	bagged	2	7		open		7
	bagged		5		open		6
Bag 20	bagged	0			open		6
					open		5
					open		5
					open		6
					open		6
					open		5
					open		6
					open		6
					open		5
					open		5
					open		6
					open		7
					open		6
					open		5
					open		6
Total fruit		**17**				**43**	
Mean no. seeds per fruit			**6.53**				**6.70**
St. Dev.			**1.42**				**1.30**

Appendix 4.3. Thrips survey by M. S. S.

Survey for thrips in *Arctostaphylos uva-ursi*

Arctostaphylos uva-ursi was examined by M. Sheehy Skeffington for the presence of thrips in mid- and late April 2018 when a majority of inflorescences were observed to have open flowers.

Methods

Permanent plots were relocated using GPS and finding the markers where possible (in all but one plot). The total number of inflorescences in each 50cm x 50cm plot and the number in bud, flower, fruit and aborted noted as in Methods in Chapter 4. A single flower was selected from each inflorescence that had at least one fully open flower, dissected and examined with a x 10 lens for the presence of any invertebrates. Care was taken to detach the intact flower before dissecting. A minimum of 10 flowers were sampled, or 10% of the total inflorescences with flowers within each plot.

As no thrips were found in Cregballymore, an extra 50cm x 50cm plot was added in a patch with abundant flowers. At Caherbullog, as one plot (CBd) had only one inflorescence (in bud still), a wider area in a semi-circle radius of 5m to the south of and adjacent to the permanent plot (no plants occurred adjacent to and to the north of the plot) was searched and a total of four inflorescences with a flower were examined. One plot (CBb) was not found exactly, but in the approximate site, two areas ca 5m x 1.5m and 7m x 3m were searched for inflorescences. The large plot size was due to the very low occurrence of inflorescences at the site. Due to the very low occurrence of inflorescences in flower, an extra 50cm x 50cm plot was selected where these were more abundant and counted as above.

Results

The number of inflorescences was much higher in the lowland Cregballymore site (CM) as noted in Chapter 4. However no thrips were found in any of the 53 flowers examined there (Table 4.1); one acarid mite was seen in one flower and observed taking away part of an anther, suggesting it was there to take pollen. Despite the extra plot examined at the Caherbullog upland site (CB), few inflorescences were found, let alone with open flowers, in the permanent plots. Of the total of 40 flowers examined, none was found to contain any invertebrates (Table 4.1). One plot was on an anthill and there was much more evidence of nectar robbing by the ants at this plot.

Table 4.1. Thrips survey carried out in April 2018 by M. Sheehy Skeffington at one lowland (CM) and one upland (CB) site. Where it was possible to relocate the original four plots (2014 counts) counts were undertaken at these plots and one additional plot was added at both sites due to low numbers of flowers; counts are the totals for five plots

Site Date	**Cregballymore (CM)** **19th April 2018**	**Caherbullog (CB)** **30th April 2018**
Total inflorescences	325	87
Bud	177	46
In flower	142	38
Aborted	4	2
In fruit	2	1
No. flowers examined	53	40
No. individual flowers with thrips	0	0
No. individual flowers without thrips	53	40
No. flowers punctured	5	>15
Total flowers examined	53	40
Total flowers with thrips	0	0
Flowers with other invertebrates	1*	0

* a single acarid mite was found in one flower at CM.