Niche separation of bryophytes in grikes of the limestone pavements of northern England

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Abstract

The limestone pavements of northern England vary greatly from the wooded pavements of Morecambe Bay to the large areas of open pavement in Yorkshire. The diverse morphology of limestone pavements underpins biodiversity allowing vegetation to occupy different ecological niches. The grikes of limestone pavements create a protected, humid and shaded space suitable for woodland plants with a bryophyte flora that is unique and species rich due to the high proportion of heterogenous microhabitats. The niche separation of bryophytes has been observed in multiple studies, typically focusing on moisture. Based on a 70-year-old study from the British Ecological Society, the niche separation of bryophytes in a matrix of depth and light is observed in the grikes of open limestone pavements. Ten plots of open pavement (less than 10% scrub cover) and seven plots of wooded pavement (mature trees, greater than 10% scrub cover) of 250 m^2 across eight sites were selected. 30 grikes at each plot were chosen using strategic random sampling and species, light levels, and grike characteristics were recorded. Data was analysed using R version 4.4.2 and generalised additive models to assess relationships between light, depth and species organisation. 3464 observations were made across all sites comprising a total of 27 species. In open pavements it was found that in the first 50 cm of the grike the light levels were variable allowing for generalist species to grow with niche overlap. Deeper down in the grike where there was a constant percentage reduction in light, there was greater niche separation. In contrast wooded pavements showed a greater overlap of species all growing at the top of the grike with a much lower diversity compared to the open pavements. These findings show that limestone pavements should be managed to allow for a mosaic of vegetation without complete tree cover.

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Declaration

I declare that the work presented in this thesis is my own work and has not been submitted in substantially the same form for the award of a higher degree elsewhere. The moss zonation diagram used in chapter 1 is from the British Ecological Society (British Ecological Society, 1954).

The word length of this thesis is 16,148.

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1. Introduction

1.1. Limestone pavements

Limestone pavements are created by multiple events over a long period of time (Webb, 2013). Limestone is a sedimentary rock made from either skeletal carbonate bodies, movement of fragments, or precipitates from water (Fookes and Hawkins, 1988). During the Pleistocene (2.6 million to 11,000 years ago), ice sheets scoured the limestone bedrock to produce a uniform surface (Webb, 2013). Following the last glacial period (Devensian glaciation) around 16,000 years ago, the features of limestone pavements were formed through dissolution of the limestone surface (Webb, 2013). Often these features developed beneath a layer of soil or peat where linear weaknesses occurred in the limestone (Webb, 2013). Over time, as soil was lost due to erosion, the unique formation of limestone pavements became visible (Webb, 2013). Some pavements formed alongside coasts, lakes or along river channels where features were created by wave, current and wind action rather than glaciation (Goldie, 1993). Limestone pavements are found across the globe from the Alps to Canada (Stevens, 2025).

Limestone pavements are primarily made up of “clints” and “grikes”. Grikes are fissures in the rock which are widened by physical, chemical, and biological weathering (Ward and Evans, 1976; Williams, 1966). Clints are the flat pieces of bedrock whose shapes are dictated by the pattern of grikes (Williams, 1966). Other smaller features are also present such as runnels which are channels on the clint surface that run down-slope into grikes (Ward and Evans, 1976; Williams, 1966). Solution cups, small, cup-shaped depressions, are formed by chemical solution erosion and are sometimes partly filled with water (Williams, 1966). They can remain damp for periods of time which allows algae, lichens and bryophytes to develop (Zseni et al., 2003). As soil forms in the depression, vascular plants will appear helping to erode the hole further (Zseni et al., 2003). The grey colour of the pavements can sometimes be caused by a lichen veneer (Webb, 2013).

1.2. Limestone pavements in Britain and Ireland

Limestone pavements are found in all countries in the British Isles and form a significant proportion of European limestone pavement (Blakesley and Buckley, 2016). The largest area in Europe is The Burren in Western Ireland with 18,000 ha of limestone pavement (Williams et al., 2009; Zseni et al., 2003). In Britain, the majority of pavements are found in Northern England (2,228 ha or around 77%) with the greatest area across Yorkshire and Cumbria (Blakesley and Buckley, 2016; Webb, 2013). Here the pavements are made up of strong and dense Carboniferous limestone creating large beds and well developed limestone pavement (Goldie, 1995; Williams, 1966). Pavements are found from sea level in Morecambe Bay, where pavements are typically wooded, up to 620 m in the open pavements of Yorkshire (Webb and Crowle, 2023). Asby Scar NNR in Cumbria has the most varied pavement in the British Isles (Vincent, 1995) and Gait Barrows NNR in Lancashire is among the most botanically rich pavements even though it is only 500 m in diameter with around 50% of the original pavement having been removed (Goldie, 1987; Webb, 2013). This pavement includes a mixture of woodland, scrub, and exposed pavement up to 3 m thick (Goldie, 1995). Also found here are rillenkarren which are rare, small runnels between sharp crests found on the pavement (Webb, 2013).

Other smaller areas of Carboniferous limestone occur in North and South Wales (Stevens, 2025). Anglesey, in North Wales, is designated as a UNESCO Global Geopark which is an internationally recognised site of geological significance (York, 2020) and Bryn Pydew (North Wales), a Wildlife Trust Local Nature Reserve, is also designated as a Regionally Important Geodiversity Site (Willis, 2011). In Scotland, Dalradian limestone in Perthshire and Ordovician limestone in North West Scotland together make up 10% of British limestone pavement (Ward and Evans, 1976).

1.3. Diversity in limestone pavements

Limestone pavements are geodiverse exhibiting geomorphological and hydrological features which contribute to the landscape (Gray, 2013) whilst also acting as a record of glacial and post-glacial history (Webb, 2013). In the past limestone pavements had a more extensive soil and vegetation cover with peat deposits containing post glaciation fragments such as juniper (*Juniperus* spp.) (Webb, 2013; Zseni et al., 2003). Woodland clearance to create calcareous grassland for grazing, led to the erosion of the soil layer to leave only patches of shallow soils on the surface (Webb and Crowle, 2023; Zseni et al., 2003). This clearance would have begun as far back as the Neolithic and accelerated during the Iron Age (Pigott and Pigott, 1963; Robinson, 2014). Rendzina soils made up of insoluble residue of weathered calcite are rare in Britain but occur in humid grikes (York, 2020). They have a high pH but are free draining with high organic matter content (York, 2020). It is possible also for soil to accumulate that is of a lower pH allowing a wider range of species such as *Calluna* to grow (British Ecological Society, 1954; Watson, 1918). The morphology of limestone pavements also provides variations in aspect and humidity allowing a mosaic of vegetation to develop occupying different ecological niches (Webb and Crowle, 2023). This geodiversity is important for ecosystem services and underpins biodiversity (Kubalíková et al., 2023; Webb, 2013).

Grikes create a humid and shaded space, as well as providing protection from grazers, and is suitable for plants typically found in woodlands with soils washed into grikes also helping to produce a botanically diverse microhabitat (Stevens, 2025; Webb, 2013). Grikes are typically dominated by ferns, bryophytes, and woodland ground flora species but a mixture of heathland and grassland species are also present (Stevens, 2025; Webb, 2013). Some plant species are rare and depend on the limestone pavement habitat to maintain populations (Webb and Crowle, 2023). For example, rigid buckler-fern (*Dryopteris villarii* (Bellardi) Woyn. ex Schinz & Thell.) is restricted to limestone pavements or allied habitats and due to grazing pressure is restricted to grikes (Webb and Crowle, 2023; York, 2020). Yorkshire sandwort (*Arenaria norvegica* subsp. *anglica* Holliday) is a localised species which grows on the shallow soils found on clints (Webb and Crowle, 2023). A significant proportion of the British population of *Actaea spicata* L. (baneberry) grows in pavements in North Yorkshire although this is typically an understory plant (von Zeipel and Eriksson, 2007; Ward and Evans, 1976). *Epipactis atrorubens* Hoffm. (dark-red helleborine) is a nationally scarce species confined to limestone habitats preferring shallow grikes (Walker, 2015). *Carex digitata* L. is another woodland species that is confined to Europe with populations in Western England and Wales (Tyler, 2002). Where this species is found, only a few individuals occur together (Tyler, 2002). Limestone pavements are not just an important habitat for plants, they are also home to invertebrates such as fritillary butterflies, whorl snails and spiders that rely on the flora and structures provided (Colebourn, 1974; Webb, 2013).

1.4. Conservation and management of limestone pavements

1.4.1. Removal of limestone

Historically, in Britain the main issue that limestone pavements faced was clint removal (Goldie, 1987). There is evidence of stone being removed to create ancient structures such as those found in Oxenber Wood, Yorkshire (Goldie, 1987). In the late medieval period, walls were built directly upon the pavement and traditionally, loose surface limestone was used (Goldie, 1993; Willis, 2011). Limestone pavement has also been removed to build roads and burnt to produce lime mortar or quick lime with lime kilns built out of clints or erratic stones from the site (Goldie, 1987; Willis, 2011).

More recently, pavements were destroyed to provide decorative stone (Webb, 2013). The trend for 'water worn' limestone began during the Victorian period and into the 1920s and 1930s rock gardens also became popular (Murphy, 2022). Removed stones are visible in areas close by to limestone pavements as decorative features, gate posts, wall tops and rockeries (Murphy, 2022; Stevens, 2025). Clints could also be purchased in garden centres (Goldie, 1993). Historically there was estimated to be 4,033 ha of limestone pavement in Britain (Webb and Crowle, 2023) however, the Ward and Evans (1976) survey of 537 individual pavements found only 16 pavements fully intact with around 2,343 ha left in total (Webb and Crowle, 2023). In areas where pavements were cleared by bulldozers, they quickly turned to grassland used for grazing with limited botanical interest (Goldie, 1987; Murphy, 2022; Webb, 2013). Limestone pavements are non-renewable landforms and removing the features destroys the biodiversity of the habitat (Webb, 2013). When clints are removed, grikes are filled in with rubble and soil or clints are removed completely to the grike base, removing the grike entirely and destroying the flora and fauna (Murphy, 2022). On newly damaged pavements there is little lichen growth which can take many years to grow back (Goldie, 1987; Rosén, 2006).

By the 1970s and 1980s removal of limestone pavement had reached a peak. Following the Ward and Evans (1976) survey, limestone pavements became protected through section 34 of the 1981 Wildlife and Countryside Act by issuing Limestone Protection Orders (LPOs) (HMSO, 1981). These orders are a legal instruction that prohibits disturbance or removal of limestone pavement by the owner or occupier of the land (Goldie, 1993). If found to be breaking an LPO, a person can be fined or imprisoned (Goldie, 1993). By 2000 all pavements were covered under the 1981 Wildlife and Countryside Act (Webb, 2013) making it the only natural environment which is protected by criminal law in the UK (Willis, 2011). When removal of limestone pavement ceased in Britain, the damage was pushed to Ireland, however protection there is increasing through the Habitats Directive of the European Union (Murphy, 2022). In Scotland protection of limestone pavements was removed in 2004 and no pavements in Wales are protected as sites are deemed small and not under threat (York, 2020) although lead mining in North Wales disturbed the pavements there (Willis, 2011).

1.4.2. Grazing

Limestone pavements have been grazed since pre-historic times (Goldie, 1987). There has been little research into the impacts of grazing on limestone pavements in Great Britain. In

The Burren farming has forged the landscape over the last 6,000 years, however, due to changes in farming practices the natural and cultural heritage of the landscape is being damaged (Williams et al., 2009). In the past animals were grazed on the pavements over winter allowing plants to grow and set seed during the summer to create botanically diverse areas (Williams et al., 2009). Typically livestock is now housed over winter, which has led to an increase in scrub encroachment and a decrease in species richness as light dependant species are shaded (Williams et al., 2009). To help improve the quality of the habitat, the Burren Farming for Conservation Programme, part of the Burren LIFE programme, was set up to replace the existing agri-environment scheme (Parr, 2014). It was farmer-focused and works on delivering conservation as a product (Parr, 2014). This allows farmers control of the management of the land with pay reflecting the condition by scoring winterages and lowland grassland (Parr, 2014). Such management practises used could include switching back to traditional, hardy cattle breeds such as Belted Galloway, Aberdeen Angus or Welsh Black over winter to create bare ground for recolonisation of favoured species (Willis, 2011) whilst also using new feedstuff and feeding systems to reduce the use of silage (Dunford, 2016).

Alvar grasslands are similar to the limestone pavements of Britain and Ireland growing on limestone bedrock with thin soils, a mosaic of vegetation similar in structure, and have a high conservation value (Rosén, 2006). They are rare, occurring in Sweden, Finland, Estonia, USA and Canada (Schaefer and Larson, 1997) but potentially we can learn practices relevant to limestone pavements from their management. On Öland in Sweden, emigration reduced land use leading to scrub and wood encroachment which further reduced grazing as the land became uneconomic (Rosén, 2006). This reduced the high level of biodiversity and the soil seed bank (Rosén, 2006). In recent years alvar grasslands have been restored by human clearing, managed grazing and good communication between interested parties (Rosén, 2006).

Overgrazing is also a problem on limestone pavements particularly by sheep or rabbits (Willis, 2011). Overgrazing reduces species diversity and the quality of ecological niches as grazing susceptible species, characteristic vegetation of clint tops, and those emerging from grikes are lost as well as removing potential woodland development (Stevens, 2025; Webb and Crowle, 2023; Willis, 2011). Rabbits are a particular problem in Yorkshire when farmers kill foxes, and due to climate change, rabbits can reproduce all year (Willis, 2011). It can be difficult to manage land with grazing animals as surrounding grassland or heathlands will require different management practises (Stevens, 2025). The number, type and intensity of animals should be considered when creating management plans. Willis (2011) provides details on how grazing different animals can impact pavements and how different management techniques can be used for conservation. For example, cows are non-selective grazers that stay away from unstable clints and grikes unlike sheep, who in large numbers can lead to overgrazing (Willis, 2011). However, allowing sheep onto pavements in August and early September can create bare soil for seedling colonisation whilst also reducing competition from woody vegetation (Willis, 2011). Also, by carefully positioning water and food, cattle can be used to trample areas of unwanted vegetation such as bracken (Willis, 2011). Using different breeds of goat can be effective for conservation as they are generalist grazers and light browsing by deer with sufficient trampling can aid seedling establishment and prevent a dense layer of ground vegetation from developing (Willis, 2011). Finally, rabbit populations should be monitored to allow control methods to be implemented before biodiversity is impacted (Willis, 2011).

There can also be issues from localised areas of nutrient enrichment due to animal droppings, fertiliser drift, dumping manure, bonfires and feeding continually in the same area (Williams et al., 2009; Willis, 2011). Nutrient enrichment allows weedy species such as nettles (*Urtica dioica* L.) and gorse (*Ulex europaeus* L.) to outcompete desirable plant species. Other negative species such as the invasive *Cotoneaster horizontalis* Decne. and farm ruderals will outcompete favoured species (Willis, 2011). Regular monitoring can be used to make sure management practices are providing high quality habitats all year round and for the long term although, due to lack of resources this rarely occurs (Blakesley and Buckley, 2016).

1.4.3. Managing wooded pavements

When wooded limestone pavements are not managed, an understory of hazel (*Corylus avellana* L.), bramble (*Rubus fruticosus* L.), blackthorn (*Prunus spinosa* L.) or hawthorn (*Crataegus monogyna* Jacq.) outcompetes favoured species and reduces diversity (Willis, 2011). There has been a reduction in coppice management in the last 100 years which reduces open spaces in lowland pavements and can shade-out light dependant species (Webb and Crowle, 2023). Where there has been planting of non-native trees, intense shade and waxy leaf litter can also lead to diversity loss (Willis, 2011). The Morecambe Bay LIFE project showed that by removing non-native species, building fencing, using traditional rotational coppicing methods and thinning as well as using traditional cattle breeds had a positive influence on limestone pavement species richness (Willis, 2011).

Furthermore non-native trees can be removed using ring barking that leaves deadwood as an additional microhabitat and avoids using chemicals (Willis, 2011).

1.4.4. Other human induced issues

Limestone pavements first became of interest to tourists in the Georgian era (Murphy, 2022). Over the years land has been purchased by organisations to create nature reserves around the limestone pavement (Goldie, 1996) such as Gait Barrows NNR or Asby Scar NNR and one third of the total area of limestone pavement lies within the Yorkshire Dales National Park (Murphy, 2022). This is extremely helpful for conserving limestone pavements however visitors can be an issue due to littering and trampling flora (Willis, 2011). Fragile plants such as bryophytes and lichens can take many years to grow back (Rosén, 2006). To aid in regeneration of pavement flora, replanting from native local stock can be used (Willis, 2011). Educating visitors will help the public to understand the habitat and improve awareness and protection (Willis, 2011).

The impacts of climate change on limestone pavements are largely unknown. Climate change is likely to affect species distributions such as the limestone fern (*Gymnocarpium robertianum* (Hoffm.) Newman) which is scattered around the UK (mostly in England and Wales) (Dines and Rumsey, 2020), but whose range might increase into different habitats (York, 2020). Whereas some nationally scarce species such as baneberry (*Actaea spicata*) might see a decrease in range, particularly out of the south and east (York, 2020). Areas such as The Burren could experience flooding or erosion, and coastal pavements of Scotland could be affected by storm surges (York, 2020). The soil chemistry may change if saline water enters the environment thus affecting which plants can grow (York, 2020). Grikes may also act as a refuge during climate change as temperatures are lower and more stable with a higher relative humidity, lower light intensity and lower air speed (York, 2020).

1.4.5. Conservation of limestone pavements

Limestone pavements can be included in a SSSI (Site of Special Scientific Interest) or SAC (Special Areas of Conservation), however these do not afford the same protection as an LPO (Goldie, 1995). In England, there are 174 LPOs, 98 sites are SSSI, and 52 sites are SAC. Examples such as Eaves Wood and Gait Barrows (Lancashire) and Humphrey Head (Cumbria) fall into both a SSSI and a SAC (Natural England, 2023). They are also a priority habitat of the 1992 European Union Habitats and Species Directive (Commission of the

European Communities, 1992), but limestone pavements are listed as Least Concern in the European Red List of Habitats (Webb and Crowle, 2023).

Much of the limestone pavement in Britain is currently not deemed to be in favourable conservation status (Webb and Crowle, 2023). For pavements to be in a favourable condition they must maintain current physical structure and low productivity soils, as well as having herbivory levels that enable the characteristic vegetation structure (Webb and Crowle, 2023). This also includes the associated bryophyte communities of which some species, like vascular plants, rely on this habitat to live.

1.5. What are bryophytes?

Bryophytes are an unofficial group of small, non-vascular, spore-producing plants that are characterized by a life cycle with alternate generations (Vanderpoorten and Goffinet, 2009). They are the only land plants to have a dominant, haploid gametophyte (green leafy plant) which alongside the diploid sporophyte (spore-producing structure) differs architecturally between the three divisions in this group (Vanderpoorten and Goffinet, 2009). They are:

Marchantiophyta. The liverworts are divided into those that are leafy with stems and leaves and thallose liverworts with no distinct stems or leaves (Atherton et al., 2010). There are around 5000 extant species of liverwort and around 300 of those are found in Britain (Atherton et al., 2010; Vanderpoorten and Goffinet, 2009). Liverworts are likely to be the first plants that colonised land 264 million years before flowering plants evolved (Porley, 2013).

Bryophyta. Mosses are either acrocarpous growing upright with capsules at the top of stems or pleurocarpous growing in wefts or mats that spread horizontally with capsules on the sides of stems (Atherton et al., 2010). There are around 12,000 species of moss with 763 species in Britain (Atherton et al., 2010; Vanderpoorten and Goffinet, 2009).

Anthocerotophyta. The hornworts are the least diverse of the three groups and are named after their horn-like sporophyte (Vanderpoorten and Goffinet, 2009). They lack leaves and resemble thallose liverworts (Atherton et al., 2010). In Britain there are four species of hornwort (Atherton et al., 2010).

There is no single evolutionary origin of bryophytes with the three divisions evolving separately from a green algae (Charophyceae) ancestor (Porley, 2013). In total, there are around 16,000 known species of bryophyte, however there is more likely to be around 22,000 species (Porley, 2013). They come in a variety of forms such as the early pioneers on mineral soils (e.g. *Riccia*), tall turfs mostly found on temperate forest floors (e.g. *Polytrichum*), cushions on rocks and trees (e.g. *Grimmia*), mats attached by rhizoids (e.g. *Homalothecium*), and fans creeping on vertical bases (e.g. *Neckera*) (Mägdefrau, 1982).

As bryophytes do not have roots, developed vascular tissue, or lignin, they do not grow tall and instead absorb water and nutrients across the whole plant surface (Porley, 2013). However, their poikilohydric lifestyle means that they can suspend metabolism and dry out to resume activity when water becomes available again (Porley, 2013). Bryophytes are found in nearly every ecosystem across all continents and can dominate the vegetation in harsh conditions where other plants would fail to survive, such as in the Antarctic which is almost entirely cryptogrammic (Longton, 1984; Vanderpoorten and Goffinet, 2009). In areas where there is more moisture, luxuriant epiphytic communities can flourish (Vanderpoorten and Goffinet, 2009) and in the tropics they can even exist as epiphylls growing on the leaves of vascular plants (Doležal et al., 2023). In Britain, the bryophyte flora far surpasses that of mainland Europe with over 60% of total European species (compared to 20% of European flowering plants) due to the humid oceanic climate (Porley and Hodgetts, 2005). Some species have their only European localities here and others are rare globally (Porley and Hodgetts, 2005).

1.6. Why are bryophytes important?

Bryophytes face pressure from habitat loss through intensification of agriculture, forestry, lack of management, housing development, competition from invasive species, and atmospheric pollution (Porley and Hodgetts, 2005). Bryophyte communities have also been destroyed through removal to be used in floristry and horticulture (Porley, 2013). Although bryophytes are small and often overlooked, they play many important roles.

1.6.1. Colonisation

Bryophytes are typically the early pioneers of bare substrates, allowing later colonisation of vascular plants and other organisms from higher trophic levels by promoting soil formation, trapping wind-blown material, and forming undecomposed organic matter (Doležal et al., 2023; Vanderpoorten and Goffinet, 2009). Bryophytes also help to stabilise soils against erosion particularly in arid areas by binding particles into stable aggregates (Vanderpoorten and Goffinet, 2009). In soils they can mediate temperature including shielding soils from heat and allowing permafrost to persist (Porley, 2013; Vanderpoorten and Goffinet, 2009). Bryophytes also show positive benefits to native plant recruitment as substrates for seedling establishment. For example, *Picea abies* (L.) H. Karst. establishment was improved by microsites of *Sphagnum* spp. and *Pleurozium* sp. on logs in native forests (Hörnberg et al., 1997).

1.6.2. Water

Bryophytes have an extremely high water holding capacity of around 1500% of their dry weight which can be released slowly to avoid loss of soil moisture (Porley, 2013; Slate et al., 2024; Vanderpoorten and Goffinet, 2009). Epiphytic bryophytes are able to intercept rainfall at greater rates than trees or vascular epiphytes, reducing flash floods and landslides and aquatic bryophyte cushions reduce water velocity as well as filtering particles (Porley and Hodgetts, 2005; Vanderpoorten and Goffinet, 2009). Climate change may affect the relationship between bryophytes and water. If there is excessive amounts of water, bryophytes may become overwhelmed and changes to evaporation and hydration cycles may stop their ability to retain water and a positive carbon balance (Slate et al., 2024).

1.6.3. Nutrient cycling

Bryophytes are an important part of nutrient cycling. Firstly, they can make nutrients available for other organisms. Through symbiosis with cyanobacteria, nitrogen is fixed from the atmosphere and can be stored in bryophyte tissue which is then leached upon decomposition (Slate et al., 2024; Vanderpoorten and Goffinet, 2009). However, it is possible that bryophytes reduce availability of nitrogen for vascular plants and microbes (Turetsky, 2003). *Sphagnum* in the form of peat fixes CO_2 for long term storage with more carbon stored in *Sphagnum* than any other genus of plant (Vanderpoorten and Goffinet, 2009). Due to their involvement in the water, carbon and nitrogen cycle, bryophytes could act as a buffer to change in many ecosystems (Slate et al., 2024).

1.6.4. As indicators

As bryophytes have short life cycles and can respond quickly to environmental changes, they are good indicators of climate change and atmospheric deposition of heavy metals (Porley and Hodgetts, 2005). Bryophyte herbarium material can be used to ascertain past levels of pollution (Porley and Hodgetts, 2005). Forbes (1994) also showed how presence-absence data on bryophytes combined with vascular plant cover data can be used to indicate discrete surface disturbances in the arctic and Frego (2007) suggests that bryophytes could be used as indicators of forest integrity.

1.7. Bryophytes in limestone pavements

The bryophyte flora of limestone pavements is unique with a high number of species (Bates, 1978; Downing, 1992). Acrocarpous mosses are more likely to be found than the larger, longer-lived pleurocarps (Downing, 1992). Species found on limestone pavements are sometimes similar to those of calcareous cliffs, rocks and walls (Watson, 1918) and the different features and geochemistry allow different communities to form (Spitale and Nascimbene, 2012) with the pH of the substrate potentially being the most important factor in determining species composition and richness (Tyler et al., 2018). Löbel et al. (2006) found that bryophyte and lichen species richness increased as soil pH increased. Calcicole (lime loving) bryophytes have some distinct morphological features such as extreme papillosity (raised structures on leaf surface), leaves with long hair points, and rolled leaves (Redfearn, 1957). Only a few limestone pavement species are obligate calcicoles and species that are restricted to calcareous rocks show concentrations of calcium much higher (16-17 times) than species found on non-calcareous rocks (Bates, 1982; Redfearn, 1957). These species may have a higher calcium requirement for permeability control and to maintain cell membranes (Bates, 1982).

In grikes, bryophytes are prominent especially where light levels are very low (Stevens, 2025). Species found here are like those found in calcareous woodland such as *Ctenidium molluscum* (Hedw.) Mitt. which is one of the best indicators of a calcareous habitat (Atherton et al., 2010; Webb and Crowle, 2023). Other examples include *Reboulia hemisphaerica* (L.) Raddi, a distinct calcicole liverwort also found under boulders (Atherton et al., 2010), *Neckera crispa* Hedw. grows on the sides of grikes, and *Tortella densa* (Lorentz & Molendo) Crundw. & Nyholm, the rarest *Tortella* species in Britain and Ireland occurs mostly in northern England and western Ireland (Blockheel et al., 2014). Redfearn (1957) found that grikes filled with humus had a more complex bryophyte flora with species such as *Pohlia cruda* (Hedw.) Lindb., *Trichostomum crispulum* Bruch, and *Ditrichum flexicaule* (Schwägr.) Brockm. growing there. Holyoak and Long (2005) found that an unshaded, damp grike in County Mayo provided a suitable habitat for the endangered *Bryum gemmiparum* De Not. which is typically found further south on sunny rocks along the river Usk (Atherton et al., 2010; Poponessi et al., 2020).

On the limestone surface, *Tortella tortuosa* (Schrad. ex Hedw.) Limpr. and *Syntrichia ruralis* (Hedw.) F. Weber & D. Mohr are the main species that form moss cushions (Sand-Jensen and Hammer, 2012). *Tortella tortuosa* is an obligate calcicole requiring calcium to survive but is found in most areas of Britain and Ireland (Atherton et al., 2010). Other species found on clint tops are *Schistidium apocarpum* (Hedw.) Bruch & Schimp. in small tufts which can detach easily from the rock when dried out, *Ctenidium molluscum* in mats, and the widespread *Schistidium crassipilum* H.H. Blom which requires bare rock to grow (British Ecological Society, 1954; Tyler et al., 2018). There are some species that grow on limestone pavements which are more typically associated with arid habitats such as *Grimmia dissimulata* E. Maier (Blockheel et al., 2014). Limestone pavements can be dry areas as water quickly infiltrates the rock (Downing, 1992). *Tortella nitida* (Lindb.) Broth. typically grows on walls and in churchyards but can grow on open limestone pavement (Blockheel et al., 2014) and *Bryum knowltonii* Barnes also exists in unshaded areas (Holyoak and Long, 2005). *Fissidens dubius* P. Beauv. is a widespread species found mostly on dry limestone but can also occur in sheltered and damp areas of the pavement (Atherton et al., 2010; Watson, 1918). After colonisation by early bryophyte species, the microclimate is improved so that less drought resistant species are able to survive (Sand-Jensen and Hammer, 2012).

The solution cups on clints often become colonised by bryophytes and add an extra microhabitat rather than being a microcosm of the site vegetation (Doddy and Roden, 2014; Lowe, 1981). Organisms that colonise the solution hollows must be adapted to frequent infilling and drying out as well as receiving direct sunlight (Doddy and Roden, 2014). In a study by Lowe (1981) bryophytes made up 10.8% of the 83 species found in solution hollows. Mosses commonly found were *Tortella tortuosa*, *Cratoneuron filicinum* (Hedw.) Spruce and *Atrichum undulatum (Hedw.) P. Beauv* (Lowe, 1981). Another species that can be found in solution cups is *Pseudocalliergon turgescens* (T. Jensen) Loeske, a very rare moss that is found on one pavement in North Lancashire (Webb and Crowle, 2023) but can also be found in central and northern Europe, Asia, Bolivia and New Guinea (Slack et al., 1988). It was also rediscovered in New York State where previously it had only been recorded as a subfossil (Slack et al., 1988). *Bryum neodamense* Itzigs. occurs mostly in other calcareous habitats but can be found in solution hollows (Blockheel et al., 2014).

Having a high proportion of heterogenous microhabitats in a small area with gradients in humidity and light allow for a high diversity of bryophytes in limestone pavements (Lundholm and Larson, 2003; Poponessi et al., 2020). During early succession, bryophyte cover and diversity is high, however over time, as organic matter accumulates, they are outcompeted by vascular plants and the diversity of the microhabitat decreases (García de León et al., 2016; Rodgers, 2018). Moss cushions hold a high density of seeds (Zamfir, 2000) and as moss cushions increase in size, the vascular species richness of the cushion also increases due to a higher humidity and water storage capacity as well as collecting nutrients from detritus (Sand-Jensen and Hammer, 2012). A cover of bryophytes also has a positive effect on moth diversity and rare moth species richness (Patton, 2022). Bryophytes can be used as a medium on which to pupate and as food for moth larvae in a water and nutrient limited environment (Patton, 2022).

However, many studies have shown a negative relationship between bryophyte cover and vascular plant cover (García de León et al., 2016; Löbel et al., 2006; Zamfir, 2000). A thick cover of moss can inhibit emergence of vascular limestone species such as those of *Arenaria serpyllifolia* L. and *Veronica spicata* L. as it is difficult for small dicotyledon seed leaves to grow through the moss mat (Zamfir, 2000). Mosses can also compete with seedlings for water particularly in dry environments and a low light intensity from increased growth of moss shoots in wet environments may also inhibit germination (Otsus and Zobel, 2004; Zamfir, 2000). Moth species which rely on vascular plant species for food will be negatively affected by a high cover of bryophytes (Patton, 2022).

Tyler et al. (2018) found that in alvar grasslands grazing had a mostly positive effect on bryophytes potentially due to reduced competition with vascular plants and disturbance stopping any species dominating. *Ditrichum flexicaule* can colonise recently disturbed areas and some species such as *Bryum argenteum* Hedw. and *Ceratodon purpureus* (Hedw.) Brid. were more common in heavily grazed areas (Tyler et al., 2018). Species negatively affected by grazing were *Hylocomium splendens* (Hedw.) Schimp., *Hypnum cupressiforme* Hedw., *Plagiomnium affine* (Blandow) T.J. Kop., rare *Tortella* species, and *Hylocomiadelphus triquetrus* (Hedw.) Ochyra & Stebel, which prefers closed vegetation (Rodgers, 2018; Tyler et al., 2018). Some bryophyte species found in alvars in North America and Europe exist on limestone pavements in Britain and Ireland such as *Myurella julacea* (Schwägr.) Schimp., *Tortella inclinata* (R. Hedw.) Limpr., *Riccia sorocarpa* Bisch., *Fissidens adianthoides* Hedw., *Polytrichum juniperinum,* and *Abietinella abietina* (Hedw.) M. Fleisch (Schaefer and Larson, 1997). Where there is little disturbance from grazing, species may move to clint tops (Stevens, 2025).

1.8. Niche separation

The niche theory is the idea that every species has a range of environmental conditions and resources within a space where it can maintain a long-term average net reproductive rate greater than one (Chase, 2011; Silvertown, 2004). It was first introduced by the zoologists Jospeh Grinnell and Charles Elton but the niche theory can be seen in many different species (Silvertown, 2004). An easy example to observe is the zonation of plants in tidal areas brought about by many factors but in particular salinity and inundation tolerance (Janousek et al., 2019). Defining the ecological niche that a species can occupy requires an understanding of the complex interactions between a multitude of different drivers such as microclimate, vegetation structure, resource availability and biotic interactions (Doležal et al., 2023). A niche can be described as either fundamental where a species can maintain a positive population in the absence of other species or a realised niche where other species are present (Chase, 2011). Niche separation (species not competing) can occur when a habitat has greater variability with resources distributed within the space and shared between species (Chase, 2011; Pernthaler, 2017). As species diversity increases, so does niche separation (M'Closkey, 1978).

1.8.1. Niche separation in bryophytes

Niche separation has been observed in bryophytes in multiple studies. The most important environmental factor influencing bryophyte organisation is moisture (Craw, 1976). This can be seen in Antarctica where the pattern of zonation was observed by Lewis Smith (1999) in three moss species whose distribution was predominately controlled by moisture availability. *Bryum argenteum* occupied the wettest areas found, *Ceratodon purpureus* occupied the driest areas, and *Bryum pseudotriquetrum* occupied the mesic ecotone (Lewis Smith, 1999). In a study by Kimmerer and Allen (1982), the interaction between water and bryophyte species growing on a bare cliff in a river shaped the organisation of the community. At the base of the cliff *Fissidens obtusifolius* Wilson grew outcompeted as it has a greater association with bare rock and the divided leaves allows flowing water to pass through with little resistance (Kimmerer and Allen, 1982). Higher upon the cliff *Conocephalum conicum* (L.) Dumort. grows. This liverwort is less tolerant of flooding and is more likely to be removed from the rock by the flow of water (Kimmerer and Allen, 1982). When there is little disturbance, these two species show niche separation and live in equilibrium, however during flooding other species colonise the rock between the two colonies, creating a higher diversity (Kimmerer and Allen, 1982). Similarly, a study of eight *Sphagnum* species from a mire adjacent to a lake in Michigan showed that distance from the edge of the water affected species cover (Vitt and Slack, 1975). Whilst there was some niche separation, a few of the species showed a niche overlap. *Sphagnum teres* (Schimp.) Ångstr. ex C. Hartm. had a narrow niche breadth occupying the area 0 – 20 m from the edge of the water with very little overlap, whereas *Sphagnum capillaceum* (*Sphagnum capillifolium* (Ehrh.) Hedw.) occupied the area 30 – 110 m from the edge of the water overlapping a few other *Sphagnum* species (Vitt and Slack, 1975). Where there is an overlap in niche it may be due to pre-emptive competition (rather than interactive competition defined by niche theory) where bryophytes are first to colonise an area and so capture resources from other possible colonising species (Young, 1997). In fact, the nature of bryophytes may contradict other aspects of niche theory. For example, many species are opportunistic and as bryophytes rely on multiple different regeneration methods, this flexibility will affect the success of a species within a community (Young, 1997).

1.8.2. Niche separation in limestone pavements

It is possible to observe niche separation in plants in limestone pavements as there is a limit to which species can occur together (Silvertown, 1983). In a study by Silvertown (1983), it was thought that the distribution of plants in grikes could potentially be influenced by grike depth and grazing. Plants not resistant to grazing will struggle to persist in shallower grikes and plants intolerant to shade will not grow well in deep grikes and so niche theory would suggest that the grike would be partitioned by grike depth (Silvertown, 1983). It was found that there was niche overlap between the two vascular plant species (*Mercurialis perennis* L. and *Geranium robertianum* L.) in relation to depth in the grike (Silvertown, 1983). This could be due to lack of interspecific competition and instead disturbance, flora dynamics, and emptiness of the habitat (Silvertown, 1983).

Another instance of niche separation being observed in the grikes of limestone pavements is from the British Ecological Society (1954) summer meeting where zonation of bryophytes in grikes in Colt Park Wood are recorded (Figure 1). For both sizes of grike, the species present changed deeper into the grike. In the narrow grike, fewer species were present with *Mnium hornum* Hedw. and *Atrichum undulatum* near the top of the grike, with *Thuidium tamariscinum* (Hedw.) Schimp. and *Plagiothecium sylvaticum* (*Plagiothecium nemorale* (Mitt.) A. Jaeger) appearing between 1 and 2 ft. At the base of the grike only *Thamnium alopericum* (*Thamnobryum alopecurum* (Hedw.) Gangulee) occurs. In the wider grike more species are present with many species at the top of the grike not observed in the narrow grike such as *Camptothecium sericeum* (*Homalothecium sericeum* (Hedw.) Schimp.)*, Ctenidium molluscum, Neckera crispa,* and *Mnium undulatum* (*Atrichum undulatum*). Species that are found higher in the narrow grikes such as *Mnium hornum* and *Thuidium tamariscinum* are found deeper in the wider grikes.

This study is rare in focusing on bryophytes in limestone pavements. However, it is 70 years old and only took place on one site. Although bryophytes are an integral part of limestone pavement flora, there have been few studies focusing on these plants.

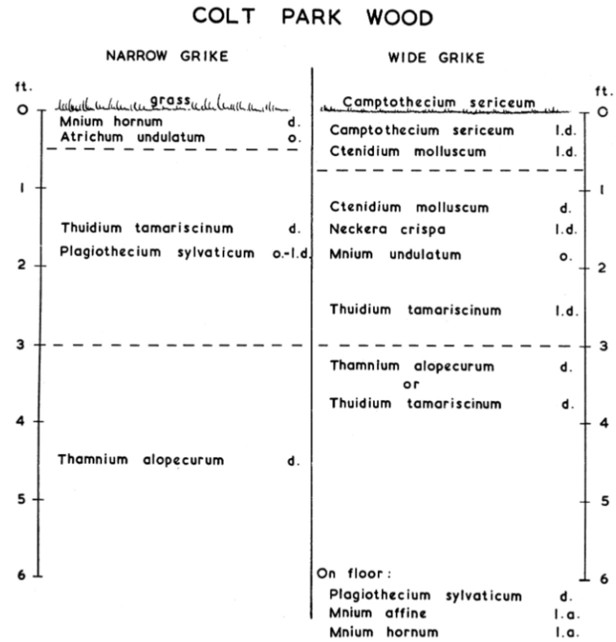

Fig. 2. Moss zonation in grikes.

Figure 1. Zonation of bryophytes in Colt Park Wood limestone pavement in narrow and wide grikes taken from BES summer meeting 1954 (British Ecological Society, 1954).

1.9. Thesis aims

The limestone pavements of northern England are variable in size, altitude, and vegetation and contain species which only occur in this habitat. Most of the work conducted on bryophytes in limestone pavements is outdated, even though pavements can be dominated by bryophytes including many rare and interesting species. Apart from the brief mention of bryophyte zonation in the British Ecological Society (1954) summer meeting, there have been no studies on bryophyte niche separation in limestone pavements. In fact, there has been very little work on niche separation in limestone pavements in general.

As grikes could act as a refuge for species from climate change, it is important to understand how plants occupy this space currently to predict how future changes could impact the rare flora found in limestone pavements. Observing the niche separation in bryophytes in grikes could help to understand how bryophytes may respond to environmental change as well as differing management practices. This thesis will aim to discover if niche separation is observed in bryophytes in the grikes of limestone pavements across sites in Northern England. It will also look at how the different sizes of grikes will affect bryophyte organisation and composition.

2. Methods

2.1. Study sites

Seventeen plots across eight sites that contain areas of limestone pavement in northern England (Table 1, Figure 2) were selected for this study. Ten plots were made up of open limestone pavement which are those that contain less than 10% scrub cover (Webb and Crowle, 2023) (Figure 3). Seven plots were made up of wooded limestone pavement which are those that have mature trees and scrub cover greater than 10% (Figure 4). Each plot comprised of 250 m^2, either in a 50 x 50 m plot or a 25 x 100 m plot. In some areas, patches of limestone pavement are small or broken up and so the entirety of the plot may not be made up of usable pavement.

Table 1. List of sites used in this study with their location, number of plots at each site, and whether plots used were open or wooded. Open pavements are those with scrub cover < 10%. Wooded pavements are those with mature trees and scrub cover > 10%.

Site Name	County	Number of Plots	Vegetation
Warton Crag	Lancashire	2	Open, Wooded
Eaves Wood	Lancashire	2	Wooded
Hyning Scout Wood	Lancashire	2	Wooded
Dalton Crags	Cumbria	2	Open, Wooded
Hutton Roof Crags	Cumbria	2	Open
Farleton Knott	Cumbria	3	Open
Oxenber Woods	North Yorkshire	1	Wooded
Ingleborough	North Yorkshire	3	Open

Figure 2. Map showing locations of sampling sites in Northern England. Sampling sites used were Warton Crag, Eaves Wood, Hyning Scout Wood, Dalton Crags, Hutton Roof Crags, Farleton Knott, Oxenber Woods and Ingleborough.

Figure 3. Open limestone pavement at Hutton Roof Crags, Cumbria (Roberts, 2025a).

Figure 4. Wooded limestone pavement at Hyning Scout Woods, Lancashire (Roberts, 2025b).

2.2. Sampling

At each plot a six-figure grid reference and the altitude in metres was first recorded. To randomly select grikes to be studied, strategic random sampling was used. Coordinates of the grikes within the plot were selected using randomly generated numbers between 1 and 100. Where there was not a grike in the coordinate selected, the nearest grike would be used. This was repeated 30 times until all grikes were marked.

The start and end of a grike was defined as a continuous, undisturbed fissure. Where a grike would intersect with another or where there was a barrier such as rubble, this would be the end of the grike. Grikes had to be 1 m or longer for selection. At each grike the minimum and maximum width, the maximum depth and the length in cm were recorded as well as the percentage cover of other non-bryophyte species. Each grike was also assigned a category based on orientation, width and depth (Figure 5). A meter rule was placed in the centre of the grike on the clint top from where specimens were recorded along the length of the rule through the depth of the grike. Only specimens growing on the rock or soil upon the rock were recorded and not those growing on other surfaces such as the trunk of a tree growing out of the grike.

1. N-S, narrow, shallow.
2. N-S, narrow, medium.
3. N-S, narrow, deep.
4. N-S, wide, shallow.
5. N-S, wide, medium.
6. N-S, wide, deep.
7. E-W, narrow, shallow.
8. E-W, narrow, medium.
9. E-W, narrow, deep.
10. E-W, wide, shallow.
11. E-W, wide, medium.
12. E-W, wide, deep.

Figure 5. Categories assigned to each grike based on grike orientation and grike depth and width. Narrow grikes are those with a minimum width < 20 cm. Wide grikes are those > 20 cm. Shallow grikes are those with a depth < 40 cm. Medium grikes are those with a depth between 40 and 100 cm. Deep grikes are those that are > 100 cm.

For each specimen the species name, specimen depth in cm (taken from the middle of the specimen), the aspect of the wall the specimen is growing on unless growing on the floor and whether the specimen is growing vertically or horizontally on the grike wall (such as on a ledge) or at the floor of the grike. In the open pavements, light levels were recorded for each specimen on the clint top closest to the specimen and then immediately after the light level aligned with the centre of the specimen. The light meter used during this study was the Skye Instruments Quantum Sensor which was taped to the bottom of a garden cane to allow it to be placed in the grike horizontally, keeping the sensor upright. In wooded pavements light levels were not taken and instead a percentage cover estimate of the canopy cover was recorded at each grike.

This process of recording the grike dimensions and specimens within the grike was repeated for 30 grikes in the plot.

Species name used were those as of Atherton et al. (2010) in Mosses and liverworts of Britain and Ireland: a field guide. Updated names are included in brackets from Tropicos.org (2025) and British Bryological Society (2025). For two genera where identifications were difficult, species were listed as *Fissidens* spp. and *Hypnum* spp.

2.3. Data analysis

Statistical analysis was carried out using R version 4.4.2 (R Core Team, 2024).

To assess the effects of grike characteristics on light, generalised additive models (GAM) were used using the *mgcv* package (Wood, 2011). Light levels recorded between clint top and specimen level were used to calculate percentage reduction in light between these two points. The relationship between depths of specimens and percentage reduction in light was tested using Spearman rank correlation and models were further compared using Akaike Information Criterion (AIC). Grike characteristics were added to the GAM to test whether they would be good predictors of percentage reduction in light. Models that exhibited a lower AIC showed which grike characteristics were good predictors. These characteristics were then added as an interaction in the GAM and models with a lower AIC showed an interaction with specimen depth and percentage reduction in light.

To test how light affects species composition within the grike, violin plots were created using *ggplot2* (Wickham, 2016). The Kruskal-Wallis test with Nemenyi post-hoc test from the *PMCMRplus* (Pohlert, 2024) was used to determine statistically significant differences between species. Generalised additive models were then used to see how predictors of percentage reduction in light interacted with specimen depth and to see which species had a relationship with these predictors that was a statistically significant non-constant function. For wooded pavements, GAMs were used to see how different grike characteristics interacted with specimen depth rather than percentage reduction in light. Regression modelling was used to see how much variability in specimen depth could be explained by light. To see if any other variables affected species composition, violin plots and Kruskal-Wallis tests with Nemenyi post-hoc tests were used to see if the aspect and position affected the species composition for each species.

To calculate niche separation of species in open pavements, methods were used from Silvertown et al. (2001). A matrix of specimen depth and percentage reduction in light was created using niche boxes where one unit equals either 10 cm or 10%. The relative abundance of each species and weighted means for depth and light was calculated for each niche box which was then used to calculate niche separation using Pianka's index (Pianka, 1973). Pianka's index (O_{kl}) is the sum of the proportional use of a resource by group one (P_{il}) multiplied by the proportional use of the resource by group two (P_{ik}) divided by the square root of the sum of P_{il}^2 multiplied by the sum of P_{ik}^2 which can be represented using the equation:

$$O_{kl} = \frac{\sum_i^n P_{il} P_{ik}}{\sqrt{\sum_i^n P_{il}^2 \sum_i^n P_{ik}^2}}$$

In this study the proportional use of the resource is the weighted mean depth or percentage reduction in light in each niche box. This was repeated for families, lifeform and division. Plots for relative abundance in niche boxes were created using Microsoft Excel and Microsoft PowerPoint (Microsoft Corporation, 2025a; Microsoft Corporation, 2025b).

To compare species compositions in open and wooded pavements, Mann-Whitney U tests were run for each species on specimen depth between open and wooded pavements. To compare different types of grikes, the categories were modified to align with previous analysis, discounting aspect. Grikes were categorised as narrow with a grike maximum width less than 30 cm and either shallow (depth less than 50 cm), medium (depth between 50 and 99 cm) and deep (over 100 cm) forming six new categories. Violin plots and Kruskal-Wallis tests with Nemenyi post-hoc tests were used to see differences between species and categories between open and wooded pavements.

The Shannon index (Shannon, 1948) was calculated for each depth unit and grike category in open and wooded pavements, and each light unit and niche box in open pavements. A comparison of mean percentage reduction in light and mean specimen depth was compared with Ellenberg light values obtained from BRYOATT (Hill et al., 2017).

3. Results

3.1. General results

In total 510 grikes were recorded, with 300 grikes in the open pavements and 210 grikes in the wooded pavements (Table 2). In the open pavements, the grikes recorded ranged from 53 cm to 620 cm in length and 12cm to 211 cm in depth with minimum widths of 1 cm to 60 cm and maximum widths of 4 cm to 98 cm. In the wooded pavements, the grikes recorded ranged from 75 cm to 985 cm in length and 10 cm to 160 cm in depth with minimum widths of 2 cm to 61 cm and maximum widths of 7 cm to 103 cm. In open pavements, category 2 grikes (narrow and medium depth) were most common with 96 of 300 grikes and in wooded pavements, category 4 (wide and shallow) grikes were more common with 81 of 210 grikes (Table 2).

Table 2. The number of grikes in open and wooded pavements for each new grike category. 1: narrow and shallow, 2: narrow and medium, 3: narrow and deep, 4: wide and shallow, 5: wide and medium, 6: wide and deep.

Category	Open Pavements	Wooded Pavements
1	65	66
2	96	28
3	33	5
4	30	81
5	51	26
6	25	4
	300	**210**

From the seventeen sites visited a total of 3464 observations (Table 3) were made with 1852 specimens recorded in open pavements and 1614 specimens recorded in wooded pavements. These records were formed of 27 species, 25 of those were found in the open pavements and 21 were found in the wooded pavements (Appendix 1). Most species occurred in both types of sites; however, two species were only found in wooded pavements and each only in one site. *Amblystegium serpens* was recorded at Oxenber Woods and *Plagiochila porelloides* was recorded at Dalton Crags. In the open sites *Anomodon viticulosus* was only recorded at Hutton Roof, *Bryum radiculosum* had one observation at Farleton Knott and *Encalypta streptocarpa* also had only one observation at

Hutton Roof. *Pseudoscleropodium purum, Reboulia hemisphaerica* and *Rhytidiadelphus squarrosus* were also only found in open sites. The most recorded species across all sites was *Ctenidium molloscum* with 732 records (Table 3).

Table 3. Species recorded in this study with total number of observations across all sites. Species name used were those as of Atherton et al. (2010). Updated names are included in brackets from Tropicos.org (2025) and British Bryological Society (2025).

Observations	Species
1	*Bryum radiculosum* Brid.
1	*Encalypta streptocarpa* Hedw.
2	*Amblystegium serpens* (Hedw.) Schimp.
2	*Climacium dendroides* (Hedw.) F. Weber & D. Mohr
3	*Rhytidiadelphus squarrosus* (Hedw.) Warnst.
5	*Plagiochila porelloides* (Torr. ex Nees) Lindenb.
9	*Anomodon viticulosus* (Hedw.) Hook. & Taylor
9	*Rhytidiadelphus triquetrus* (*Hylocomiadelphus triquetrus* (Hedw.) Ochyra & Stebel)
17	*Hypnum resupinatum* Taylor
19	*Neckera complanata* (Hedw.) Huebener
21	*Reboulia hemisphaerica* (L.) Raddi
22	*Pseudoscleropodium purum* (Hedw.) M. Fleisch.
33	*Hypnum lacunosum* (*Hypnum cupressiforme* var. *lacunosum* Brid.)
42	*Hypnum cupressiforme* Hedw.
62	*Ditrichum gracile* (*Flexitrichum gracile* (Mitt.) Ignatov & Fedosov)
68	*Didymodon insulanus* (De Not.) M.O. Hill
76	*Kindbergia praelonga* (Hedw.) Ochyra
96	*Homalothecium sericeum* (Hedw.) Schimp.
196	*Plagiomnium undulatum* (Hedw.) T.J. Kop.
225	*Thuidium tamariscinum* (Hedw.) Schimp.
231	*Fissidens spp.*
240	*Scapania aspera* M. Bernet & Bernet
288	*Neckera crispa* Hedw.
323	*Tortella tortuosa* (Schrad. ex Hedw.) Limpr.
363	*Eurhynchium striatum* (Schreb. ex Hedw.) Schimp.
378	*Thamnobryum alopecurum* (Hedw.) Gangulee
732	*Ctenidium molluscum* (Hedw.) Mitt.
3464	**27**

3.2. Light

In open pavements, the percentage reduction in light from clint top to specimen level within the grike showed a significant non-linear relationship with specimen depth (p-value < 0.001). As the depth of the specimen increases, so does the percentage reduction in light (Figure 6). In the first 50 cm of the grike, the percentage reduction in light increases rapidly, however there is a greater spread of data over this distance with other variables likely affecting light in the upper area of the grike.

It was found that the percentage reduction in light did not differ significantly between different aspects or where specimens were growing with no definite aspect (Figure 7) (p-value = 0.5176). This overlap can also be seen in Figure 8.

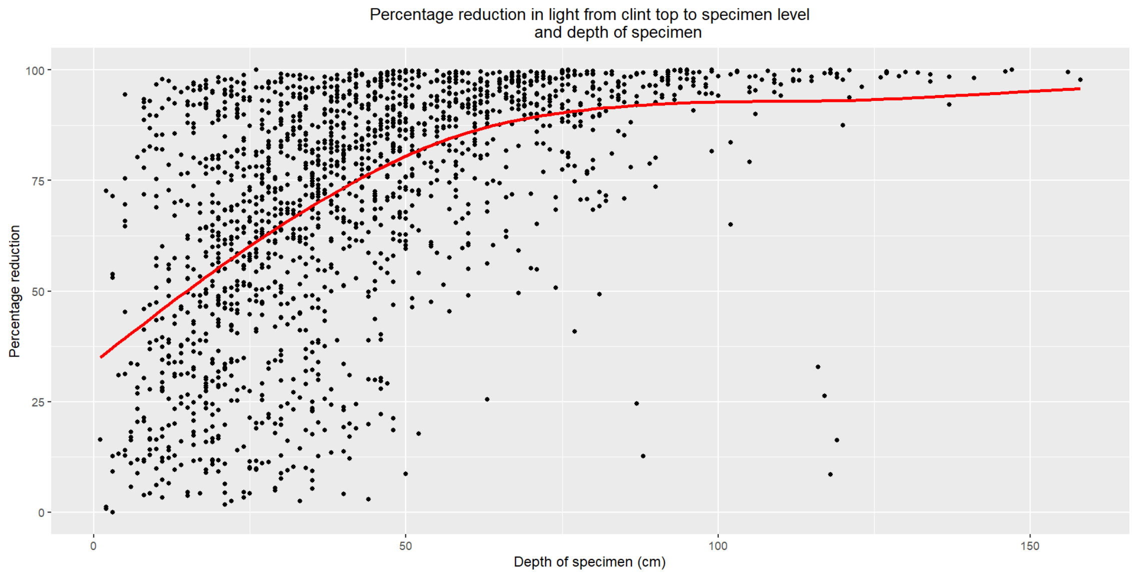

Figure 6. The relationship between specimen depth and percentage reduction in light from clint top to specimen level. Significant non-linear relationship (p-value < 0.001) with percentage reduction in light increasing as depth of specimen increases.

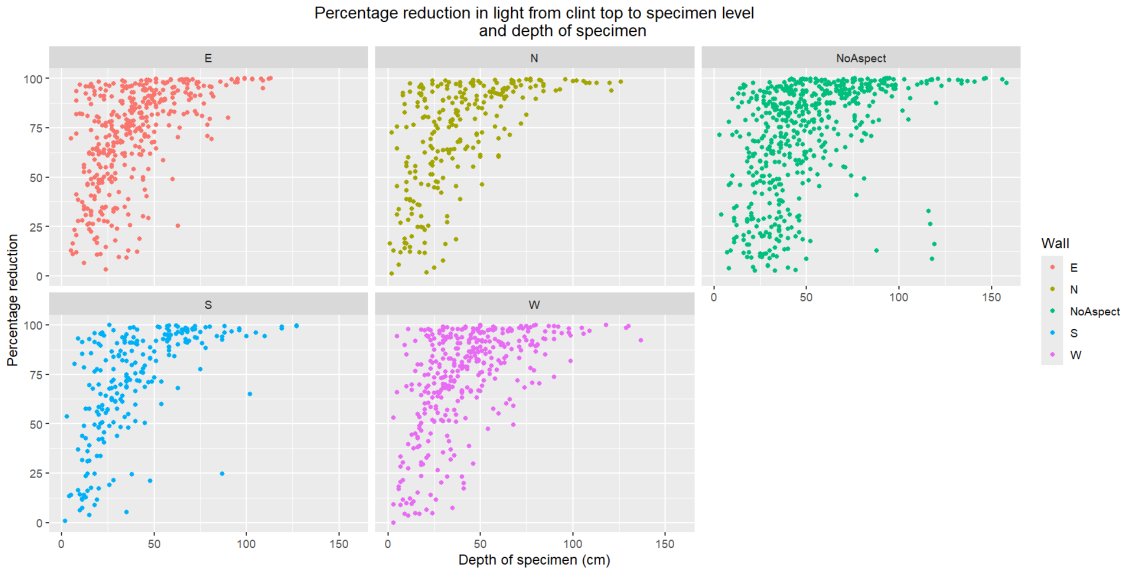

Figure 7. The percentage reduction in light for each aspect. From left to right: East, North, No Aspect, South, West. There was no significant difference in percentage reduction in light between aspects (p-value = 0.5176).

Other grike characteristics such as grike length, grike minimum and maximum width and percentage cover of other species were shown to be possible predicters of percentage reduction in light alongside specimen depth. In Figure 8 the relationship between different grike characteristics and percentage reduction in light can be seen. The percentage reduction in light increases with grike length from 0 cm to around 120 cm and again from 300 cm to 500 cm. Grike minimum and maximum width both show a decrease in percentage reduction in light as the width of the grike increases. There is some increase in percentage reduction in light as percentage cover increases but it is minimal. When added to the model as interactions with percentage reduction in light, grike length and grike maximum width improved the model and likely influence percentage reduction in light alongside specimen depth.

When the grike is long and the specimen deep, the percentage reduction in light is greatest (Figure 9). When the specimen is higher up in the grike and the grike is less than 300 cm long, the percentage reduction in light is lowest. When the maximum width of the grike is low and the specimen is deep, the percentage reduction in light is highest, and conversely when the maximum width is high and the specimen depth is higher in the grike, the percentage reduction in light is lowest (Figure 10). It is likely that the spread of data seen in Figure 6, particularly when the depth of the specimen is low and the percentage reduction in light is high, occurs in situations where the grike is longer than 300 cm and has a low maximum width.

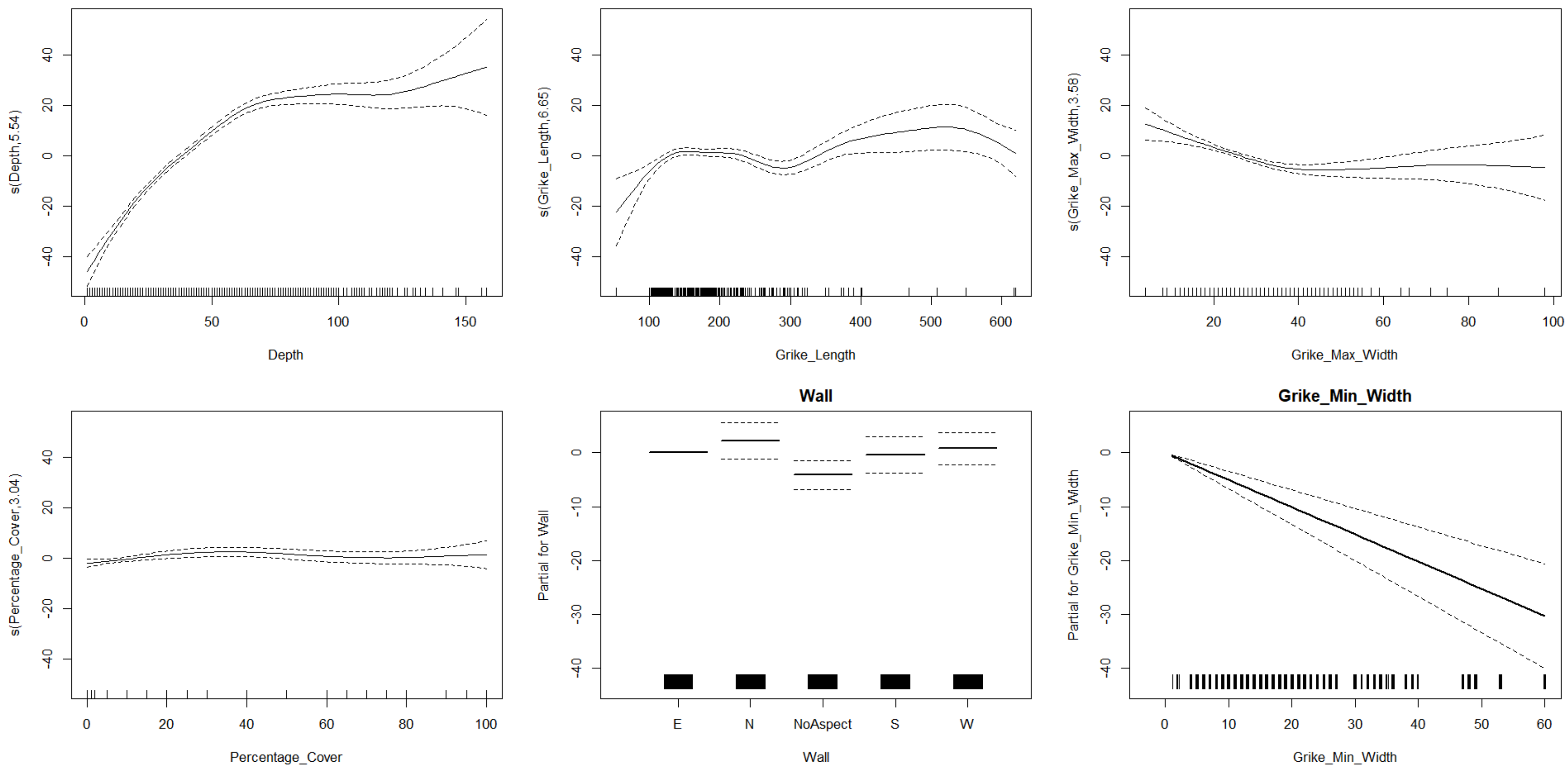

Figure 8. Generalised additive model with potential predictors of percentage reduction in light. Plots showing as follows from left to right: depth of specimen, grike length, grike maximum width, percentage cover of other species, aspect, and grike minimum width against percentage reduction of light.

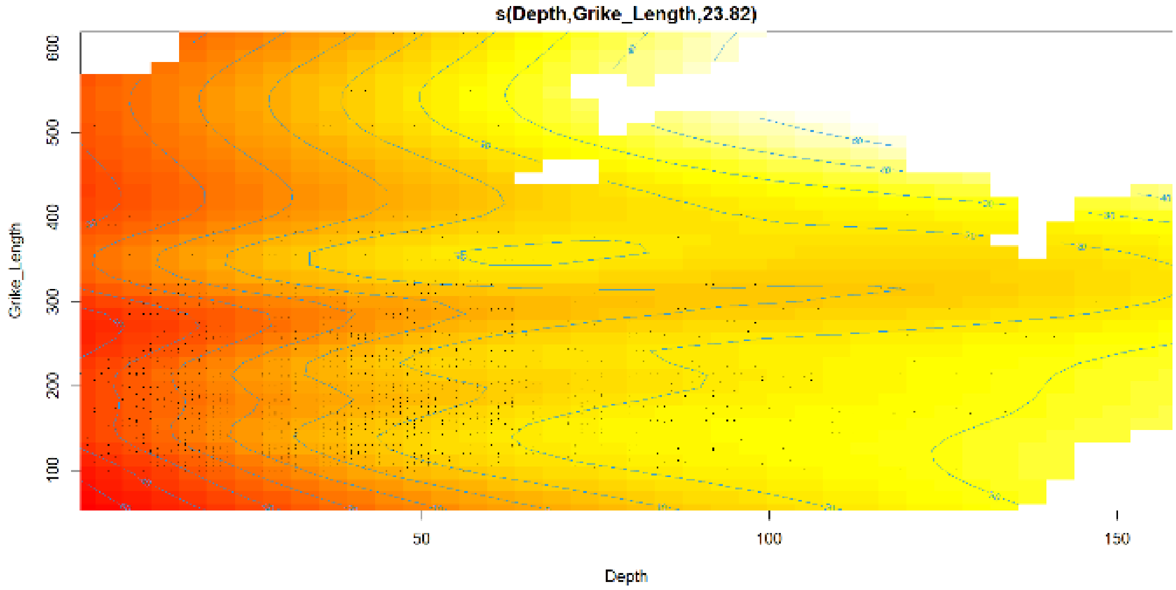

Figure 9. Interaction between grike length and specimen depth with percentage reduction in light from generalised additive model. Lighter areas show where percentage reduction in light is greatest.

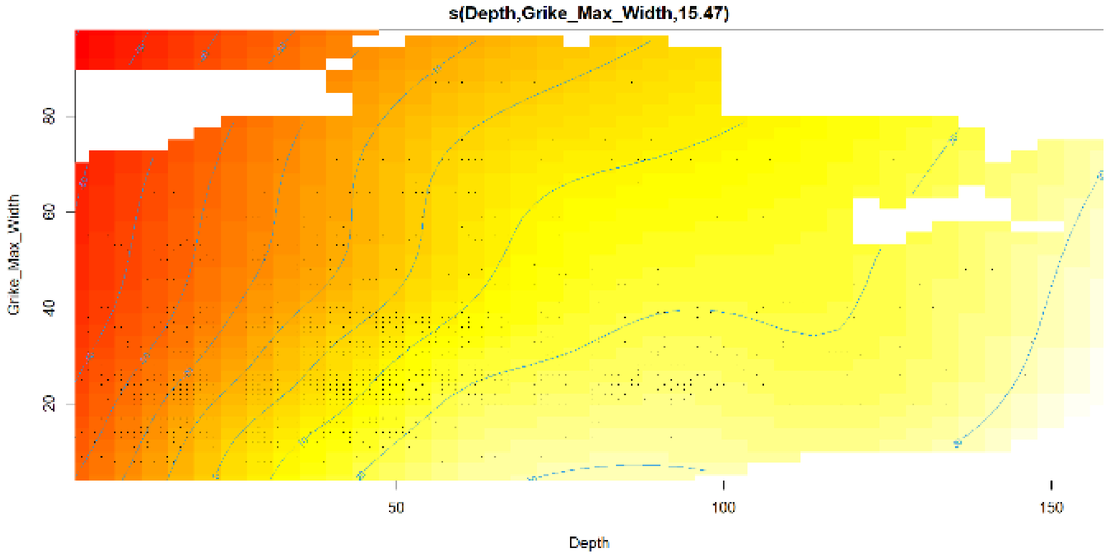

Figure 10. Interaction between grike maximum width and specimen depth with percentage reduction in light from generalised additive model. Lighter areas show where percentage reduction in light is greatest.

3.3. Open limestone pavements

Species organisation in grike by depth and percentage reduction in light

Figure 11 shows the organisation of species by depth within the grikes of open limestone pavements. This plot shows which species grow near the top of the grike such as *Tortella tortuosa* and *Homalothecium sericeum*, and species which grow deeper in the grike such as *Neckera complanata*. Figure 12 shows how the same species are distributed within the grike by percentage reduction in light. *Neckera complanata* which grows between around 40 cm and 125 cm (Figure 11) grows where the percentage reduction in light is close to 100% (Figure 12). Whereas *Reboulia hemisphaerica* grows from around 10 cm to 150 cm but again where the percentage reduction in light is closer to 100%. In contrast, *Homalothecium sericeum* grows predominantly around 30 cm but grows where the percentage reduction in light is anywhere from 0 to 100%. This can be seen in other species which grow mostly higher up in the grike such as *Ctenidium molloscum, Didymodon insulanus,* and *Ditrichum gracile. Pseudoscleropodium purum* grows in a short depth range of around 10 cm to 80 cm which is reflected in the percentage reduction in light it grows at, typically above 75%. However, *Neckera crispa* also has a small depth range, predominately within the first 50 cm, but has a much wider range of percentage reduction in light it will grow in from 0 to 100%.

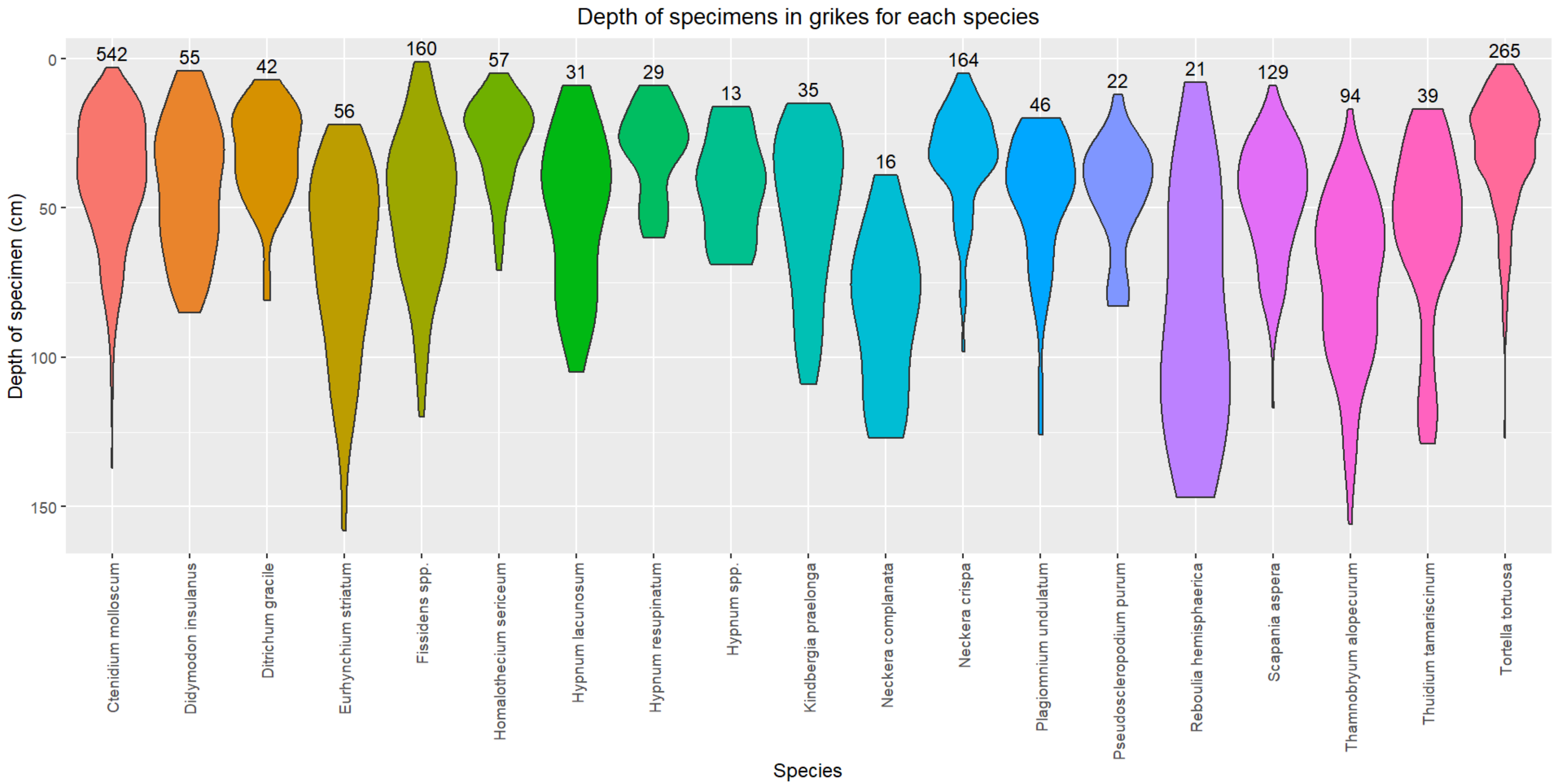

Figure 11. Violin plot for depths of specimens for each species in open pavements. Number of records for each species displayed. Species with less than ten records removed.

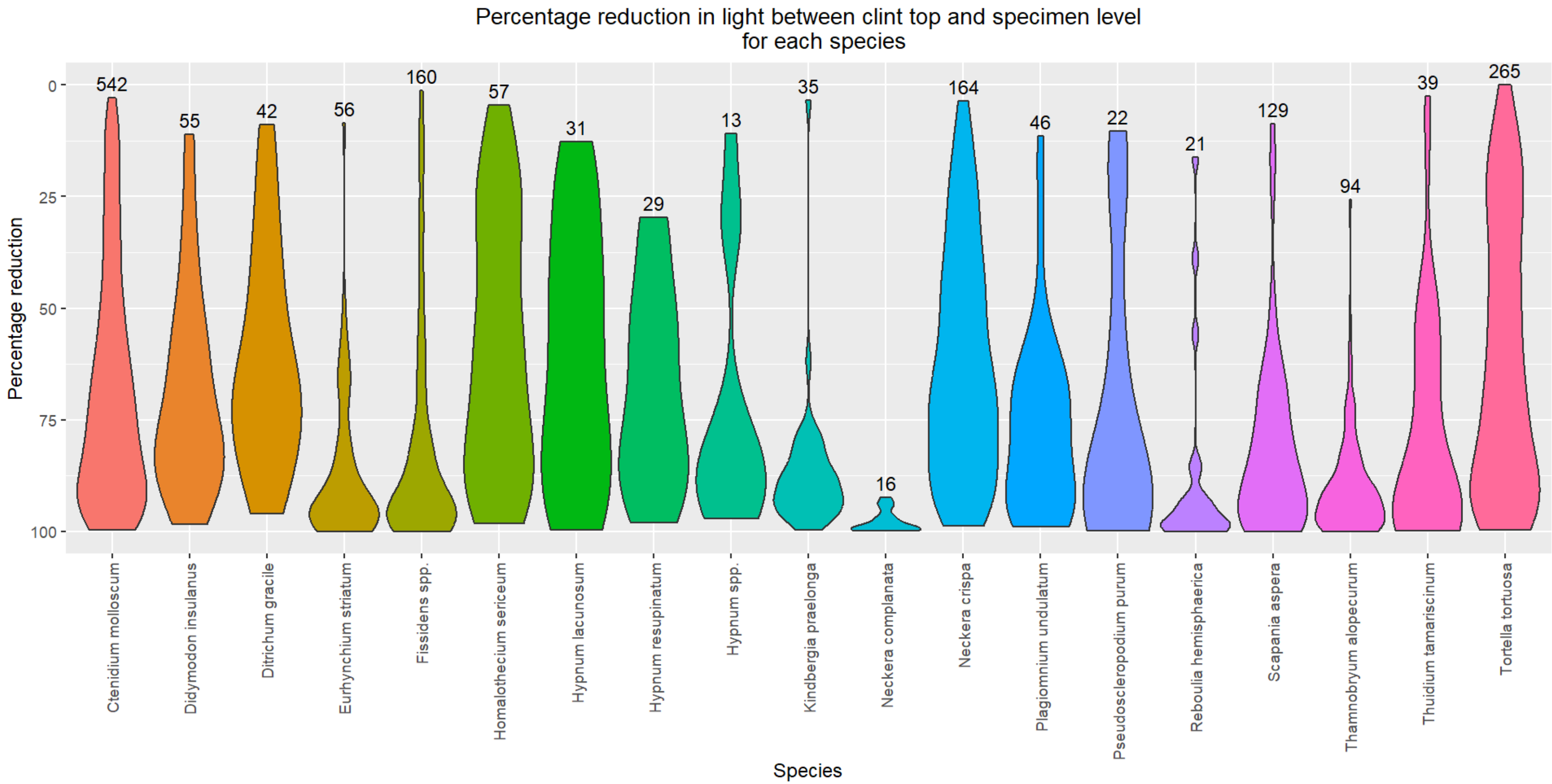

Figure 12. Violin plot for percentage reduction in light from clint top to specimen level for each species. Higher percentage reduction in light exist where conditions are darker within the grike compared to surface. Number of records for each species displayed. Species with less than ten records removed.

When comparing Figure 11 and Figure 12 it is clear that species have varying depth ranges within the grike however, most species grow where the percentage reduction in light is closer to 100% and species will either grow across a range light levels such as *Ctenidium molloscum* and *Tortella tortuosa* or species will grow where the percentage reduction in light is high such as *Neckera complanata* and *Kindbergia praelonga*. These differences are likely from other grike characteristics affecting species organisation in the grike.

Grike maximum width and grike length

As seen above, grike maximum width and grike length (Figure 9 and Figure 10) are potential influencers of percentage reduction in light alongside specimen depth. It is possible that these factors can influence where in the grike the species is growing. *Reboulia hemisphaerica* grows at all depths but where the percentage reduction in light is close to 100%. This pattern could be influenced by grike maximum width as *R. hemisphaerica* grows in grikes with a maximum width of around 30 cm or lower (Figure 13). The narrower grikes having a greater percentage reduction in light (Figure 10) would allow *R. hemisphaerica* to grow higher up in the grike. For most species grike maximum width was a statistically significant predictor of species depth. The only species to not have a p-value < 0.05 in the model were *Ditrichum gracile, Homalothecium sericeum, Hypnum resupinatum, Hypnum spp., and Pseudoscleropodium purum*. Species which show a prominent interaction between grike maximum width and grike depth are shown in Figure 14 to Figure 18. *Eurhynchium striatum* and *Kindbergia praelonga* show a decrease in specimen depth as grike maximum width increases. Whereas *Neckera complanata, Plagiomnium undulatum,* and *Reboulia hemisphaerica* show an increase in depth as the grike maximum width increases.

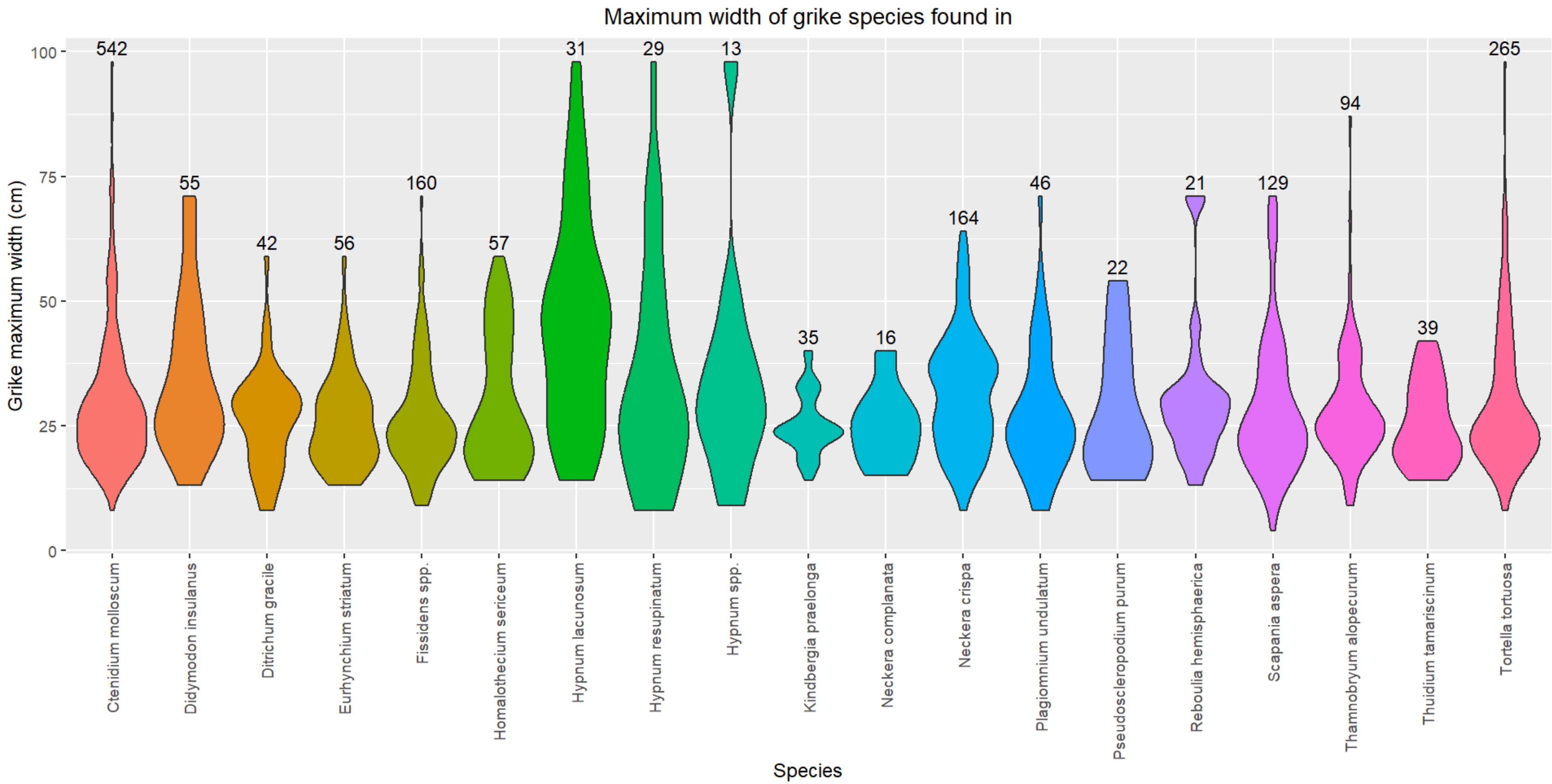

Figure 13. Violin plot for the maximum width of the grike each species was found growing in, in open pavements. Number of records for each species displayed. Species with less than ten records removed.

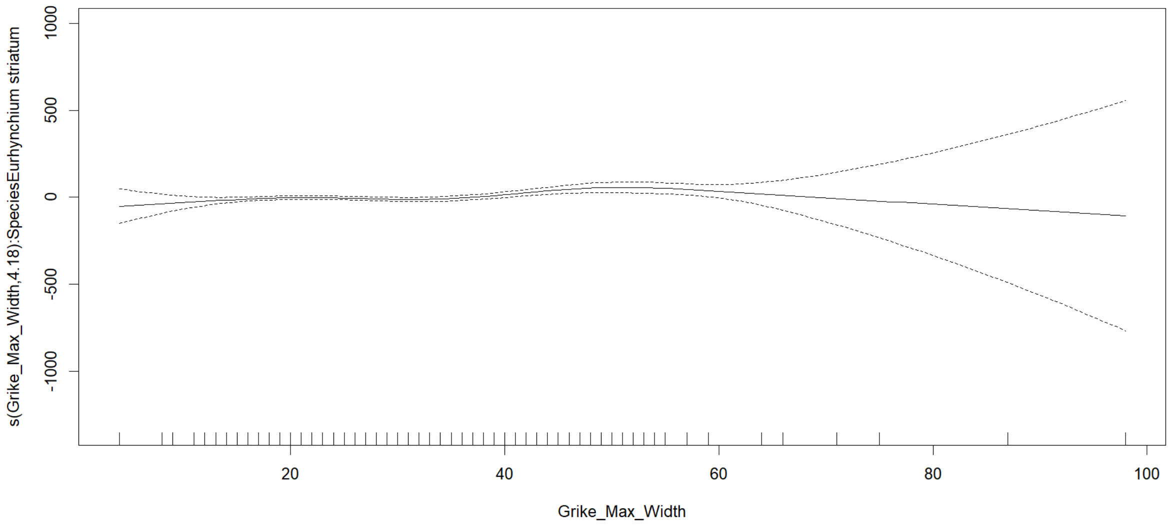

Figure 14. Interaction between grike maximum width and specimen depth (y-axis) in open pavements for Eurhynchium striatum from generalised additive model.

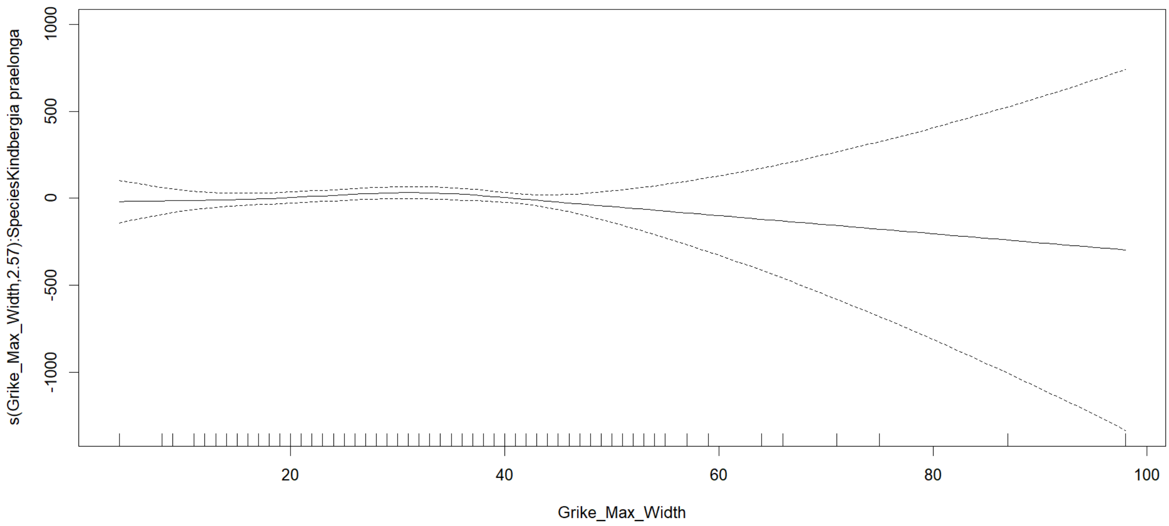

Figure 15. Interaction between grike maximum width and specimen depth (y-axis) in open pavements for Kindbergia praelonga from generalised additive model.

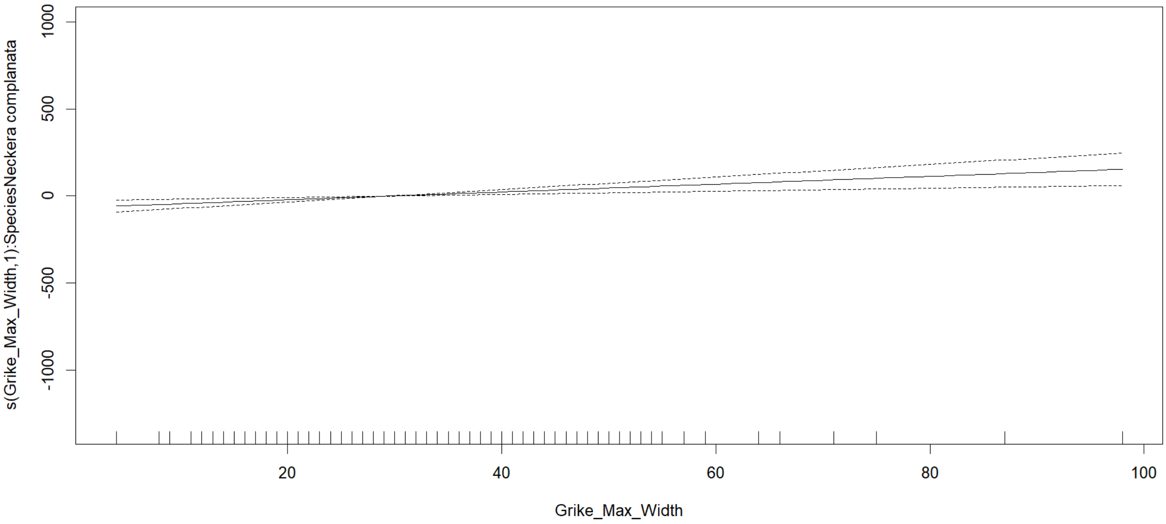

Figure 16. Interaction between grike maximum width and specimen depth (y-axis) in open pavements for Neckera complanata *from generalised additive model*.

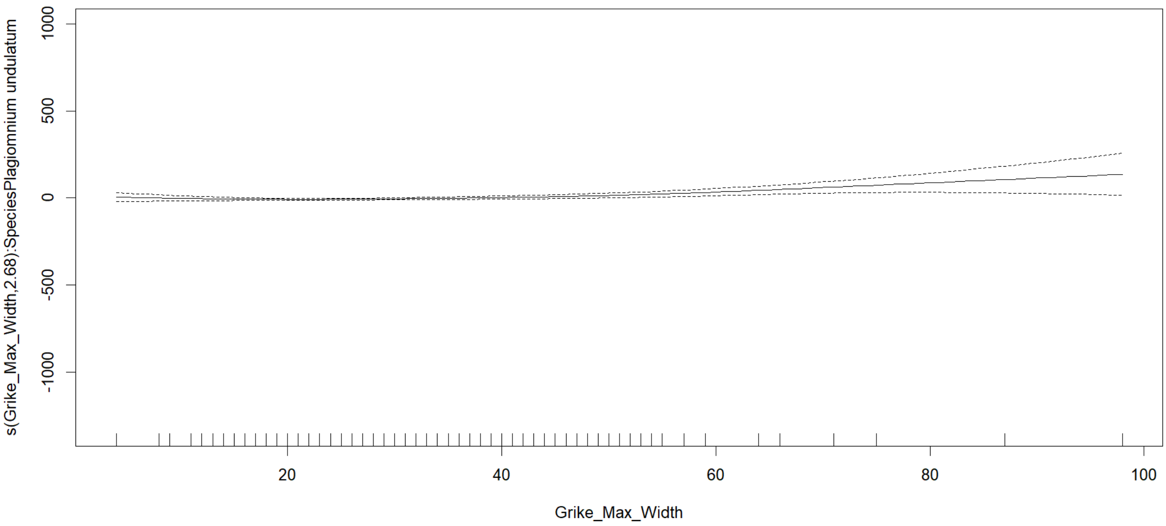

Figure 17. Interaction between grike maximum width and specimen depth (y-axis) in open pavements for Plagiomnium undulatum *from generalised additive model*.

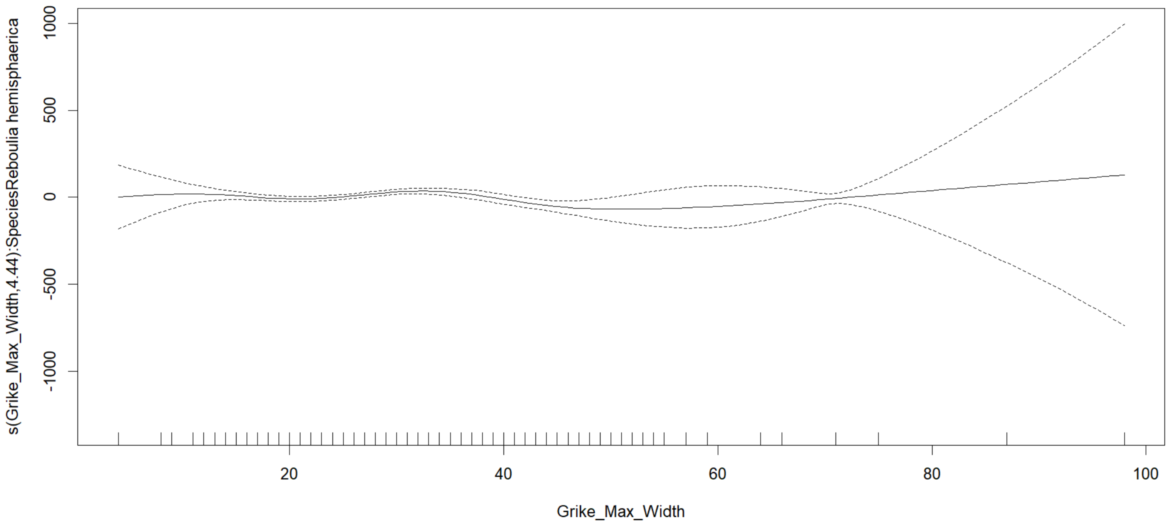

Figure 18. Interaction between grike maximum width and specimen depth (y-axis) in open pavements for Reboulia hemisphaerica *from generalised additive model.*

Grike length is also a potential factor influencing species depth. However, fewer species have a p-value < 0.05 in this model compared with grike maximum width. These species are *Ctenidium molloscum* (Figure 19), *Ditrichum gracile* (Figure 20), *Neckera complanata* (Figure 21), and *Scapania aspera* (Figure 22) which show an increase in specimen depth as grike length increases. *Thamnobryum alopecurum* (Figure 23) and *Thuidium tamariscinum* (Figure 24) also show an increase in specimen depth as grike length increases but then begins to decrease at 450 cm for *Thamnobryum alopecurum* and 500 cm for *Thuidium tamariscinum*.

The relationship between grike length and grike maximum width with light would likely combine to influence species organisation within the grike. For example, *Ctenidium molloscum* tends to grow in grikes less than 200 cm long (Figure 25) and in grikes less than 30 cm wide (Figure 13) which could account for *Ctenidium molloscum* growing in the first 50 cm of the grike, but where percentage reduction in light is higher than 50%.

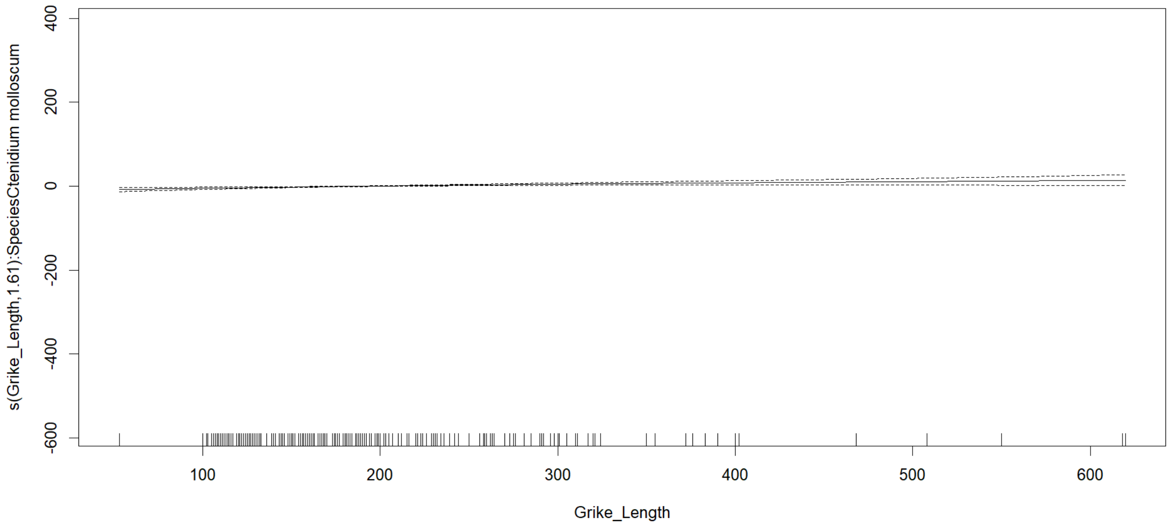

Figure 19. Interaction between grike length and specimen depth (y-axis) in open pavements for <u>Ctenidium molloscum</u> *from generalised additive model*.

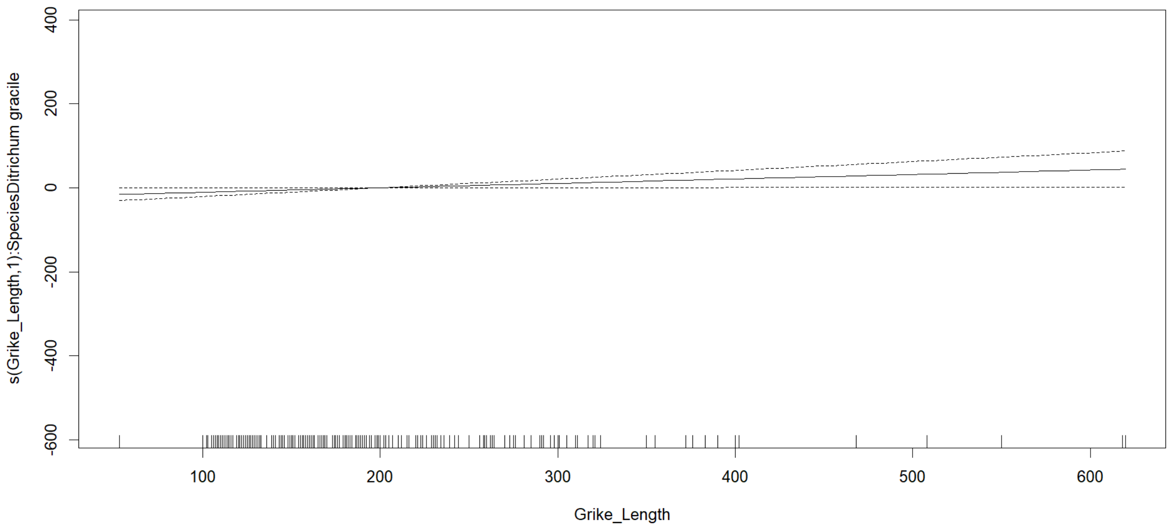

Figure 20. Interaction between grike length and specimen depth (y-axis) in open pavements for <u>Ditrichum gracile</u> *from generalised additive model*.

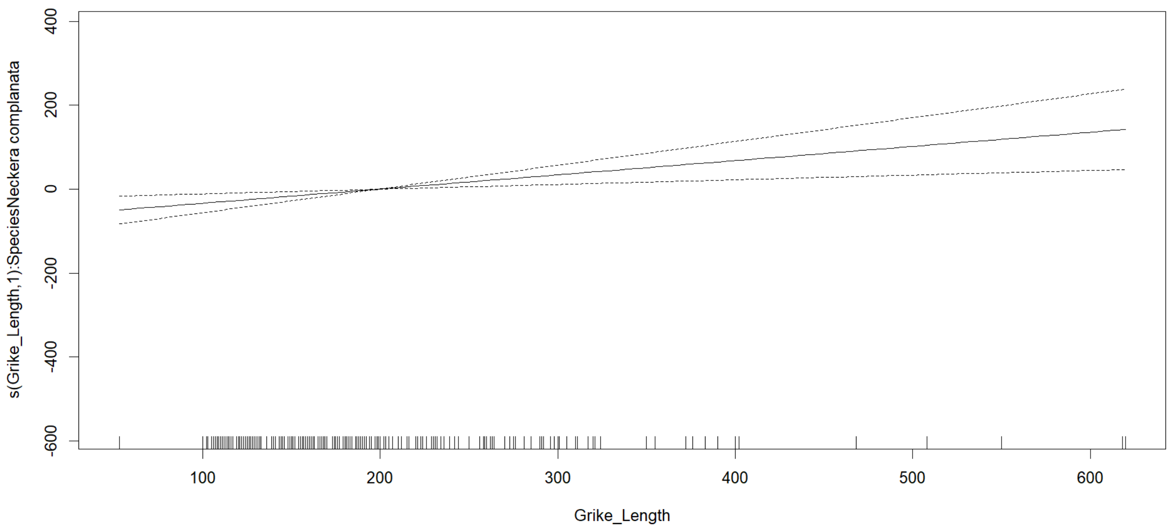

Figure 21. Interaction between grike length and specimen depth (y-axis) in open pavements for Neckera complanata *from generalised additive model.*

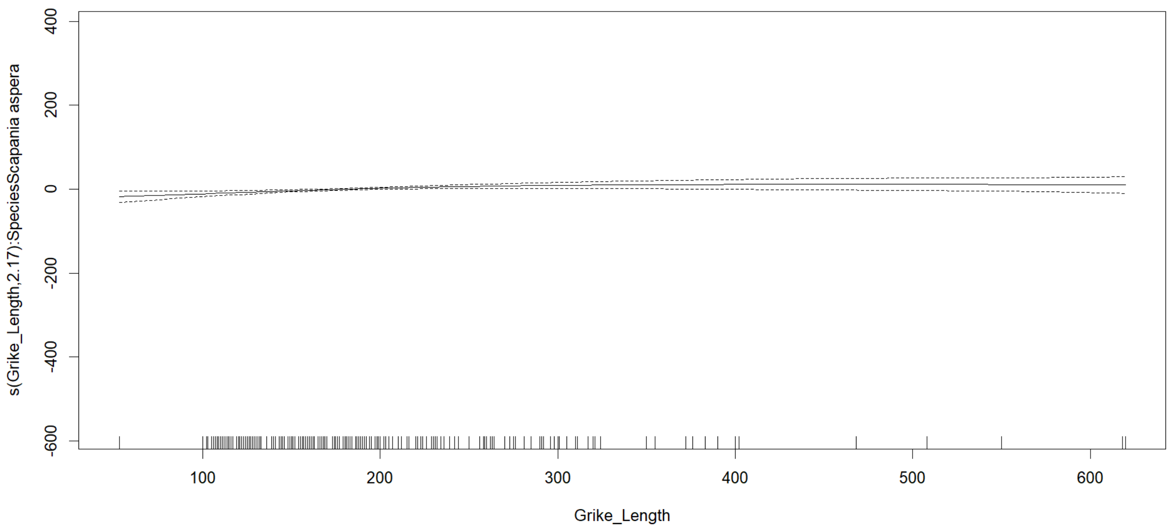

Figure 22. Interaction between grike length and specimen depth (y-axis) in open pavements for Scapania aspera *from generalised additive model.*

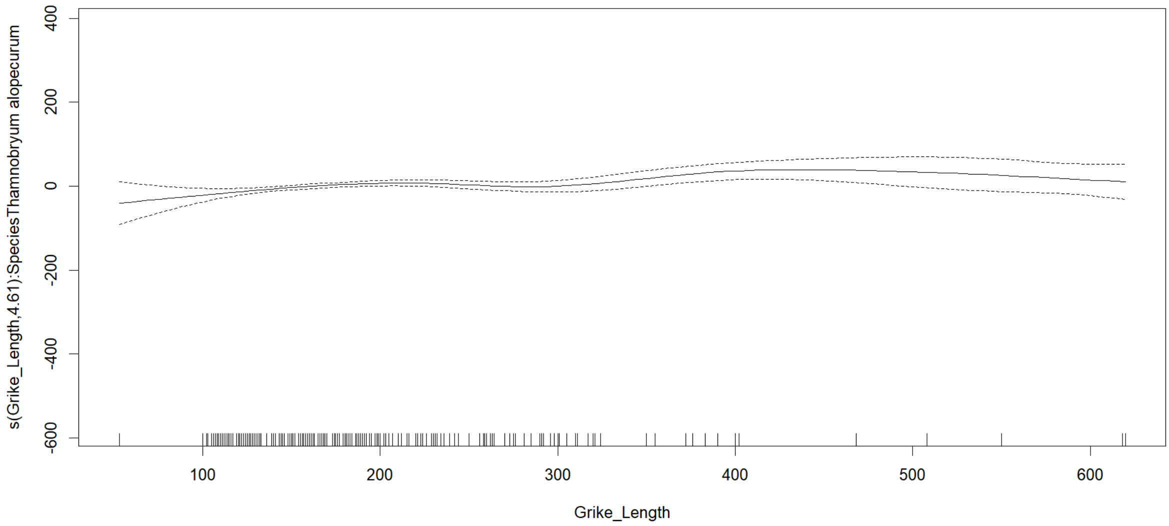

Figure 23. Interaction between grike length and specimen depth (y-axis) in open pavements for <u>Thamnobryum alopecurum</u> *from generalised additive model*.

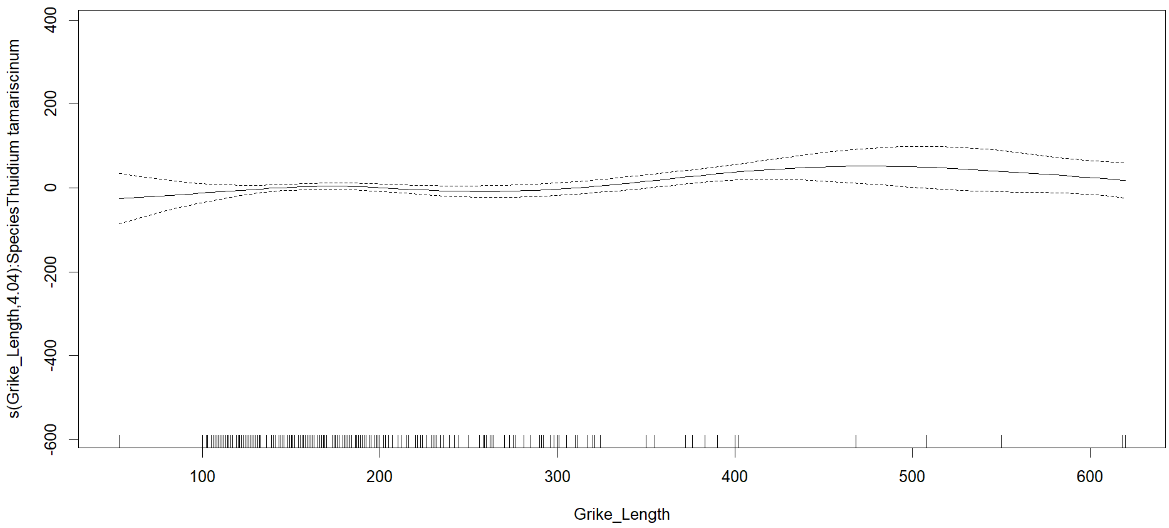

Figure 24. Interaction between grike length and specimen depth (y-axis) in open pavements for <u>Thuidium tamariscinum</u> *from generalised additive model*.

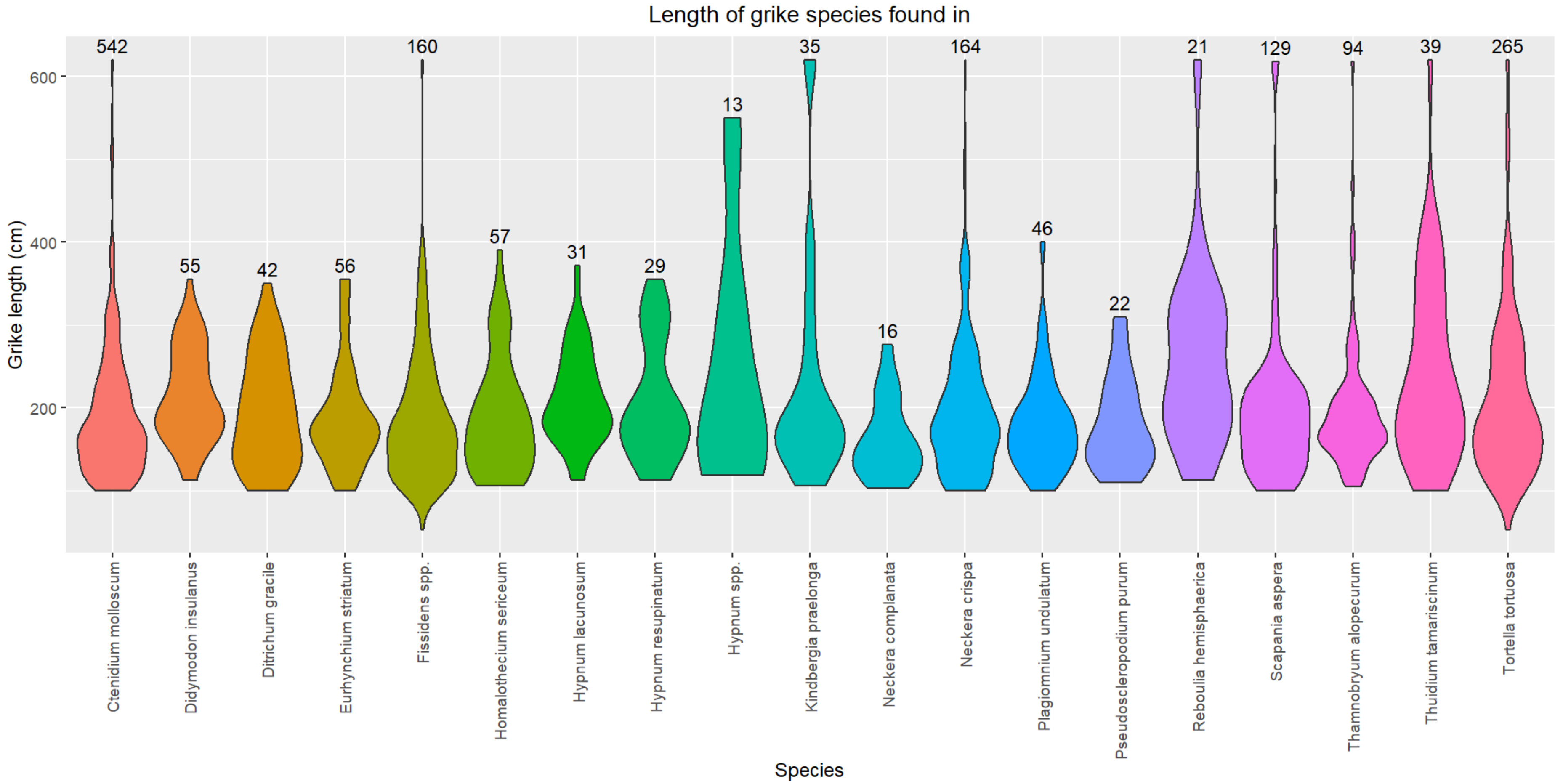

Figure 25. Violin plot for each species distributed by grike length in open pavements. Number of records for each species displayed. Species with less than ten records removed.

Using a regression model, it can be seen that light is a good predictor for specimen depth for most species. Only three species showed a p-value greater than 0.05 in the model. These were *Hypnum resupinatum, Hypnum spp.,* and *Pseudoscleropodium purum.* It is likely that although light is a factor in determining species depth within the grike alongside grike maximum width and grike length, there could be other factors which determine where species grow within the grike that are not based on grike characteristics.

Position in grike

The only species to show any significant difference between position growing in the grike and percentage reduction in light was *Plagiomnium undulatum* (Figure 26). When growing at the base of the grike, specimens typically were growing at a lower percentage reduction in light compared to when growing horizontally in the grike (p-value = 0.0433). There was no statistical difference between the base of the grike and growing horizontally with growing vertically on the grike wall. In Figure 12, *Plagiomnium undulatum* can be seen growing typically where the percentage reduction in light is greater than 50%.

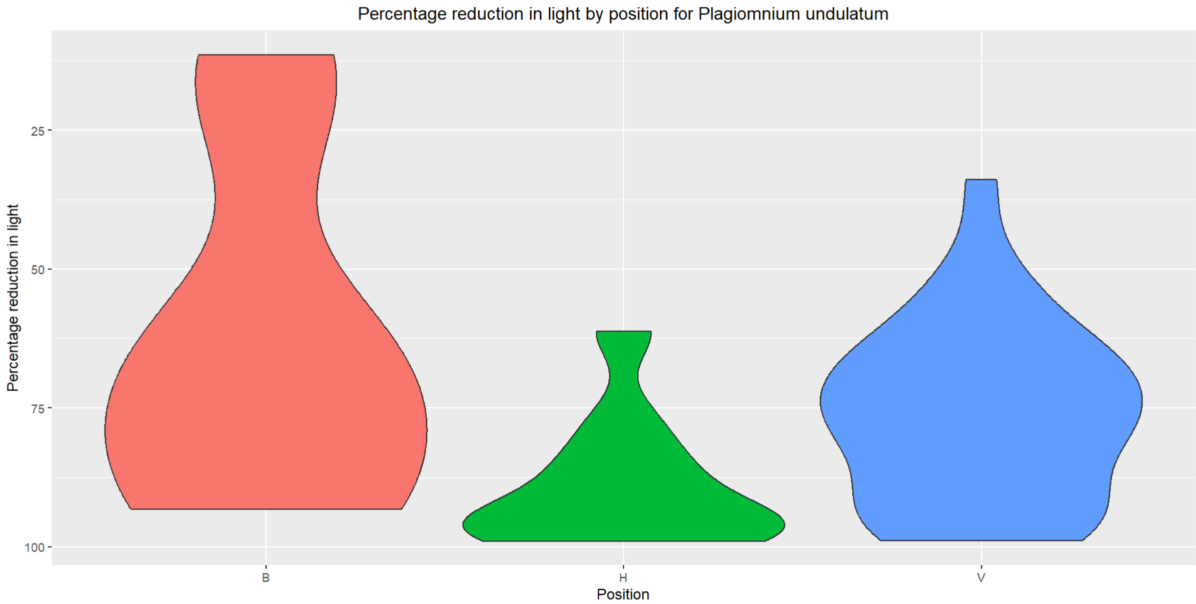

Figure 26. Violin plot for percentage reduction in light in different positions within the grike for Plagiomnium undulatum*. Where percentage reduction is highest, conditions are darker in the grike compared to the surface. From left to right: base of the grike, horizontal surface, growing vertically on grike wall.*

Overlap between species

When organised in a matrix of depth x percentage reduction in light by relative abundance it is easy to see an area within the grike where there is a greater mix of families and where in the grike certain families and therefore species are more dominant (Figure 27). The area of the grike with the greatest number of families exists where depth is less than 90 cm and percentage reduction in light is greater than 60%. There is a greater relative abundance of Hypnaceae is most niche boxes (blue), however Pottiaceae (yellow) does also dominate particularly higher up in the grike. The niche box with the greatest diversity is where the depth is between 50 and 59 cm and percentage reduction in light is between 90 and 99 %. In fact, the percentage reduction in light level with the greatest diversity is 90 to 99%.

The species which have statistically different distributions in specimen depth and percentage reduction in light can be seen in Appendix 2 and Appendix 3. The niche overlap between each species can also be seen in the Appendix 5. Species which have a greater difference between specimen depths such as *Thuidium tamariscinum* and *Tortella tortuosa* have a p-value <0.001 which aligns with a niche overlap value of 0.119. As can be seen in Figure 11 there is a small overlap between specimen depth for these two species. Whereas species such as *Ctenidium molloscum* and *Ditrichum gracile* which grow across a similar depth range have a niche overlap of 0.693. Species which grow at similar depths can also show a niche overlap in percentage reduction in light. *Kindbergia praelonga* and *Thuidium tamariscinum* which grow at similar depths have a niche overlap in percentage reduction in light of 0.847. When comparing niche overlaps between families (Table 4) there is typically a greater niche overlap in percentage reduction in light between families than there is between depths. Flexitrichaceae shows a niche overlap with most other families. The only species present in this family is *Ditrichum gracile* which grows mostly below 50 cm however across the range of percentage reduction in light. Aytoniaceae shows niche separation with most families. This is another family with only one species (*Reboulia hemisphaerica*) which grows across all depths, but where percentage reduction in light is close to 100%.

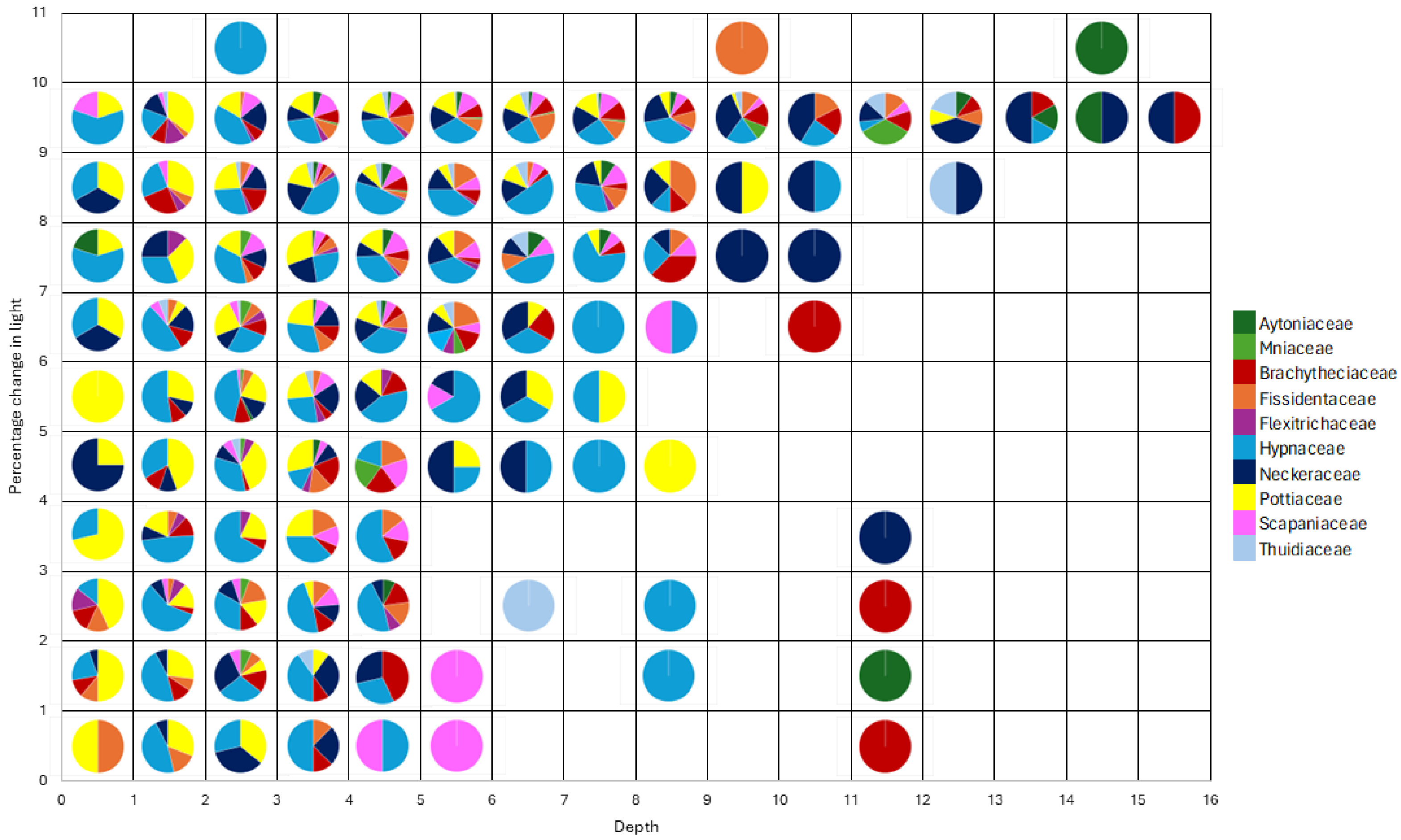

Figure 27. Relative abundance of each family in each niche box in open pavements where each unit represents 10 cm (depth) or 10% (percentage reduction in light).Relative abundance in each niche box is the number of specimens for a family divided by total number of specimens.

Table 4. Pianka's index of niche overlap for depth and percentage reduction in light between families in open pavements. Shading from white (niche separation) to dark green (niche overlap).

		Depth	Light
Aytoniaceae	Mniaceae	0.043915747	0.30929499
	Brachytheciaceae	0.030905908	0.07978777
	Fissidentaceae	0.049158217	0.089779304
	Flexitrichaceae	0.267120814	0.303494226
	Hypnaceae	0.091289444	0.250282357
	Neckeraceae	0.069574392	0.1451522
	Pottiaceae	0.06038715	0.14080947
	Scapaniaceae	0.082073596	0.245006361
	Thuidiaceae	0.039573934	0.10634578
Mniaceae	Brachytheciaceae	0.061297605	0.329702205
	Fissidentaceae	0.058768573	0.235151259
	Flexitrichaceae	0.306373349	0.601997144
	Hypnaceae	0.093199967	0.510983206
	Neckeraceae	0.078722756	0.374102452
	Pottiaceae	0.090982034	0.538399949
	Scapaniaceae	0.145503044	0.474671964
	Thuidiaceae	0.062787749	0.403201666
Brachytheciaceae	Fissidentaceae	0.104679291	0.24555436
	Flexitrichaceae	0.371676196	0.380940356
	Hypnaceae	0.312541917	0.471289301
	Neckeraceae	0.424732021	0.522282401
	Pottiaceae	0.246378138	0.509461397
	Scapaniaceae	0.133724828	0.31930734
	Thuidiaceae	0.064709988	0.181169272
Fissidentaceae	Flexitrichaceae	0.384011158	0.252931931
	Hypnaceae	0.254118026	0.381170887
	Neckeraceae	0.180163869	0.324201252
	Pottiaceae	0.208661886	0.325783823
	Scapaniaceae	0.230716073	0.371623172
	Thuidiaceae	0.072636419	0.147251147
Flexitrichaceae	Hypnaceae	0.6974315	0.603147458
	Neckeraceae	0.523574983	0.410928108
	Pottiaceae	0.517360093	0.752347661
	Scapaniaceae	0.473052029	0.478940667

	Thuidiaceae	0.392231655	0.439802931
Hypnaceae	Neckeraceae	0.707230917	0.604196651
	Pottiaceae	0.500167157	0.61504267
	Scapaniaceae	0.268330728	0.462680004
	Thuidiaceae	0.132980211	0.310108327
Neckeraceae	Pottiaceae	0.365662876	0.479665169
	Scapaniaceae	0.149196326	0.334936962
	Thuidiaceae	0.095237088	0.225459478
Pottiaceae	Scapaniaceae	0.196481085	0.459842062
	Thuidiaceae	0.128367224	0.268461223
Scapaniaceae	Thuidiaceae	0.243168237	0.272613434

3.4. Wooded limestone pavements

Species organisation in grike by depth

Figure 28 shows the depth of each species in wooded pavements. Here, all species grow near the top of the grike, with the majority of specimens found in the top 25 cm. However, there is still a significant difference between species (p-value < 0.001) with Table 5 showing which species differ significantly (p-value <0.05). *Tortella tortuosa* grows in the top 15 cm of the grike and has the greatest number of significant differences with other species in wooded pavements, particularly with those that grow deeper down in the grike such as *Thamnobryum alopecurum* and *Fissidens* spp.

Table 5. P-values of post-hoc test below 0.05 for depths of specimens in wooded pavements. Where p-value is below 0.05, there is a significant difference in specimen depths between species.

	Ctenidium molloscum	***Ditrichum gracile***	***Eurhynchium striatum***	***Plagiomnium undulatum***	***Thuidium tamariscinum***	***Tortella tortuosa***
Fissidens spp.	0.008	0.041	0.002	0.010	0.003	3.088E-07
Neckera crispa	8.950E-05	0.012	3.544E-06	0.0002	2.621E-05	1.281E-09
Thamnobryum alopecurum	0.001		9.381E-06	0.002	0.0002	1.002E-08
Tortella tortuosa	0.040		0.037			
Scapania aspera						0.0003
Kindbergia praelonga						0.0490

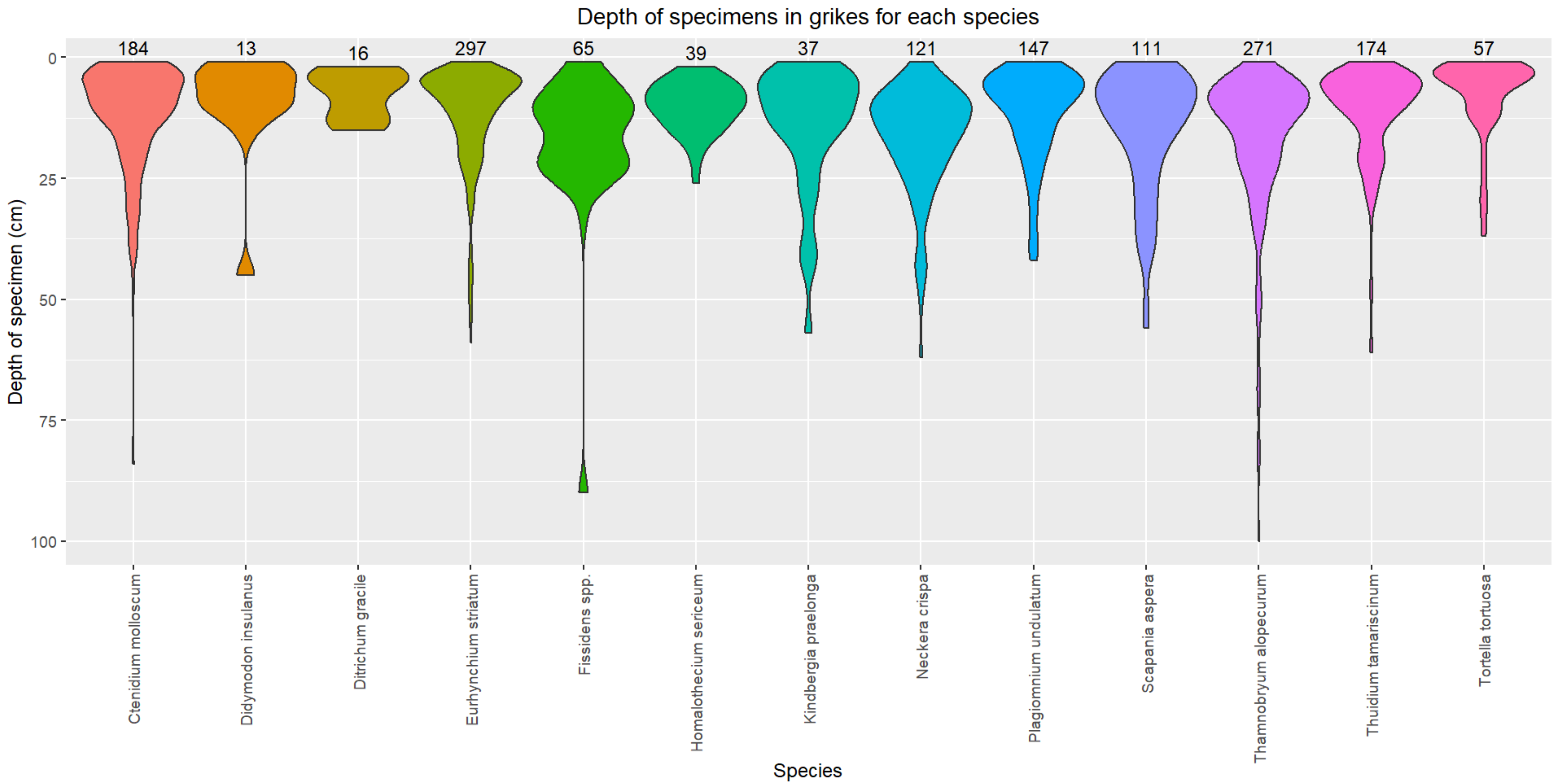

Figure 28. Violin plot for specimen depth of each species in wooded pavements. Number of records for each species displayed. Species with less than ten records removed.

There was no significant correlation between specimen depth and canopy cover (p-value = 0.252). However, canopy cover could be a predictor of specimen depth (p-value < 0.05) for *Ctenidium molloscum, Fissidens* spp.*, Kindbergia praelonga, Scapania aspera,* and *Thamnobryum alopecurum*. Figure 29 to Figure 33 show the relationship between canopy cover and specimen depth for these species. All species apart from *Fissidens* spp. show a decreasing trend in specimen depth as canopy cover increases, i.e. as canopy cover increases, species move higher up the grike. Whereas *Fissidens* spp. exhibits an increase in depth before peaking at 40% canopy cover where the specimen depth then decreases and plateaus as canopy cover increases.

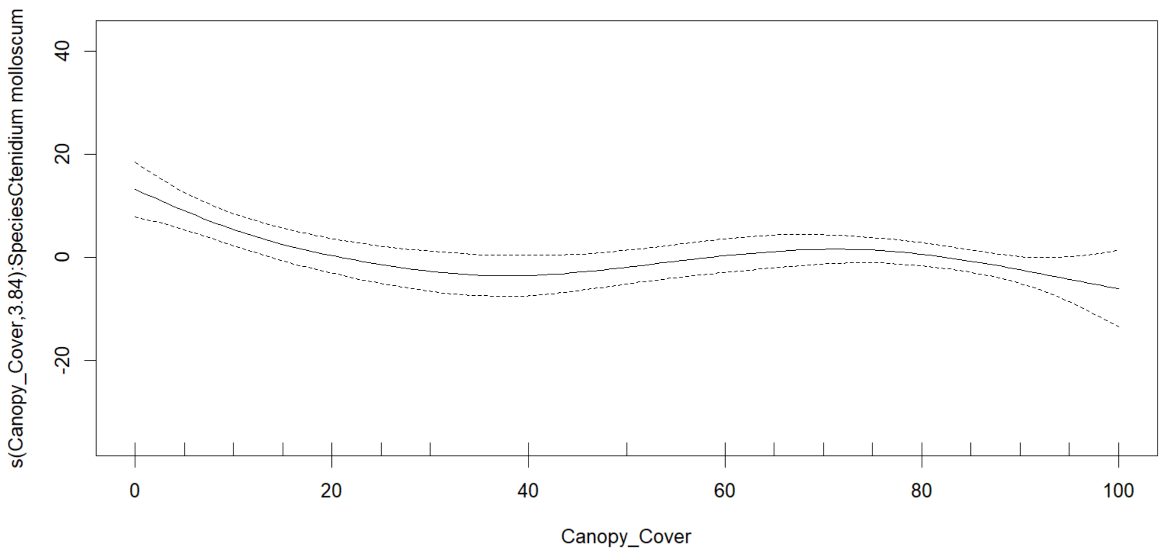

Figure 29. Interaction between canopy cover and specimen depth (y-axis) in wooded pavements for <u>Ctenidium molloscum</u> *from generalised additive model*.

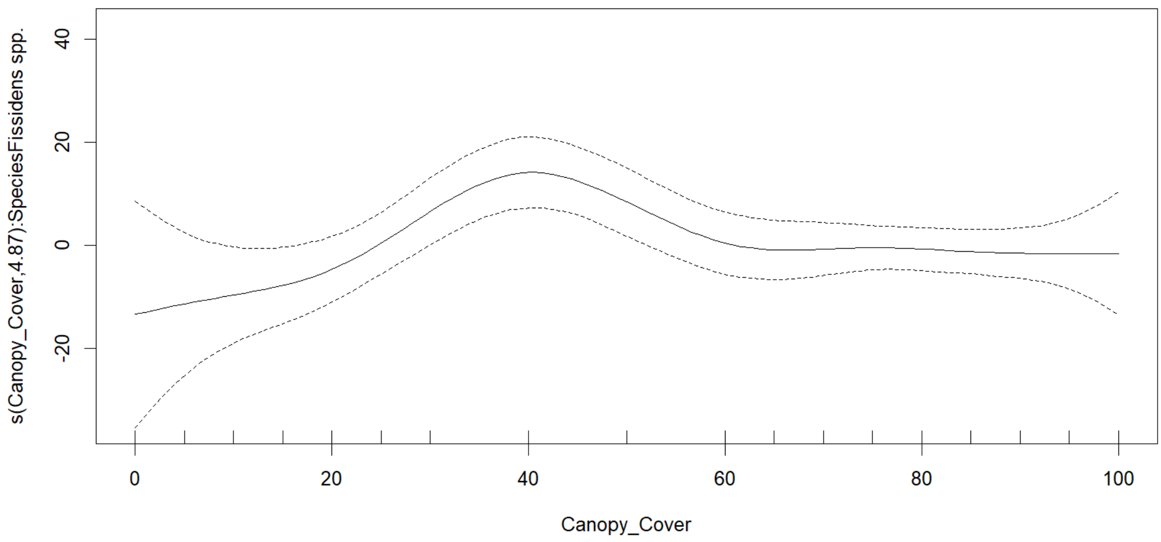

Figure 30. Interaction between canopy cover and specimen depth (y-axis) in wooded pavements for Fissidens *spp. from generalised additive model.*

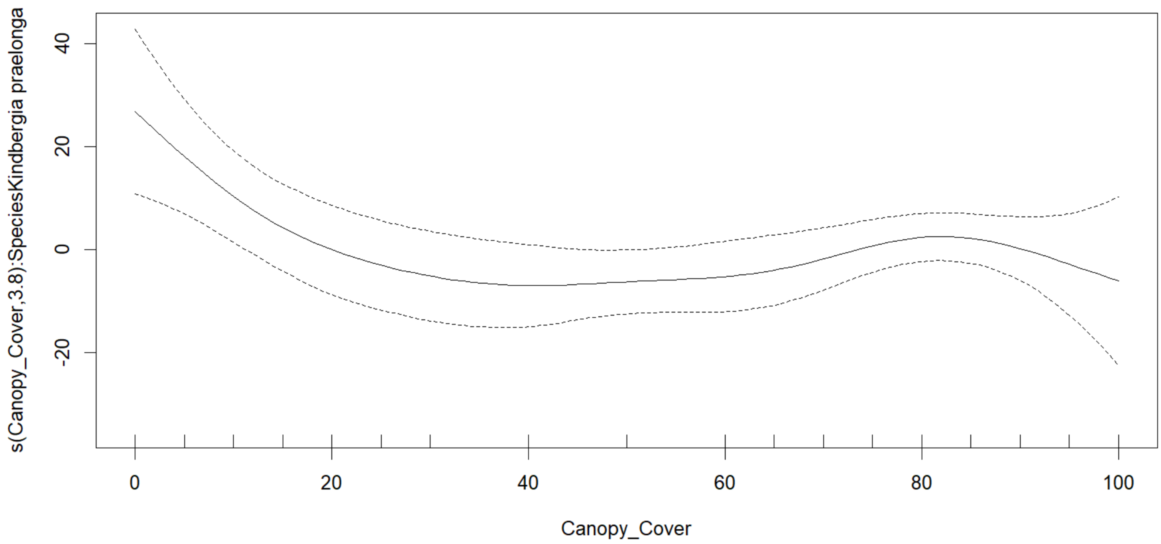

Figure 31. Interaction between canopy cover and specimen depth (y-axis) in wooded pavements for Kindbergia praelonga *from generalised additive model.*

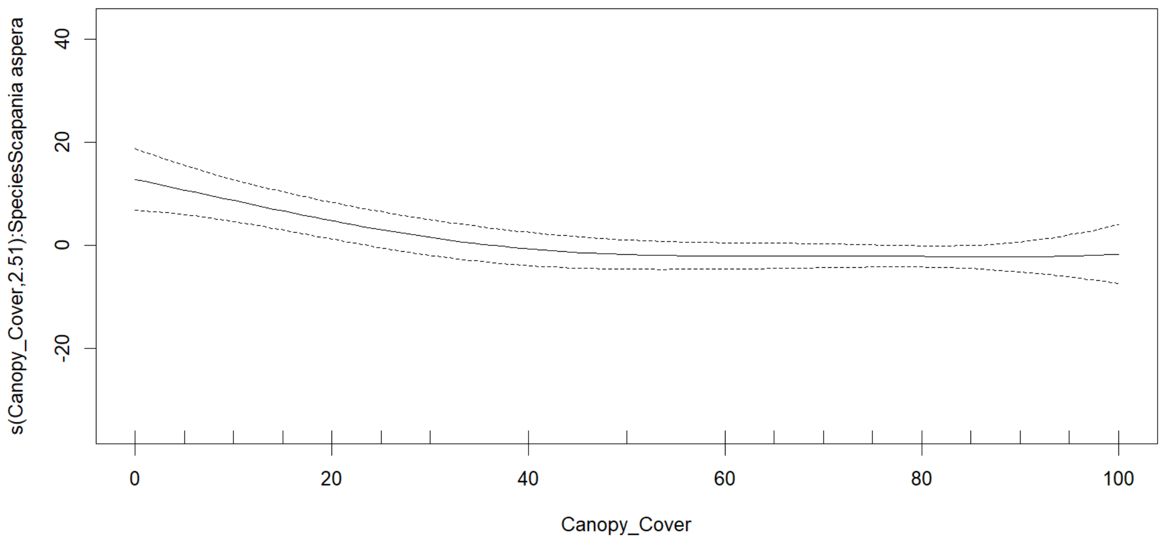

Figure 32. Interaction between canopy cover and specimen depth (y-axis) in wooded pavements for Scapania aspera *from generalised additive model.*

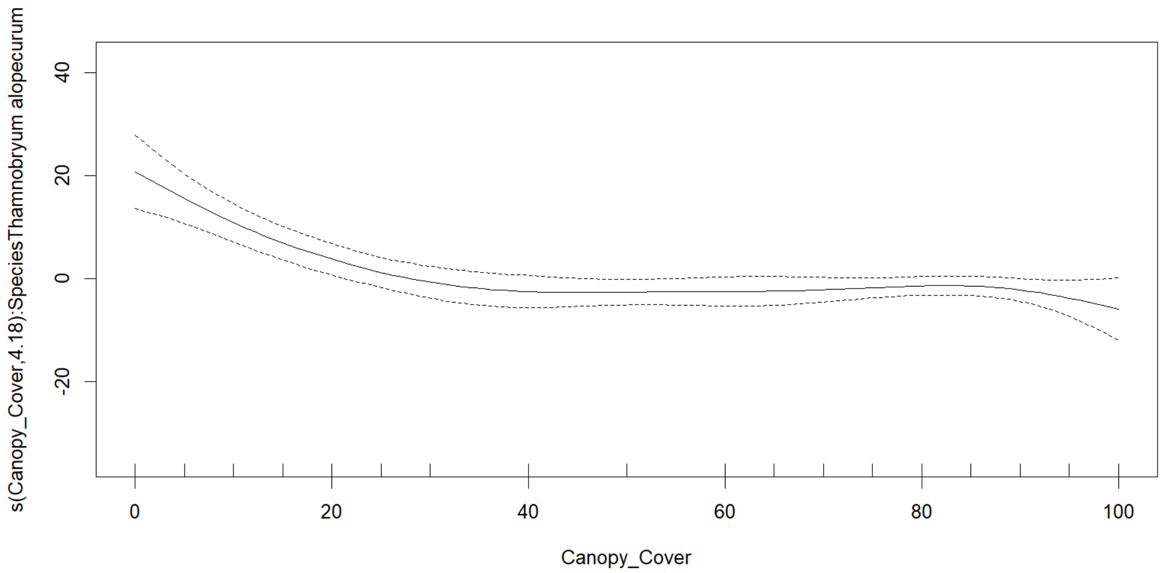

Figure 33. Interaction between canopy cover and specimen depth (y-axis) in wooded pavements for Thamnobryum alopecurum *from generalised additive model.*

Grike maximum width and grike depth

Using a generalised additive model, grike maximum width and grike depth were found to be potential characteristics that interact with specimen depth in wooded pavements. The species that showed a relationship between grike maximum width and specimen depth (p-value < 0.05)

are *Fissidens* spp., *Neckera crispa, Plagiomnium undulatum,* and *Thuidium tamariscinum*. Figure 34 to Figure 37 show the relationship for each of these species between grike maximum width and specimen depth. *Neckera crispa, Plagiomnium undulatum,* and *Thuidium tamariscinum* show a positive relationship, as grike maximum width increases, specimen depth also increases. *Fissidens* spp. shows an increasing trend with grike maximum width, peaking at 65 cm before decreasing with grike maximum width.

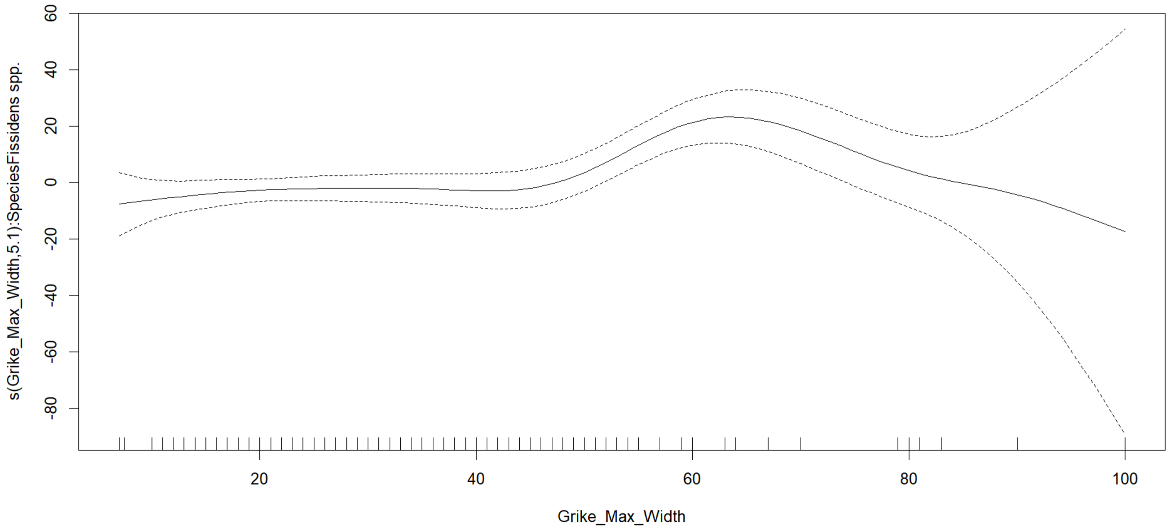

Figure 34. Interaction between grike maximum width and specimen depth (y-axis) for Fissidens spp. from generalised additive model.

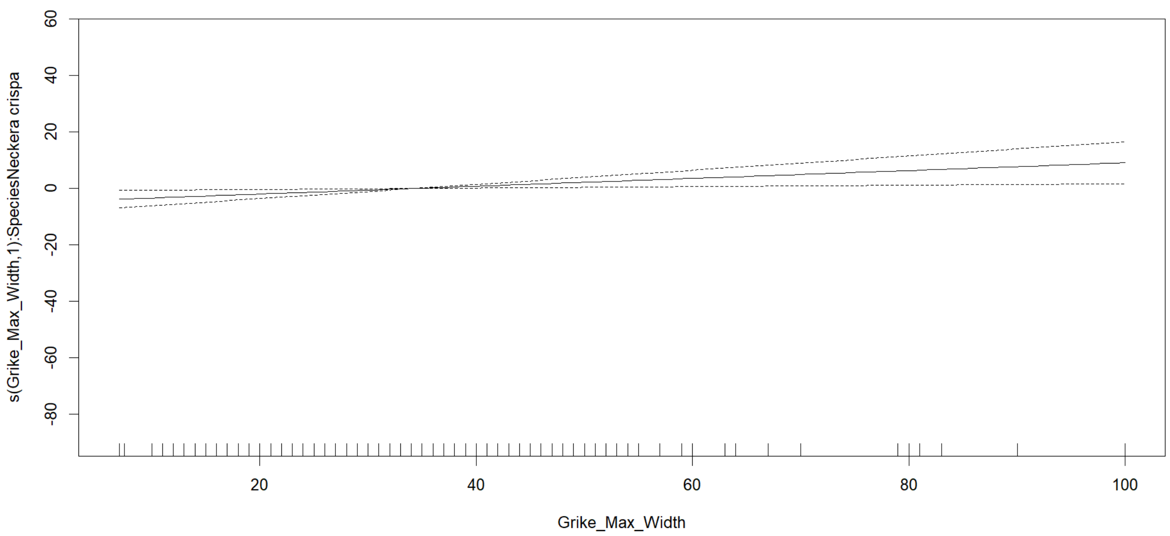

Figure 35. Interaction between grike maximum width and specimen depth (y-axis) for Neckera crispa from generalised additive model.

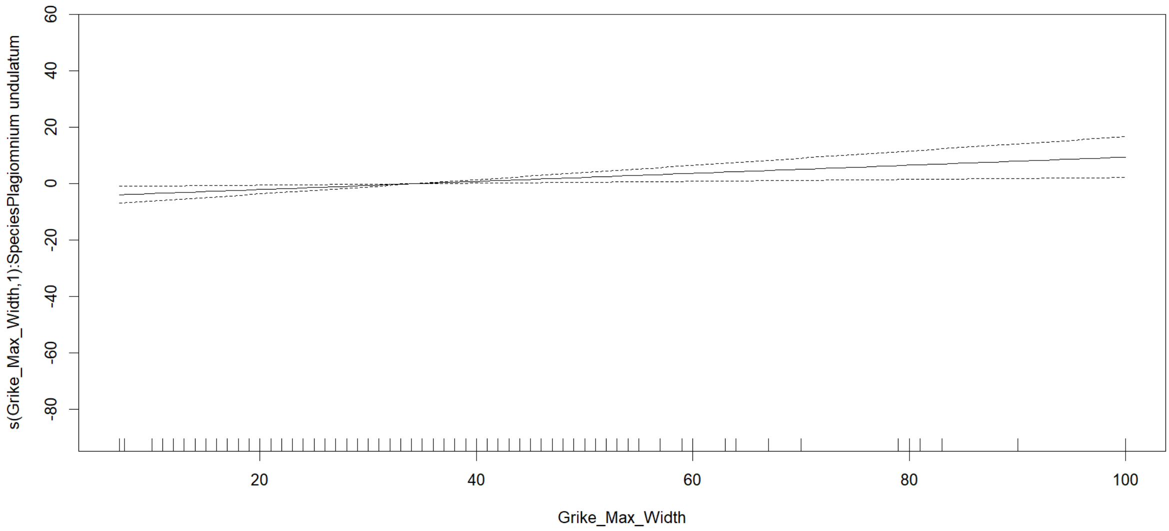

Figure 36. Interaction between grike maximum width and specimen depth (y-axis) for Plagiomnium undulatum from generalised additive model.

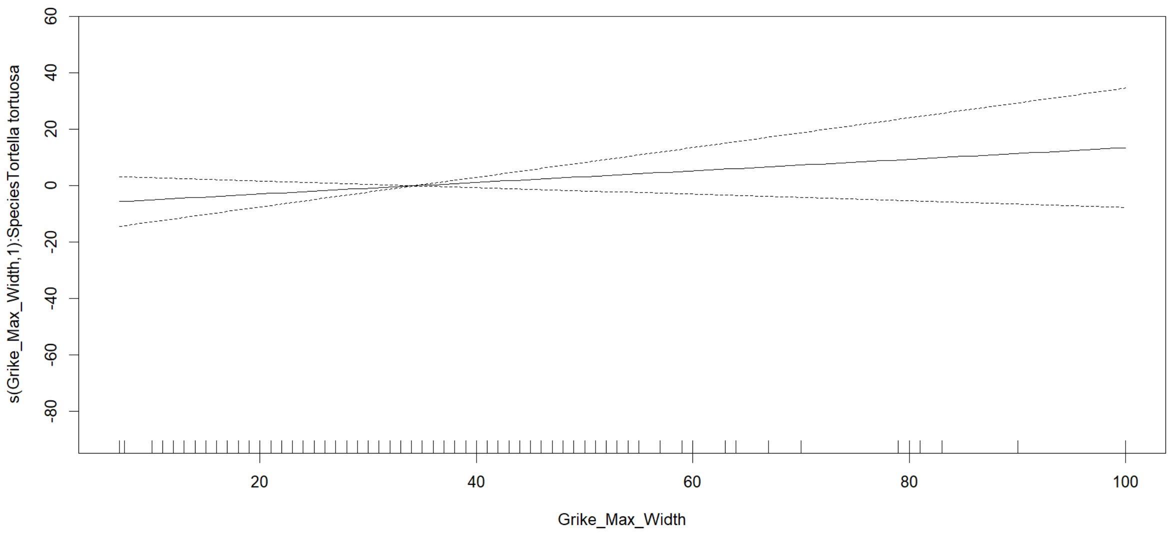

Figure 37. Interaction between grike maximum width and specimen depth (y-axis) for Thuidium tamariscinum from generalised additive model.

For grike depth, all species apart from *Ditrichum gracile* and *Homalothecium sericeum* showed a relationship between grike depth and specimen depth (p-value < 0.05). Although the species in wooded pavements are typically only growing in the top 25 cm of the grike, they are growing in grikes of varying depths. Figure 38 shows the depths of grikes species are growing in.

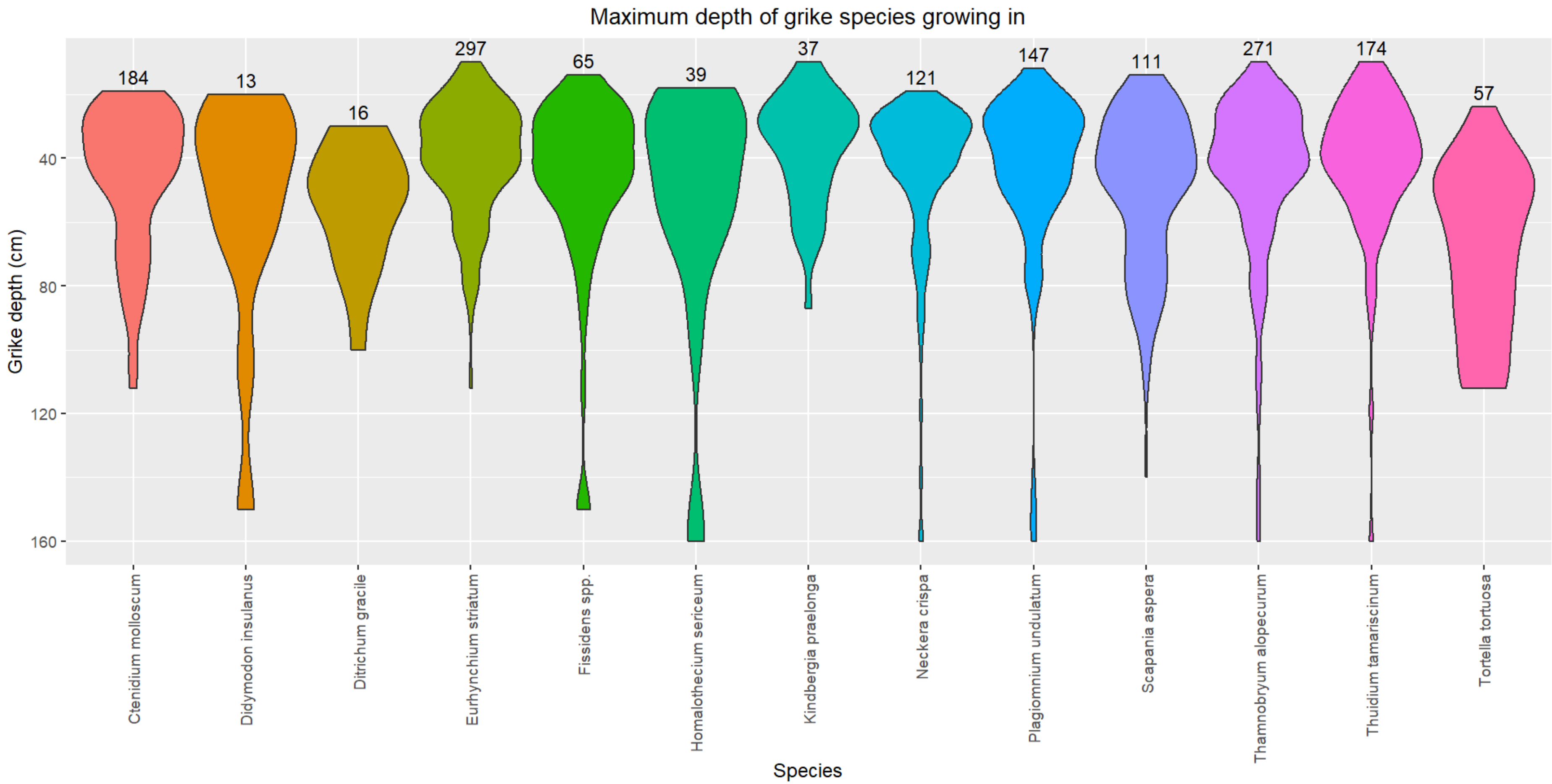

Figure 38. Violin plot for maximum depths of grike species growing in, in wooded pavements. Number of records for each species displayed. Species with less than ten records removed.

Position in grike

The two species which showed a significant difference between specimen depth for each position were *Kindbergia praelonga* and *Thamnobryum alopecurum* (Figure 39). For *Kindbergia praelonga* there was statistically significant difference in specimen depth between specimens growing horizontally and specimens growing at the base of the grike (p-value = 0.00548) and specimens growing vertically (p-value = 0.0258). Specimens growing horizontally in the grike are higher up in the grike between 0 and 15 cm. For *Thamnobryum alopecurum,* there was a statistically significant difference between all positions (Table 6). Specimens growing at the base of the grike grow between 10 and 80 cm, whereas specimens growing horizontally or vertically grow higher up in the grike, mostly between 0 and 25 cm.

Table 6. P-values for differences between specimen depths at different positions in the grike (base of grike, growing on a horizontal surface, growing vertically on grike wall) for Thamnobryum alopecurum *in wooded pavements.*

Thamnobryum alopecurum	**B**	**V**
H	0.0003	0.013
V	0.015	-

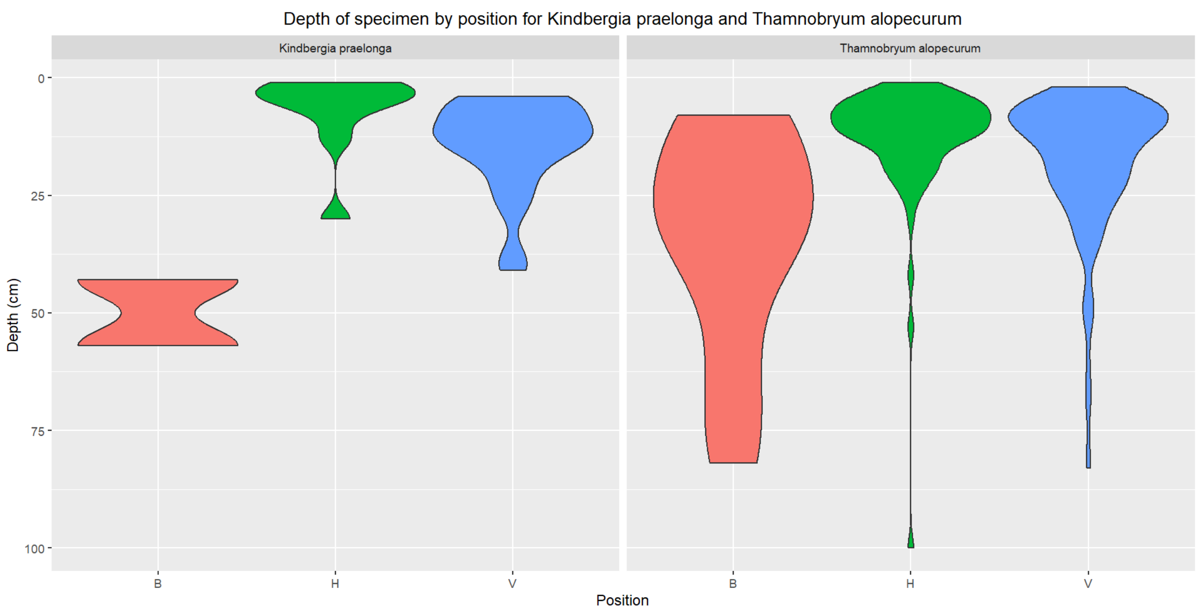

Figure 39. Violin plots for specimen depth by position (base of grike, growing on a horizontal surface, growing vertically on grike wall) for Kindbergia praelonga *and* Thamnobryum alopecurum *in wooded pavements.*

3.5. Comparison

Open and wooded pavements

Figure 40 shows the depths of specimens in open and wooded pavements for species found in both types of pavements. For each species there is a statistical difference (p-value < 0.05) between specimen depths for open and wooded pavements. All species show a much smaller depth range in wooded pavements compared to open pavements.

Although niche overlap was not calculated for wooded pavement species, the niche overlap in open pavements can be compared with differences in species distributions in wooded pavements. In open pavements *Ctenidium molloscum* and *Eurhynchium striatum* have a niche overlap in depth of 0.128, so show a separation in distribution. Whereas in wooded pavements, *Eurhynchium striatum* grows much higher in the grike compared to in the open pavements and there is no statistical difference between the distributions of *Ctenidium molloscum* and *Eurhynchium striatum* in the wooded pavements (p-value = 1.00). The niche overlap between *Thamnobryum alopecurum* and *Tortella tortuosa* in depth in open pavements was 0.155 but these species still show a difference between specimen depths in wooded pavements (p-value < 0.001). The smallest niche overlap by depth to occur between species found in both pavements is between *Kindbergia praelonga* and *Plagiomnium undulatum* of 0.0317, however these two species do not show a statistical difference in depth in both open (p-value = 1.00) and wooded pavements (p-value = 0.998). The species that have the smallest niche overlap by light are *Fissidens* spp. and *Kindbergia praelonga* of 0.101, however there is also no statistical difference between these species in open pavements (p-value = 1.00). *Fissidens* spp. and *Kindbergia praelonga* also show no difference in depth in wooded pavements (p-value = 0.859). The greatest niche overlap to occur by depth and light is between *Ctenidium molloscum* and *Hypnum* spp. of 1.24, however the number of records for *Hypnum* spp. are low. The greatest niche overlap in depth, not including *Hypnum* spp. is between *Didymodon insulanus* and *Kindbergia praelonga* of 0.802. These two species also exhibit and overlap in depth in wooded pavements (p-value = 0.928). The greatest niche overlap in light excluding *Hypnum* spp. is between *Kindbergia praelonga* and *Thuidium tamariscinum* of 0.847 which also showed no difference in depth in wooded pavements (p-value = 0.992). *Kindbergia praelonga* has both the greatest and smallest niche overlap with other species but does not have a statistical difference in either depth or light. However, a species *K. praelonga* does have a statistically significant difference between in depth and light is with *Homalothecium sericeum* (p-value < 0.001, p-value <0.01) and a low niche overlap of 0.166 and 0.228. There were some species which showed a difference in depths in the wooded pavements but not the open pavements. Most notably with *Neckera crispa*. For example, *Neckera crispa* and *Ditrichum gracile* have a statistical difference of p-value = 1.00 in open pavements and niche overlap of 0.661 but have a p-value < 0.05 in wooded pavements.

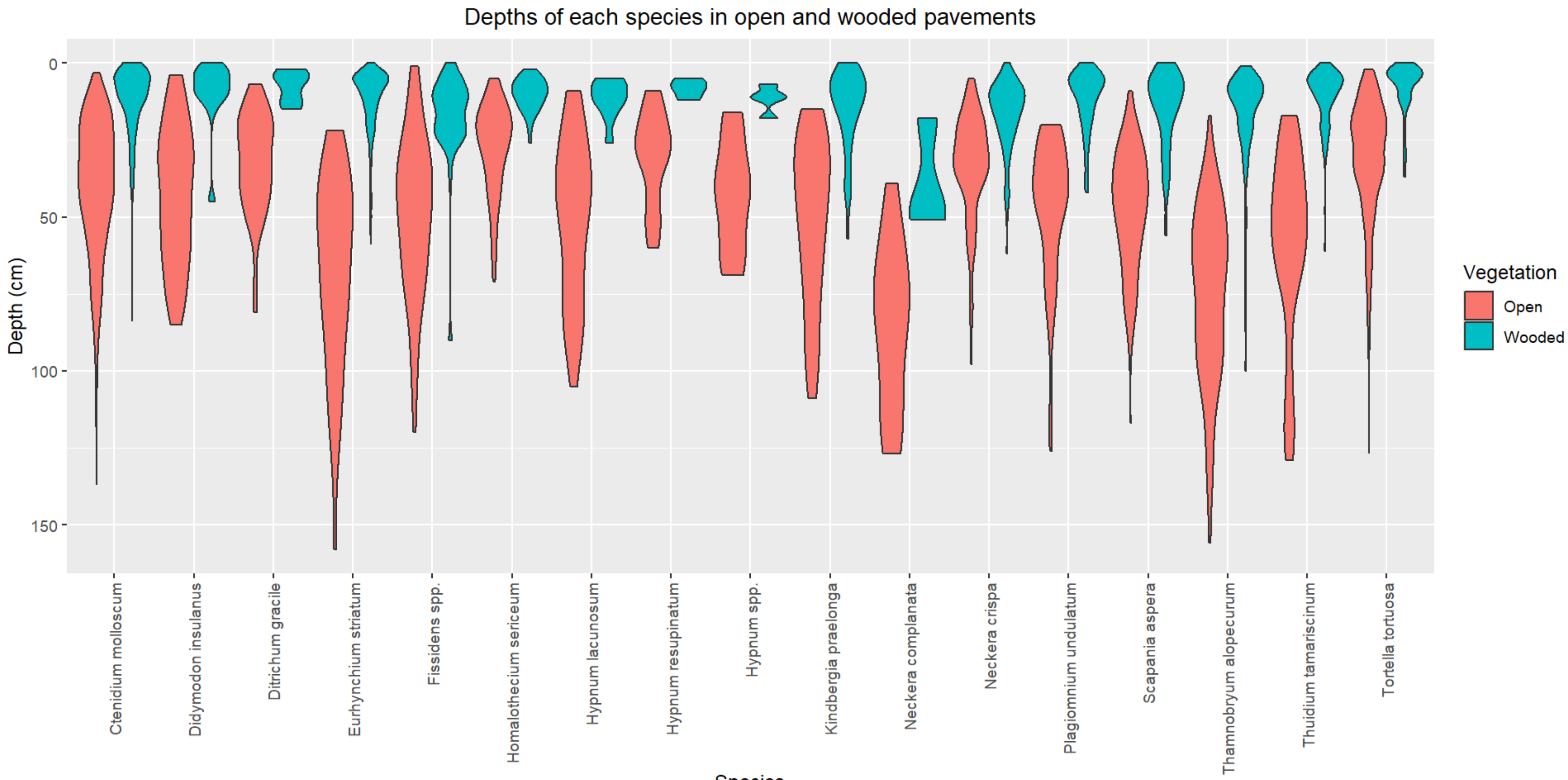

Figure 40. Violin plot for specimen depths of species in open (red) and wooded (blue) pavements.

Grike categories

In open pavements there was no statistical difference between species in categories 1 (narrow, shallow) and 4 (wide, shallow). Only some species showed differences between categories. These were *Didymodon insulanus*, *Ditrichum gracile, Hypnum resupinatum, Kindbergia praelonga, Plagiomnium undulatum,* and *Thuidium tamariscinum* (Table 7). Most differences occurred between category 1 (narrow, shallow) and category 6 (wide, deep). Figure 41 and Figure 42 show the specimen depths for species found in these categories. For the species that show differences between these grikes, all species grow further down the grike in the wide, deep grikes. For example, *Kindbergia praelonga* grows between 20 and 30 cm in category 1 grikes and around 100 cm in category 6 grikes and *Thuidium tamariscinum* grows between 20 and 40 cm in category 1 grikes and below 100 cm in category 6 grikes. All species are found in category 6 grikes, and these grikes also have the highest Shannon index of all open grike categories. *Neckera complanata* and *Reboulia hemisphaerica* are missing from category 1 grikes and this category has the lowest diversity value. Species are also missing from category 3 grikes (*Hypnum* spp.) and category 4 (*Kindbergia praelonga*).

Table 7. Species with a p-value < 0.05 for specimen depth between categories in open pavements. Where p-value is below 0.05, there is a significant difference in specimen depth between categories.

Species	**Category**	**1**	**2**	**4**
Didymodon insulanus	**5**	0.039	0.039	
	6	0.018	0.008	0.028
Ditrichum gracile	**6**	0.022		
Hypnum resupinatum	**6**	0.027		
Kindbergia praelonga	**2**	0.005		
	3	0.014		
	6	0.017		
Plagiomnium undulatum	**6**	0.027		
Thuidium tamariscinum	**6**	0.019	0.012	

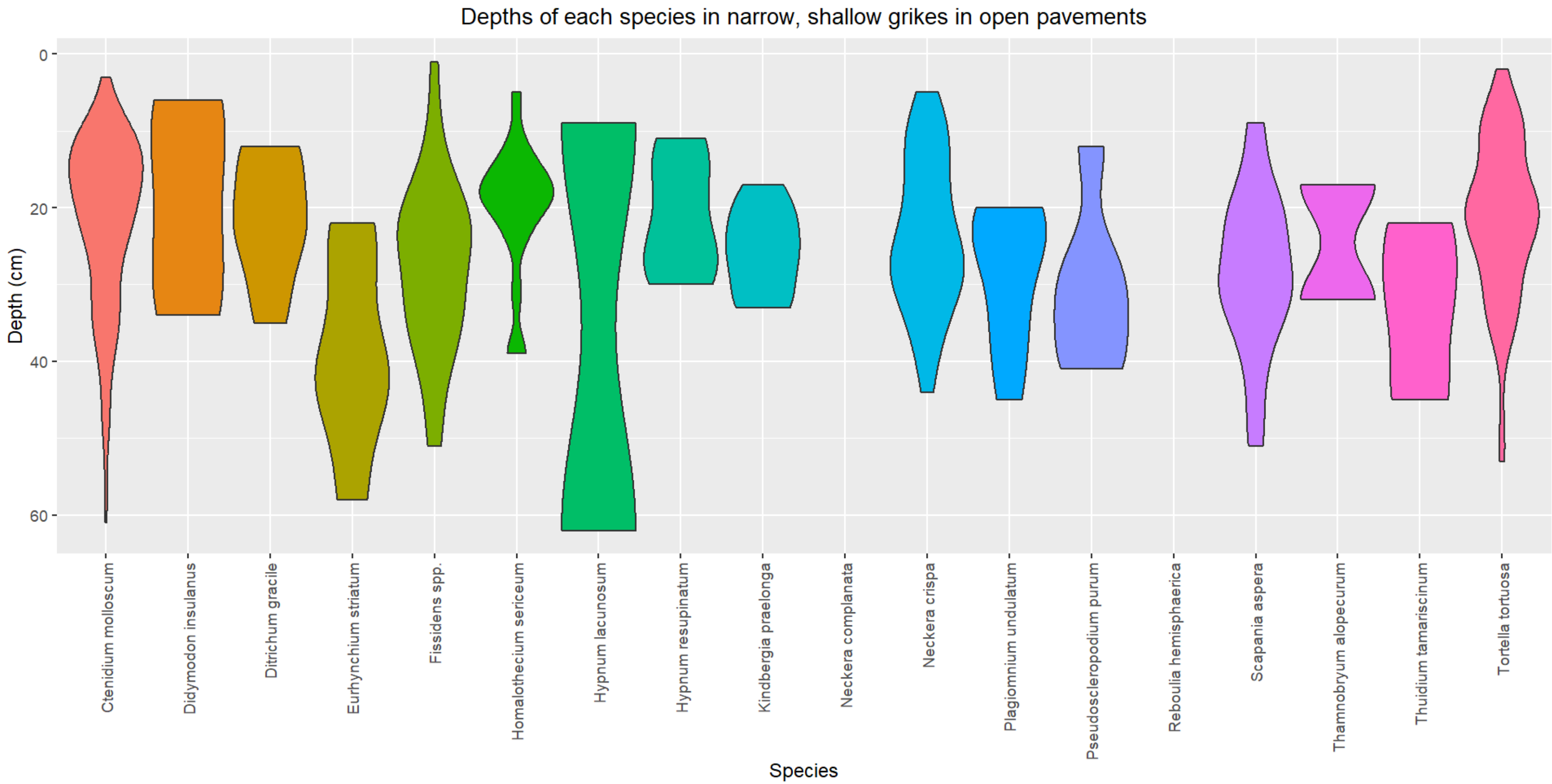

Figure 41. Violin plot for specimen depth of species in category 1 (narrow, shallow) grikes in open pavements. Category 1 grikes are those that are less than 30 cm grike maximum width and less than 50 cm grike depth.

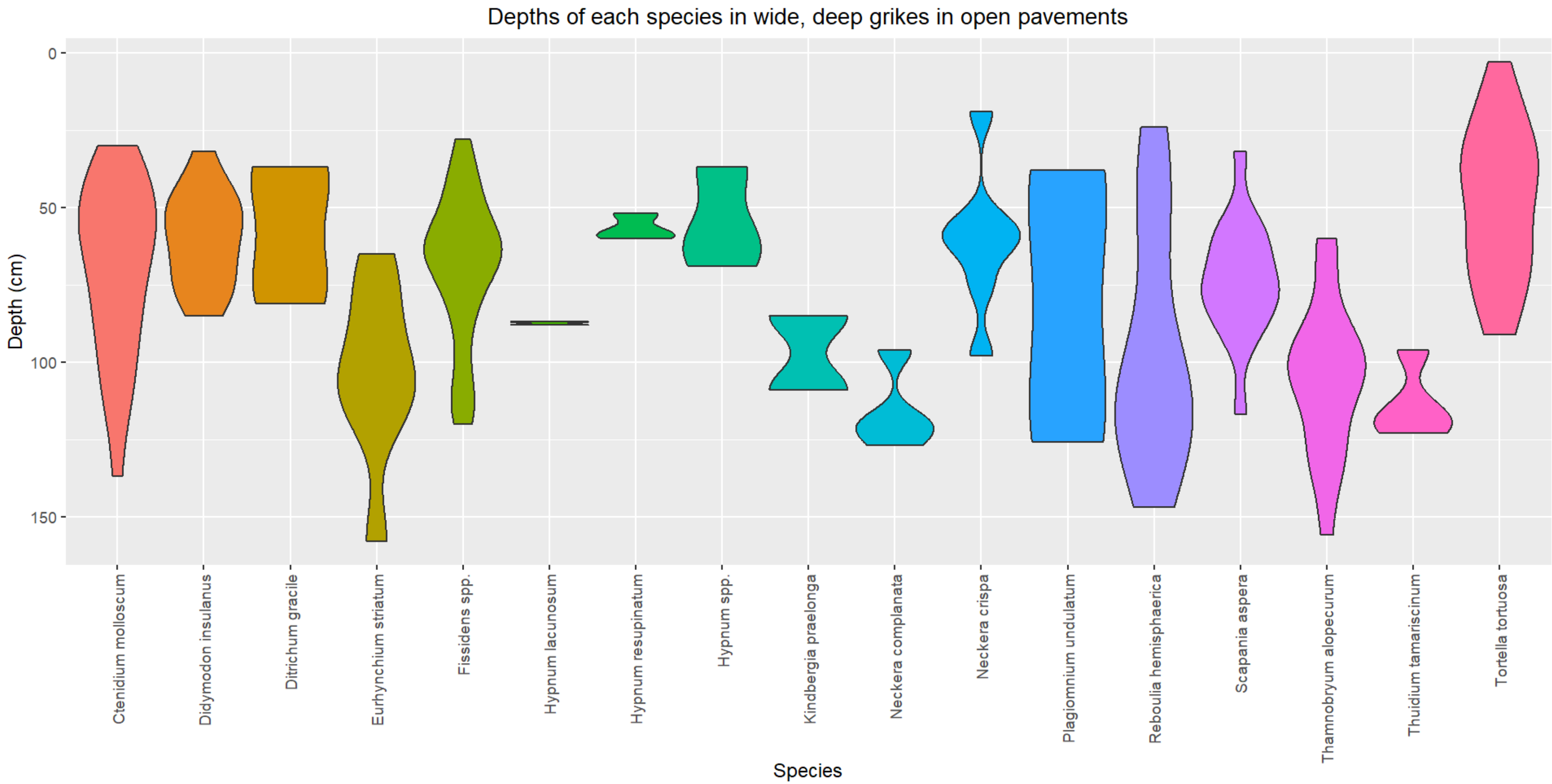

Figure 42. Violin plot for specimen depth of species in category 6 (wide, deep) grikes in open pavements. Category 6 grikes are those that are greater than 30 cm grike maximum width and with a grike depth greater than 100 cm.

In wooded pavements there was no statistical difference between species in category 3 grikes (narrow, deep) and category 6 grikes (wide, deep). In both of these deep grikes, fewer species were recorded, seven in narrow grikes and six in wide grikes. The only other grikes to have species missing was in category 4 (*Ditrichum gracile* and *Tortella tortuosa*). The only species to show differences between categories in wooded pavements were *Ctenidium molloscum, Fissidens* spp., *Thuidium tamariscinum,* and *Tortella tortuosa* (Table 8). The categories with the most differences between species are category 1 (narrow, shallow) and category 5 (wide, medium). Figure 43 and Figure 44 show the specimen depths for each species in these grikes. Like in the open pavements, species that show differences in depths between these two grike types, grow further down the grike in the wide, medium grikes. In wooded pavements, the category with the highest diversity was category 2 (narrow, medium) and the category with the lowest diversity was category 3 (narrow, deep).

Table 8. Species with a p-value < 0.05 for specimen depth between categories in wooded pavements. Where p-value is below 0.05, there is a significant difference in specimen depth between categories.

Species	**Category**	**1**	**2**
Ctenidium molloscum	**3**	0.035	
	5	0.021	
Fissidens spp.	**5**	0.040	
	6	0.047	
Thuidium tamariscinum	**5**	0.031	0.039
Tortella tortuosa	**3**	0.008	0.003

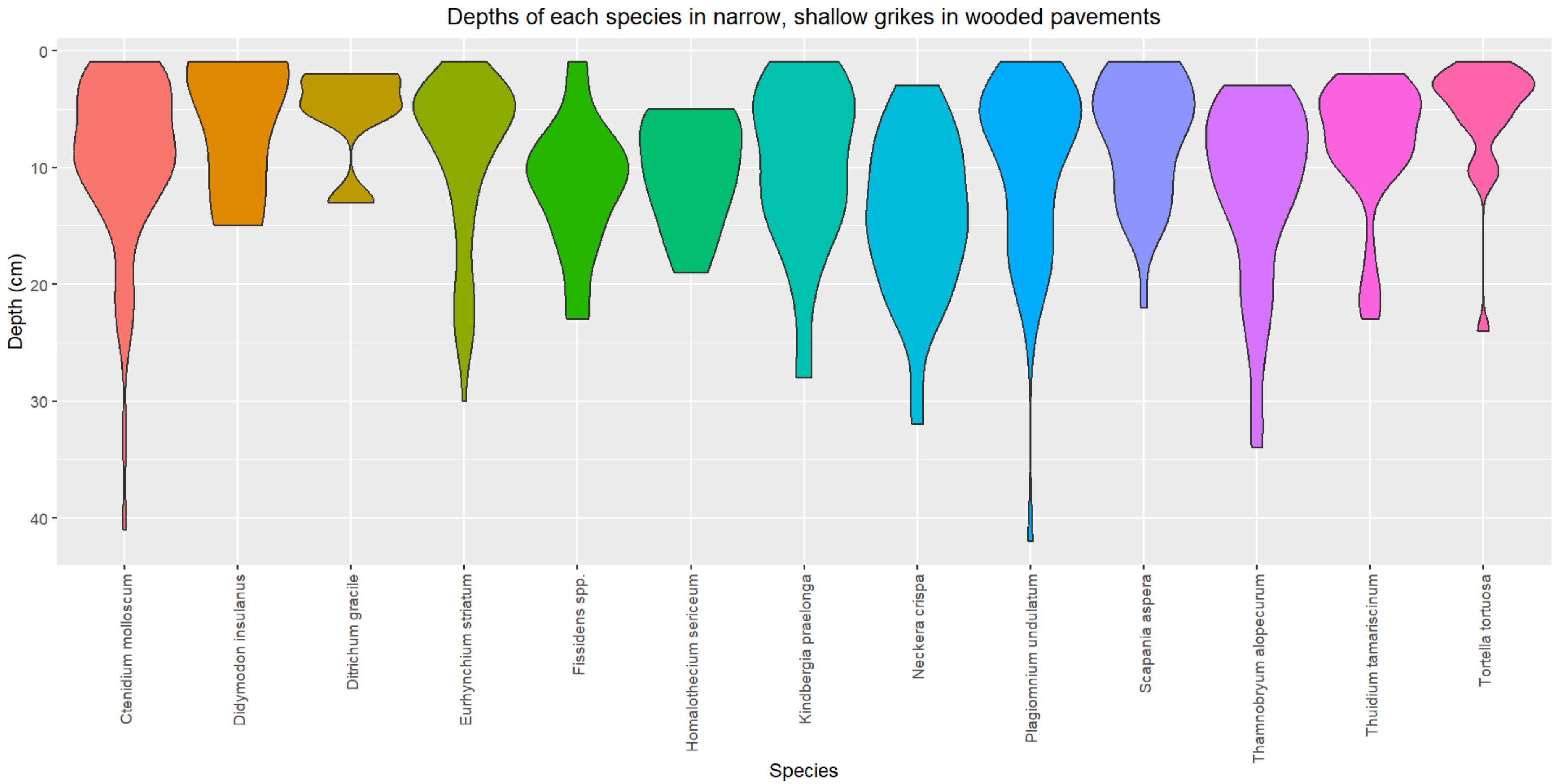

Figure 43. Violin plot for specimen depth of species in category 1 (narrow, shallow) grikes in wooded pavements. Category 1 grikes are those that are less than 30 cm grike maximum width and less than 50 cm grike depth.

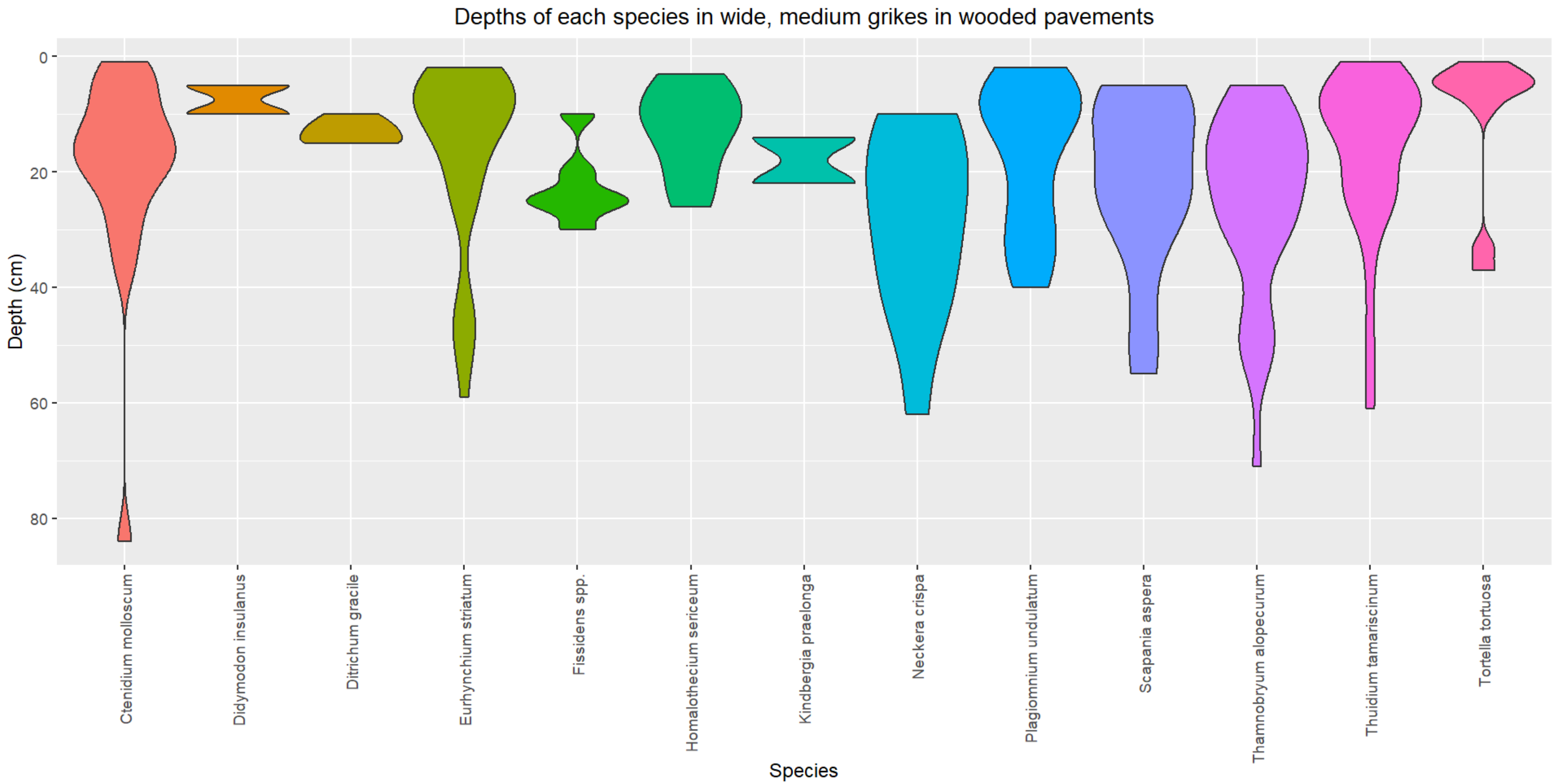

Figure 44. Violin plot for specimen depth of species in category 5 (wide, medium) grikes in wooded pavements. Category 5 grikes are those that are greater than 30 cm grike maximum width and between 50 cm and 99 cm grike depth.

Although Figure 40 shows a statistically significant difference for each species' depth between open and wooded pavements, when species are separated by category, there is not a difference in depth between open and wooded pavements for some species (Table 9). Only *Ctenidium molloscum* and *Thuidium tamariscinum* show a difference (p-value < 0.05) for all categories between open and wooded pavements. Some species such as *Didymodon insulanus* only showed a difference between open and wooded pavements in one category (wide, medium). *Neckera complanata* only had specimens growing in both open and wooded pavements for one category (narrow, shallow).

Open pavements showed a higher diversity in categories 2, 3, 4, 6 compared to wooded pavements. For specimen depth, the depth range with the greatest diversity in open pavements was 80 – 89 cm, whereas in wooded pavements it was 10 – 19 cm. The diversity by depth was only higher in wooded pavements compared to open pavements for the first 19 cm where upon the diversity becomes higher for every depth range in open pavements.

Table 9. P-values for each species for specimen depths between open and wooded pavements for each category. Shaded boxes are those where the p-value > 0.05. A '-' marks categories where the species was either only growing in open or wooded pavements or neither. Where p-value is below 0.05, there is a significant difference in specimen depths between open and wooded pavements.

Species	Category 1	Category 2	Category 3	Category 4	Category 5	Category 6
Ctenidium molloscum	3.14E-18	4.18E-14	0.035	1.83E-14	5.04E-09	-
Didymodon insulanus	0.110	0.081	0.242	0.100	0.041	0.263
Ditrichum gracile	0.007	0.005	-	0.540	0.003	0.289
Eurhynchium striatum	8.50E-05	1.16E-09	0.142	0.0002	6.38E-05	-
Fissidens spp.	4.53E-07	0.0001	0.034	0.007	0.002	0.172
Homalothecium sericeum	0.001	0.001	0.540	0.002	0.028	-
Hypnum lacunosum	0.699	0.056	-	0.0384	0.011	-
Hypnum resupinatum	0.023	0.242	-	-	-	-
Hypnum spp.	-	-	-	0.374	-	-
Kindbergia praelonga	0.0001	0.004	-	0.183	0.171	-
Neckera complanata	0.540	-	-	-	-	-
Neckera crispa	1.06E-05	0.004	0.242	2.86E-08	0.037	0.018
Plagiomnium undulatum	2.78E-05	2.05E-07	0.245	0.007	0.002	0.108
Scapania aspera	5.62E-09	3.31E-05	0.022	0.001	4.11E-06	0.193
Thamnobryum alopecurum	0.072	8.35E-10	0.001	-	9.22E-07	0.005
Thuidium tamariscinum	0.006	1.10E-06	-	0.032	0.0002	0.029
Tortella tortuosa	5.19E-09	1.72E-08	0.001	0.104	0.0002	-

4. Discussion

4.1. Bryophytes in limestone pavements

In the limestone pavements of northern England, a variety of bryophyte flora grows. In the open pavements, *Ctenidium molloscum, Neckera crispa* and *Tortella tortuosa* dominate, and in the wooded pavements these species are replaced with *Eurhynchium striatum, Thamnobryum alopecurum* and *Thuidium tamariscinum*. *Thamnobryum alopecurum* particularly is found to replace *Neckera crispa* in deeper shade (Blockheel et al., 2014). Although slightly less present in the wooded pavements, *Ctenidium molloscum* was the most frequently recorded moss in this study. The ability of *C. molloscum* to grow in a range of conditions allows it to dominate here and elsewhere being a widespread species, albeit slow growing (Blockheel et al., 2014; Furness and Grime, 1982). *Reboulia hemisphaerica* on the other hand is scarce with a locally frequent distribution across the UK, found here only in the open limestone pavements (Blockheel et al., 2014). Colonies of *R. hemisphaerica* have been lost recently from where it grows on hedge banks and along lanes from changing management practices (Blockheel et al., 2014) but grikes of limestone pavements where it is moist in winter and drier in summer could become a refuge for this species (Blockheel et al., 2014). Another limestone pavement species that has seen a decline in other habitats is *Flexitrichum gracile* (*Ditrichum gracile*) which does not have a wide distribution across the UK but can colonise well in the north and west (Blockheel et al., 2014). Although none of the species found here are particularly rare there were a few species that were only found at one site, for example *Plagiochila porelloides* was only found in a wooded pavement at Dalton Crags and *Anomodon viticulosus* was only found in an open pavement at Hutton Roof. This could be due to the grike sampling area size or due to the number of sites visited. The species richness was higher overall in the open pavements (25 species in open pavements compared to 21 in wooded pavements) however the bryophyte cover is much less. Figure 3 and Figure 4 show the typical difference between open and wooded pavements with wooded pavements typically being covered in a mat of bryophytes that extend from the clint tops into the grikes. Many of the species found here are not specific to the grikes of limestone pavements but are similar to those found in calcareous woodlands (Webb and Crowle, 2023), however from this study it was found that bryophytes species react differently to the light available in the grike.

4.2. Light levels and species distributions in open pavements

In the grikes of open limestone pavements, the percentage reduction in light (from the clint top to within the grike) became greater further down the grike. In simpler terms, the deeper down the grike, the darker it is compared to the surface. However, in the first 50 cm of the grike, there was both a rapid increase in the percentage reduction in light and a large spread of data. In this top portion of the grike, the light is more variable where light levels can be similar to that of the surface or much darker and the same light level as that found at the bottom of the grike. This variability in light is possibly affected by the maximum width of the grike and the grike length as seen in Figure 9 and Figure 10. The light varies across different grike lengths and as the grike maximum width increases, it becomes lighter. Yarranton and Beasleigh (1968) found that width along with depth and aspect was significant in the distribution of species within the grike as they affected light levels. Here, aspect was not found to affect the light in the grike as expected.

Species that grow in the first 50 cm of the grike where light is so variable are likely to be generalists such as *Ctenidium molloscum*, which was found mostly growing above 50 cm and where the percentage reduction in light was greater than 50% but predominantly closer to 100% as seen in Figure 11 and Figure 12. Zechmeister (1995) found that *Ctenidium molloscum* had increased growth in shady and humid sites but with an Ellenberg value of 7 (well-lit, sometimes occurring in partial shade (Ellenberg, 1974; Hill et al., 2017)) this species can thrive at the top of the grike. *Tortella tortuosa* is another species which grows predominantly above 50 cm in the open pavements being particularly well suited to the variable conditions, growing where the percentage reduction in light is anywhere from 0 to 100%. This species also has an Ellenberg value of 7 (Hill et al., 2017), typically found growing on the clint surface being a pioneer species of limestone (Ivimey-Cook, 1965). *Neckera crispa* is similar to *T. tortuosa* in its growing conditions but with a lower Ellenberg value (6, semi-shade to well-lit (Hill et al., 2017)). *N. crispa* is typically found in shaded or sheltered sites with the walls of grikes being a well-known location (Blockheel et al., 2014).

Once below 50 cm in the open pavements, the conditions become more constant. Deeper down in the grike, the grike length plays a greater role in affecting light levels compared to grike maximum width. Some species that grow deeper into the grike are *Eurhynchium striatum, Neckera complanata, Reboulia hemisphaerica, and Thamnobryum alopecurum*. These four species all require the percentage reduction in light to be above 80% but can grow across a range of depths. *Eurhynchium striatum* and *Thamnobryum alopecurum* both can grow as high up as 25 cm whilst growing down to the bottom of the deepest grikes. However, this is likely to occur in narrower, shorter grikes where the percentage reduction in light is highest, similar to what was found by Dickinson et al. (1963). *Thamnobryum alopecurum* has the lowest Ellenberg light value found here (3, shade dwelling plants (Hill et al., 2017)).

For most species, the variability in depth could be explained by light however, there were three species (*Hypnum resupinatum, Hypnum spp.,* and *Pseudoscleropodium purum*) where light was not an indicator of species depth in the open pavements. This could be due to the small sample size of these species (29, 13, 22 records respectively) and *Hypnum* spp. can be discounted as there were only 13 records of unidentified *Hypnum* species. Another variable that was recorded was the position of the specimen in the grike. However, only one species (*Plagiomnium undulatum*) showed any difference between positions in the grike so it is not a deciding factor in species organisation. Yarranton and Beasleigh (1969) found two air layers within grikes, with the top air layer being more variable and continuous with that of the surface, like that of the light levels in this study. It is possible that other environmental variables are affecting where *H. resupinatum* and *P. purum* grow. However, their positions could be due to competition with other species, specifically other families. Brachytheciaceae (*P. purum*) did not exhibit any niche overlap with other families above a value of 0.5, so this species is potentially occupying a niche space alone. Hypnaceae only shows a niche overlap with Neckeraceae, Flexitrichaceae and Pottiaceae despite occurring is most niche boxes. *Hypnum resupinatum* and *Pseudoscleropodium purum*, which is a very large moss (Blockheel et al., 2014), are potentially filling a niche space not occupied by other species more affected by light.

How each species occupies a niche can be described going vertically down the grike in the open pavements. Although all grikes are different, this description gives an idea of what a grike in an open limestone pavement might resemble. Beginning at the top of the grike, near the surface will be *Homalothecium sericeum* followed by *Ctenidium molloscum, Flexitrichum gracile, Hypnum resupinatum,* and *Tortella tortuosa*, although *Ctenidium molloscum* and *Flexitrichum gracile* are more likely to be found in narrower and shorter grikes. These species all exhibit a niche overlap with each other. In grikes that are wider, *Neckera crispa* will appear, having some overlap with *Flexitrichum gracile* and *Hypnum resupinatum*. When moving slightly deeper into the grike, species such as *Didymodon insulanus, Hypnum lacunosum, Plagiomnium undulatum, Pseudoscleropodium purum, Scapania aspera,* and *Thuidium tamariscinum* begin to appear. Some niche overlap still occurs here such as between *Ctenidium molloscum* and *Didymodon insulanus* or *Scapania aspera* with *Flexitrichum gracile* and *Hypnum resupinatum*. Deeper still into the grike where light levels are much lower, the woodland species begin to appear such as *Eurhynchium striatum, Fissidens* spp., *Kindbergia praelonga* and *Thamnobryum alopecurum*. Species that appear higher up in the grike no longer grow other than *Scapania aspera, Thuidium tamariscinum* and *Didymodon insulanus* which has a niche overlap with many species that grow deeper down. However, the other species typically occupy their own niche space. Near the bottom of the grike *Thamnobryum alopecurum* continues to grow and the only other species found here are *Neckera complanata* and *Reboulia hemisphaerica* which grow in the darkest parts of the grike in their own niche space. Although, *Reboulia hemisphaerica* may be found higher up in the grike, it will be where it is narrow and in much greater shade.

4.3. Light levels and species distributions in wooded pavements

The distribution of species in the grikes of wooded pavements differs vastly from that of the open limestone pavements. In the wooded pavements, all species grow at the top of the grike with many mostly existing in the top 15 cm. *Fissidens* spp. had the greatest distribution, potentially influenced by canopy cover, growing deepest in the grike at 40% cover. However, this could also be due to difficulty in identifying *Fissidens* species and this genus exhibits a range of Ellenberg light values (Hill et al., 2017). Although light was not measured here, it is much darker, even at the surface. Interestingly, *Neckera crispa* which was found higher up in the grikes of open pavements, was able to grow deeper than other species in the wooded pavements. As with open pavements, the grike maximum width was important allowing *N. crispa* to grow deeper when the maximum width is greater. There are likely other factors affecting *N. crispa* considering the similarity between the distributions in both pavements. For *Thamnobryum alopecurum,* the distribution within the grike is reduced greatly being limited to the first 40 cm, reducing further when the canopy cover increased. As a robust, woodland species that can cover large areas, it is possible that either light is greatly important, or there are other interacting factors. *Neckera crispa* and *Thamnobryum alopecurum* had a niche separation in the open pavements, however, show no difference between their distributions in wooded pavements. As there is likely to be greater competition happening at the top of the grike, the area in which a species can grow is potentially important. Grike depth was found to be an interacting factor in species depth in wooded pavements. Although this could be a correlation between the two variables, more space in the grike will allow species to spread further if conditions allow. Tattersall (personal communication) found that with increasing canopy cover, the proportion of light at the surface and within the grike (at 25 cm) reach a point where they intersect. Therefore, species may be able to grow deeper into the grike, where there is space, when light levels are similar to and less variable than at the surface, allowing for more species to occur.

4.4. Conservation implications

Although there is a greater diversity at the top of the grike in wooded pavements, where bryophytes are abundant and can cover the whole surface of the grike, these plants have both positive and negative effects within a woodland ecosystem (Glime, 2024). Therefore, when planning the conservation of limestone pavements, it is important to consider all species within the ecosystem, including bryophytes. They are often recorded as just a singular group (Glime, 2024), when it is obvious that each bryophyte species responds differently to the environment found in limestone pavements. Although there is a greater mass of bryophytes in the wooded limestone pavements, it is constrained to the top of the grike with the species no longer occupying their own niches as seen in the open pavements and overall, the open limestone pavements have a greater bryophyte diversity. Different studies show that a mat of bryophytes can be both helpful and harmful to other plant species (García de León et al., 2016; Sand-Jensen and Hammer, 2012; Zamfir, 2000) and it is possible that this is also not good for the bryophytes themselves. To completely rewild open limestone pavements so that they are covered by a thick canopy will reduce bryophyte diversity and likely those of other plants. There was also only a handful of records of bryophyte species that were found solely in the wooded pavements.

With the grikes of limestone pavements likely to become a refuge as climate changes (York, 2020), it is important to consider what could benefit from allowing the limestone pavements to remain open or with a mosaic of vegetation. In the open limestone pavements, the greatest diversity is found in the first 50 cm of the grike when the light is low. Bryophytes should be included in the management of sites, and so by allowing for different light levels to occur within the grikes will allow a greater number of species to grow. For example, allowing scrub in some areas and in others removing it and having some trees and denser cover, as well as considering grike characteristics, allowing both generalist and specialist species to grow occupying their own niche space.

4.5. Future work and conclusion

This study is a gateway for further research on bryophytes in the grikes of limestone pavements of which there has been very little. As the only environmental factor that was recorded here was light, further study should focus on humidity, temperature and pH which have been found to also affect grike vegetation (Yarranton and Beasleigh, 1969). Combining environmental variables, and recording them in the wooded pavements as well, would provide a more comprehensive overview of bryophyte organisation in grikes. As grike maximum width is important in both the open and wooded pavements, it would be useful to record the grike width at the point of the specimen rather than minimum and maximum width of the grike overall. Any further study that focuses on the bryophytes of limestone pavements would be useful in the management of these sites. Whilst there are those that look at how bryophytes affect the growth of vascular plants (e.g. (Zamfir, 2000)), bryophytes should be studied in their own right. Bryophytes are well known as soil developers, but the impact that this can have on limestone pavements is little studied. There is also little understanding of how bryophytes might respond to climate change or nutrient pollution even though bryophytes have an impact on terrestrial cycles (Slate et al., 2024). As slow growing plants, long ranging studies would be beneficial and research should also look to that which has been done on alvar grasslands (Campeau, 2013; Tyler et al., 2018) whose similarity to limestone pavements can provide examples of where research is lacking.

Overall, this study shows how greatly the grikes of open and wooded limestone pavements differ in bryophyte flora. The open pavements have a greater bryophyte diversity which extends deep into the grike allowing species to occupy their own niche creating an interesting pattern from generalist species at the top of the grike where the light is variable, down to the dark depths of the grike where only a few species can thrive. The change in light throughout the grike was important for nearly all species found in the open limestone pavements and the characteristics of the grike, mainly grike maximum width and grike length, were impacting the how the light varies within the grike.

The wooded pavements, although being covered in large swathes of bryophytes are less diverse overall, and do not exhibit such an organisation as seen in the open limestone pavements. Even though there is a greater diversity at the top of the grike in wooded pavements compared to the open pavements, the composition is congruous with that of the surface with bryophytes growing together. There is also a limited depth to which bryophytes can extend into the grikes of wooded pavements even for typical woodland species. For wooded pavements as well as open pavements, grike width played an important role in the organisation of bryophytes, by affecting the light that enters the grike but also potentially due to space. In the open pavements there was a greater diversity in the wide and deep grikes, however in the wooded pavements the greatest diversity was found in the narrow, medium grikes. With such differences between the open and wooded limestone pavements it is important to allow both type of communities to grow, especially in a habitat with such limited space.

Appendix

Appendix 1. Species recorded in this study in open and wooded pavements with number of observations for each species across both types of sites. Including total number of species and observations.

Open Pavements	Observations	Wooded Pavements	Observations
Anomodon viticulosus	9	*Amblystegium serpens*	2
Bryum radiculosum	1	*Climacium dendroides*	1
Climacium dendroides	1	*Ctenidium molloscum*	185
Ctenidium molloscum	547	*Didymodon insulanus*	13
Didymodon insulanus	55	*Ditrichum gracile*	16
Ditrichum gracile	46	*Eurhynchium striatum*	307
Encalypta streptocarpa	1	*Fissidens spp.*	69
Eurhynchium striatum	56	*Homalothecium sericeum*	39
Fissidens spp.	162	*Hypnum cupressiforme*	10
Homalothecium sericeum	57	*Hypnum lacunosum*	4
Hypnum cupressiforme	32	*Hypnum resupinatum*	4
Hypnum lacunosum	29	*Kindbergia praelonga*	41
Hypnum resupinatum	13	*Neckera complanata*	3
Kindbergia praelonga	35	*Neckera crispa*	124
Neckera complanata	16	*Plagiochila porelloides*	5
Neckera crispa	164	*Plagiomnium undulatum*	150
Plagiomnium undulatum	46	*Rhytidiadelphus triquetrus*	2
Pseudoscleropodium purum	22	*Scapania aspera*	111
Reboulia hemisphaerica	21	*Thamnobryum alopecurum*	284
Rhytidiadelphus squarrosus	3	*Thuidium tamariscinum*	186
Rhytidiadelphus triquetrus	7	*Tortella tortuosa*	57
Scapania aspera	129		
Thamnobryum alopecurum	94		
Thuidium tamariscinum	39		
Tortella tortuosa	266		
25	**1851**	**21**	**1613**

Appendix 2. P-values of post-hoc test below 0.05 for depths of species in open pavements. Where p-value is below 0.05, there is a significant difference in the specimen depths between species.

	Ctenidium molloscum	***Didymodon insulanus***	***Ditrichum gracile***	***Eurhynchium striatum***	***Homalothecium sericeum***	***Hypnum resupinatum***	***Neckera complanata***	***Neckera crispa***	***Thamnobryum alopecurum***	***Tortella tortuosa***
Ctenidium molloscum					0.003		7.892E-06			2.398E-06
Didymodon insulanus					0.016		0.002		1.827E-07	0.023
Ditrichum gracile							9.155E-07		3.894E-13	
Eurhynchium striatum	2.462E-08	0.007	3.0061E-07		5.940E-13	1.655E-06				1.242E-13
Fissidens spp.	0.008			0.009	9.348E-08		0.013	8.813E-07	1.084E-07	9.234E-13
Hypnum lacunosum					0.002				0.023	0.003
Hypnum resupinatum							1.325E-06		1.929E-11	
Kindbergia praelonga					0.001			0.043	0.009	0.001
Neckera crispa				3.09175E-12			2.90791E-08			0.001
Plagiomnium undulatum					0.001		0.022		0.0002	0.001

Pseudoscleropodium purum									0.021	
Reboulia hemisphaerica	8.110E-05	0.015	1.035E-05		3.280E-09	1.544E-05	3.446E-10	2.265E-07		1.686E-09
Scapania aspera	0.027		0.014		2.984E-07	0.021	0.015	5.803E-06	5.412E-07	3.821E-11
Thamnobryum alopecurum	1.929E-13				1.685E-13			3.797E-14		0
Thuidium tamariscinum	0.032		0.004		1.277E-06	0.005		8.866E-05		3.135E-07

Appendix 3. P-values for post-hoc test below 0.05 for percentage reduction in light for species in open pavements. Where the p-value is below 0.05, there is a significant difference in percentage reduction in light between species.

	Eurhynchium striatum	***Fissidens spp.***	***Kindbergia praelonga***	***Neckera complanata***	***Reboulia hemisphaerica***	***Scapania aspera***	***Thamnobryum alopecurum***	***Thuidium tamariscinum***
Ctenidium molloscum	6.78E-07	1.513E-09	0.013	7.058E-08	0.001	3.291E-06	2.155E-13	
Didymodon insulanus	0.0002	0.001	0.046	6.815E-07	0.002	0.011	3.57E-07	
Ditrichum gracile	1.873E-06	6.249E-06	0.001	9.600E-09	4.359E-05	8.821E-05	1.281E-09	0.009
Fissidens spp.				0.027				
Homalothecium sericeum	2.979E-07	4.088E-07	0.001	3.918E-09	2.428E-05	1.201E-05	2.925E-11	0.006
Hypnum lacunosum	0.0004	0.003	0.030	6.789E-07	0.001	0.014	3.912E-06	
Hypnum resupinatum	0.008571863			1.24029E-05	0.0115242		0.000245014	
Hypnum spp.				0.030				
Neckera crispa	2.660E-10	6.121E-13	5.942E-05	2.542E-10	3.125E-06	6.065E-10	2.020E-13	0.001
Plagiomnium undulatum				0.001			0.025	
Pseudoscleropodium purum				0.033				
Tortella tortuosa	7.170E-10	3.682E-13	0.002	8.405E-10	9.945E-06	7.418E-10	1.840E-13	0.002

Appendix 4. Mean percentage reduction in light in open pavements, mean specimen depth for open and wooded pavements for species, and Ellenberg light values for species found in open and wooded pavements by Ellenberg light values.

Species	Mean Percentage Reduction in Light	Mean Open Pavement Depth (cm)	Mean Wooded Pavement Depth (cm)	Ellenberg Light
Thamnobryum alopecurum	89.83840426	75.15957447	16.57570423	3
Fissidens spp.	80.8690625	49.11111111	17.37681159	4
Hypnum resupinatum	67.11433333	30.93103448	8.25	4
Eurhynchium striatum	86.90482143	67.55357143	11.79478827	5
Kindbergia praelonga	86.29428571	51.11428571	14.85365854	5
Neckera complanata	97.899375	84.6875	38.33333333	5
Plagiomnium undulatum	76.80652174	47.43478261	11.58666667	5
Thuidium tamariscinum	79.44615385	58.1025641	11.21236559	5
Didymodon insulanus	68.94254545	42.8	9.538461538	6
Hypnum spp.	72.79846154	42.84615385	11.75	6
Neckera crispa	62.44536585	33.8902439	16.58064516	6
Ctenidium molloscum	68.65579336	40.26142596	11.97567568	7
Ditrichum gracile	61.63619048	31.47826087	7.46875	7
Homalothecium sericeum	59.34649123	27.63157895	10.15384615	7
Hypnum lacunosum	61.17741935	50.40625	11.7	7
Scapania aspera	81.84333333	47.46511628	14.64864865	7
Tortella tortuosa	61.31101887	31.22932331	7.745614035	7

Appendix 5. Pianka's index of niche overlap between each species for depth and percentage reduction in light in open pavements. Values of niche overlap graded from white (niche separation) to dark green (niche overlap).

		Depth	Light
Ctenidium molloscum	*Didymodon insulanus*	0.392127263	0.526480863
	Ditrichum gracile	0.692550224	0.60027839
	Eurhynchium striatum	0.127645505	0.355696455
	Fissidens spp.	0.246295453	0.365041236
	Homalothecium sericeum	0.415199579	0.425328672
	Hypnum spp.	1.243768501	1.04669828
	Hypnum lacunosum	0.102416388	0.254183138
	Hypnum resupinatum	0.638039911	0.417119135
	Kindbergia praelonga	0.097185836	0.198905376
	Neckera complanata	0.2452766	0.425325269
	Neckera crispa	0.338431223	0.43194735
	Plagiomnium undulatum	0.09010591	0.502473441
	Pseudoscleropodium purum	0.452287168	0.617213201
	Reboulia hemisphaerica	0.085791087	0.230691413
	Scapania aspera	0.236436796	0.465067622
	Thamnobryum alopecurum	0.194806039	0.366396541
	Thuidium tamariscinum	0.127961097	0.302746299
	Tortella tortuosa	0.318697252	0.527272087
Didymodon insulanus	*Ditrichum gracile*	0.658636029	0.692958772
	Eurhynchium striatum	0.183372747	0.360847714
	Fissidens spp.	0.227231997	0.274768176
	Homalothecium sericeum	0.447910579	0.468228532
	Hypnum spp.	0.698286871	0.619801546
	Hypnum lacunosum	0.08976493	0.23907212
	Hypnum resupinatum	0.410198539	0.378888825
	Kindbergia praelonga	0.80236483	0.648447258
	Neckera complanata	0.206562886	0.399930065
	Neckera crispa	0.429060581	0.524038078
	Plagiomnium undulatum	0.188236843	0.563916368
	Pseudoscleropodium purum	0.353894138	0.550411002
	Reboulia hemisphaerica	0.166312009	0.263084384
	Scapania aspera	0.419507482	0.448473053
	Thamnobryum alopecurum	0.636187816	0.698078409
	Thuidium tamariscinum	0.651592405	0.721997883
	Tortella tortuosa	0.279833981	0.514035214
Ditrichum gracile	*Eurhynchium striatum*	0.301373837	0.32994637
	Fissidens spp.	0.396409882	0.255198756
	Homalothecium sericeum	0.608277476	0.601639044
	Hypnum spp.	1.042839892	0.93390231
	Hypnum lacunosum	0.435020945	0.31969371
	Hypnum resupinatum	0.652474936	0.568393637
	Kindbergia praelonga	0.267143134	0.323730543
	Neckera complanata	0.309951874	0.499722001

	Neckera crispa	0.66106207	0.566382176
	Plagiomnium undulatum	0.292224238	0.60320076
	Pseudoscleropodium purum	0.566988932	0.632918616
	Reboulia hemisphaerica	0.276029998	0.303767132
	Scapania aspera	0.488644257	0.469186444
	Thamnobryum alopecurum	0.565720456	0.439022588
	Thuidium tamariscinum	0.402939349	0.441879275
	Tortella tortuosa	0.491155978	0.763836027
Eurhynchium striatum	*Fissidens spp.*	0.126471807	0.255932563
	Homalothecium sericeum	0.399892747	0.354452074
	Hypnum spp.	0.525266749	0.539934248
	Hypnum lacunosum	0.051082372	0.166507991
	Hypnum resupinatum	0.258559941	0.246485622
	Kindbergia praelonga	0.035603434	0.121118019
	Neckera complanata	0.143127191	0.295081451
	Neckera crispa	0.207158696	0.349933137
	Plagiomnium undulatum	0.071841709	0.375140769
	Pseudoscleropodium purum	0.196903332	0.345309851
	Reboulia hemisphaerica	0.038334473	0.126337328
	Scapania aspera	0.530513633	0.514231779
	Thamnobryum alopecurum	0.373811937	0.500713906
	Thuidium tamariscinum	0.04862434	0.177764396
	Tortella tortuosa	0.115939412	0.318999128
Fissidens spp.	*Homalothecium sericeum*	0.242141069	0.234124983
	Hypnum spp.	0.680315991	0.522866748
	Hypnum lacunosum	0.061028645	0.126628336
	Hypnum resupinatum	0.357696001	0.203565511
	Kindbergia praelonga	0.05773381	0.100605378
	Neckera complanata	0.123140298	0.176984281
	Neckera crispa	0.363901609	0.356951696
	Plagiomnium undulatum	0.058934236	0.234924016
	Pseudoscleropodium purum	0.24377701	0.321763751
	Reboulia hemisphaerica	0.046545396	0.087566899
	Scapania aspera	0.234336699	0.374167578
	Thamnobryum alopecurum	0.134593141	0.198248575
	Thuidium tamariscinum	0.073863876	0.145931933
	Tortella tortuosa	0.178285809	0.318999128
Homalothecium sericeum	*Hypnum spp.*	0.892210482	0.840709229
	Hypnum lacunosum	0.131081655	0.233065972
	Hypnum resupinatum	0.550682023	0.384981116
	Kindbergia praelonga	0.165563818	0.227778661
	Neckera complanata	0.364391713	0.415806774
	Neckera crispa	0.396893862	0.421019144
	Plagiomnium undulatum	0.214005373	0.487161186
	Pseudoscleropodium purum	0.397707662	0.57208364
	Reboulia hemisphaerica	0.208929446	0.314290656
	Scapania aspera	0.308533341	0.396253578
	Thamnobryum alopecurum	0.688597701	0.452340688

	Thuidium tamariscinum	0.179848527	0.27912029
	Tortella tortuosa	0.330653879	0.532788359
Hypnum spp.	*Hypnum lacunosum*	0.335546793	0.447123259
	Hypnum resupinatum	0.730799427	0.648226722
	Kindbergia praelonga	0.303643946	0.316685315
	Neckera complanata	0.574160212	0.553282774
	Neckera crispa	1.056739242	0.869939197
	Plagiomnium undulatum	0.319246918	0.614619127
	Pseudoscleropodium purum	0.759789965	0.719065733
	Reboulia hemisphaerica	0.373168532	0.325954841
	Scapania aspera	0.758735071	0.823860582
	Thamnobryum alopecurum	0.735765972	0.549415767
	Thuidium tamariscinum	0.455416435	0.43726833
	Tortella tortuosa	0.849425122	0.980382101
Hypnum lacunosum	*Hypnum resupinatum*	0.308767527	0.548778832
	Kindbergia praelonga	0.035690074	0.105914026
	Neckera complanata	0.127460071	0.180943963
	Neckera crispa	0.118332561	0.260888177
	Plagiomnium undulatum	0.052280508	0.345062497
	Pseudoscleropodium purum	0.192553896	0.30372867
	Reboulia hemisphaerica	0.042121587	0.133971439
	Scapania aspera	0.100229234	0.354037278
	Thamnobryum alopecurum	0.088249685	0.185892979
	Thuidium tamariscinum	0.111281691	0.262281777
	Tortella tortuosa	0.076274674	0.270179141
Hypnum resupinatum	*Kindbergia praelonga*	0.187207812	0.174733166
	Neckera complanata	0.328106578	0.47971269
	Neckera crispa	0.567044151	0.329769875
	Plagiomnium undulatum	0.203757466	0.445942237
	Pseudoscleropodium purum	0.334932374	0.364309329
	Reboulia hemisphaerica	0.36313322	0.282715537
	Scapania aspera	0.412841764	0.558188354
	Thamnobryum alopecurum	0.399730795	0.257312991
	Thuidium tamariscinum	0.389687948	0.310376894
	Tortella tortuosa	0.456417734	0.478818549
Kindbergia praelonga	*Neckera complanata*	0.067380369	0.157089432
	Neckera crispa	0.150590883	0.366590225
	Plagiomnium undulatum	0.031652274	0.221023296
	Pseudoscleropodium purum	0.118743954	0.217308214
	Reboulia hemisphaerica	0.02917529	0.089749944
	Scapania aspera	0.261447142	0.170487512
	Thamnobryum alopecurum	0.41002934	0.518061355
	Thuidium tamariscinum	0.697689654	0.846746973
	Tortella tortuosa	0.06657712	0.176414582
Neckera complanata	*Neckera crispa*	0.211649797	0.372222545
	Plagiomnium undulatum	0.070507189	0.414334809
	Pseudoscleropodium purum	0.294529296	0.509147995

	Reboulia hemisphaerica	0.257280433	0.32124488
	Scapania aspera	0.156973158	0.363350774
	Thamnobryum alopecurum	0.154920562	0.218897891
	Thuidium tamariscinum	0.100893121	0.210804523
	Tortella tortuosa	0.164063359	0.434084933
Neckera crispa	*Plagiomnium undulatum*	0.23836297	0.401425285
	Pseudoscleropodium purum	0.409735691	0.616002393
	Reboulia hemisphaerica	0.191231237	0.207054764
	Scapania aspera	0.426775244	0.550653678
	Thamnobryum alopecurum	0.34327734	0.384022917
	Thuidium tamariscinum	0.240287762	0.392918376
	Tortella tortuosa	0.267417017	0.449851782
Plagiomnium undulatum	*Pseudoscleropodium purum*	0.116952023	0.431228353
	Reboulia hemisphaerica	0.042673636	0.309713469
	Scapania aspera	0.137553187	0.47967616
	Thamnobryum alopecurum	0.184055109	0.518977643
	Thuidium tamariscinum	0.062164913	0.403579714
	Tortella tortuosa	0.094129161	0.538126666
Pseudoscleropodium purum	*Reboulia hemisphaerica*	0.109125339	0.213198355
	Scapania aspera	0.276594102	0.447961627
	Thamnobryum alopecurum	0.268953857	0.337076336
	Thuidium tamariscinum	0.224572736	0.358830211
	Tortella tortuosa	0.320878562	0.66072016
Reboulia hemisphaerica	*Scapania aspera*	0.084234343	0.248345491
	Thamnobryum alopecurum	0.083080816	0.139940741
	Thuidium tamariscinum	0.040071492	0.10512428
	Tortella tortuosa	0.063275906	0.142927039
Scapania aspera	*Thamnobryum alopecurum*	0.430322662	0.431356686
	Thuidium tamariscinum	0.242378866	0.274565019
	Tortella tortuosa	0.178041203	0.429975076
Thamnobryum alopecurum	*Thuidium tamariscinum*	0.357531838	0.530493996
	Tortella tortuosa	0.155499386	0.304734569
Thuidium tamariscinum	*Tortella tortuosa*	0.119479088	0.264253934

References

Atherton, I., Bosanquet, S. D. & Lawley, M. 2010. *Mosses and liverworts of Britain and Ireland: a field guide,* Plymouth, British Bryological Society.

Bates, J. 1978. The influence of metal availability on the bryophyte and macrolichen vegetation of four rock types on Skye and Rhum. *The Journal of Ecology,* 6**,** 189–198.

Bates, J. 1982. The role of exchangeable calcium in saxicolous calcicole and calcifuge mosses. *New Phytologist,* 90**,** 239–252.

Blakesley, D. & Buckley, P. 2016. *Grassland restoration and management,* Exeter, Pelagic Publishing Ltd.

Blockheel, T. L., Bosanquet, S. D. S., Hill, M. O. & Preston, C. D. 2014. *Atlas of British and Irish bryophytes,* Newbury, Pisces Publications.

British Bryological Society. 2025. *British Bryological Society* [Online]. Available: https://www.britishbryologicalsociety.org.uk/ [Accessed 2025].

British Ecological Society 1954. Summer Meeting at Malham Tarn. *Journal of Animal Ecology,* 23**,** 404–409.

Campeau, S. 2013. Establishing alvar mosses on quarry floors: A necessary step in the restoration of quarries to alvars. *Final Report to the Ontario Aggregate Resources Corporation (TOARC). Bryophyta Technologies inc., Lambton, Quebec*.

Chase, J. M. 2011. Ecological niche theory. *In:* Scheiner, S. M. & Willig, M. R. (eds.) *The theory of ecology.* Chicago: University of Chicago Press, 93–108.

Colebourn, P. 1974. The influence of habitat structure on the distribution of Araneus diadematus Clerck. *The Journal of Animal Ecology***,** 401–409.

Commission of the European Communities 1992. Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. *Official Journal of the European Union,* 206**,** 50.

Craw, R. 1976. Streamside bryophyte zonations. *New Zealand journal of botany,* 14**,** 19–28.

Dickinson, C. H., Pearson, M. & Webb, D. A. Some micro-habitats of the Burren, their micro-environments and vegetation. Proceedings of the Royal Irish Academy. Section B: Biological, Geological, and Chemical Science, 1963. JSTOR, 291–302.

Dines, T. D. & Rumsey, F. J. 2020. Gymnocarpium robertianum (Hoffm.) Newman. *In:* Stroh, P. A., Humphrey, T. A., Burkmar, R. J., Pescott, O. L., Roy, D. B. & Walker, K. J. (eds.) *BSBI Online Plant Atlas*.

Doddy, P. & Roden, C. M. The nature of the black deposit occurring in solution hollows on the limestone pavement of the Burren, Co. Clare. Biology and Environment: Proceedings of the Royal Irish Academy, 2014. JSTOR, 71–77.

Doležal, J., Korznikov, K., Altman, J., Fibich, P., Řeháková, K., Lltonga, E. N., Majeský, L. & Dančák, M. 2023. Ecological niches of epiphyllous bryophytes along Afrotropical elevation gradient. *Oikos,* 5**,** e09772.

Downing, A. J. 1992. Distribution of bryophytes on limestones in eastern Australia. *The Bryologist,* 95**,** 5–14.

Dunford, B. 2016. The Burren Life Programme: An Overview. Dublin: National Economic and Social Council.

Ellenberg, H. 1974. Zeigerwerte der Gefässpflanzen Mitteleuropas. *Scripta geobotanica,* 9**,** 1–97.

Fookes, P. & Hawkins, A. 1988. Limestone weathering: its engineering significance and a proposed classification scheme. *Quarterly Journal of Engineering Geology and Hydrogeology,* 21**,** 7–31.

Forbes, B. C. 1994. The importance of bryophytes in the classification of human-disturbed high arctic vegetation. *Journal of Vegetation Science,* 5**,** 877–884.

Frego, K. A. 2007. Bryophytes as potential indicators of forest integrity. *Forest ecology and management,* 242**,** 65–75.

Furness, S. & Grime, J. 1982. Growth rate and temperature responses in bryophytes: II. A comparative study of species of contrasted ecology. *The Journal of Ecology***,** 525–536.

García de León, D., Neuenkamp, L., Gerz, M., Oja, E. & Zobel, M. 2016. Secondary succession in alvar grasslands–do changes in vascular plant and cryptogam communities correspond? *Folia geobotanica,* 51**,** 285–296.

Glime, J. M. 2024. Roles of bryophytes in forest sustainability—positive or negative? *Sustainability,* 16**,** 2359.

Goldie, H. 1993. The legal protection of limestone pavements in Great Britain. *Environmental Geology,* 21**,** 160–166.

Goldie, H. 1996. The limestone pavements of great Asby scar, Cumbria, UK. *Environmental Geology,* 28**,** 128–136.

Goldie, H. S. 1987. Human impact on limestone favement. *Endins: publicació d'espeleologia***,** 71–82.

Goldie, H. S. 1995. Major protected sites of limestone pavements in Great Britain. *Acta Geographica Szegediensis. Special Issue: Environmental Effects on Karst Terrains (ed.) Barany-Kevei, I., Szeged***,** 61–92.

Gray, M. 2013. *Geodiversity: valuing and conserving abiotic nature*, John Wiley & Sons.

Hill, M. O., Preston, C. D., Bosanquet, S. D. S. & Roy, D. B. 2017. BRYOATT – Attributes of British and Irish Mosses, Liverworts and Hornworts. Available: https://www.brc.ac.uk/biblio/bryoatt-attributes-british-and-irish-mosses-liverworts-and-hornworts-spreadsheet.

HMSO. 1981. Wildlife and Countryside Act (amended 1985). HMSO. London.

Holyoak, D. & Long, D. G. 2005. Notable records of mosses (Bryopsida) from Co Mayo, including four species new to Ireland. *The Irish Naturalists' Journal,* 28**,** 7–10.

Hörnberg, G., Ohlson, M. & Zackrisson, O. 1997. Influence of bryophytes and microrelief conditions on Picea abies seed regeneration patterns in boreal old-growth swamp forests. *Canadian Journal of Forest Research,* 27**,** 1015–1023.

Ivimey-Cook, R. 1965. The vegetation of solution cups in the limestone of the Burren, Co. Clare. *Journal of Ecology,* 53**,** 437–445.

Janousek, C. N., Thorne, K. M. & Takekawa, J. Y. 2019. Vertical zonation and niche breadth of tidal marsh plants along the northeast Pacific coast. *Estuaries and Coasts,* 42**,** 85–98.

Kimmerer, R. W. & Allen, T. 1982. The role of disturbance in the pattern of a riparian bryophyte community. *American Midland Naturalist***,** 370–383.

Kubalíková, L., Balková, M. & Zapletalová, D. 2023. Where geodiversity meets biodiversity and culture: a case study from the abandoned limestone quarries of Hády (Brno, Czech Republic). *In:* Kubalíková, L., Coratza, P., Pál, M., Zwoliński, Z., Irapta, P. N. & van Wyk de Vries, B. (eds.) *Visages of Geodiversity and Geoheritage.* London: Geological Society of London, 167–180.

Lewis Smith, R. 1999. Biological and environmental characteristics of three cosmopolitan mosses dominant in continental Antarctica. *Journal of Vegetation Science,* 10**,** 231–242.

Löbel, S., Dengler, J. & Hobohm, C. 2006. Species richness of vascular plants, bryophytes and lichens in dry grasslands: the effects of environment, landscape structure and competition. *Folia Geobotanica,* 41**,** 377–393.

Longton, R. 1984. The role of bryophytes in terrestrial ecosystems. *The Journal of the Hattori Botanical Laboratory,* 55**,** 147–163.

Lowe, C. J. 1981. *Some aspects of the ecology of limestone solution-hollows at gait barrows, north Lancashire (Doctoral dissertation).* Durham University.

Lundholm, J. T. & Larson, D. W. 2003. Temporal variability in water supply controls seedling diversity in limestone pavement microcosms. *Journal of Ecology,* 91**,** 966–975.

M'Closkey, R. T. 1978. Niche separation and assembly in four species of Sonoran Desert rodents. *The American Naturalist,* 112**,** 683–694.

Mägdefrau, K. 1982. Life-forms of Bryophytes. *In:* Smith, A. J. E. (ed.) *Bryophyte Ecology.* Dordrecht: Springer Netherlands, 45–58.

Microsoft Corporation 2025a. Microsoft Excel. Office 365 ed.: Microsoft Corporation.

Microsoft Corporation 2025b. Microsoft PowerPoint. Office 365 ed.: Microsoft Corporation.

Murphy, P. J. 2022. The Paradox of the Pavements–How the Cultural Value of Limestone Pavements Resulted in Widespread Damage to These Landforms Across Northern Britain and What Has Been Done about it. *Geoconservation Research,* 5**,** 321–326.

Natural England. 2023. Limestone Pavement Orders England. Available: https://naturalengland-defra.opendata.arcgis.com/datasets/Defra::limestone-pavement-orders-england/explore [Accessed 28 Jan 2025].

Otsus, M. & Zobel, M. 2004. Moisture conditions and the presence of bryophytes determine fescue species abundance in a dry calcareous grassland. *Oecologia,* 138**,** 293–299.

Parr, S. 2014. The Burren Farming for Conservation Programme – a 'blended' approach to agri-environment. *Conservation Land Management,* 12**,** 15–19.

Patton, J. 2022. *The Effect of Habitat Condition and Vegetation on the Moth Communities of the Limestone Habitats at Hutton Roof and Farleton Knott Sites of Special Scientific Interest, North West England (Masters thesis).* Lancaster University.

Pernthaler, J. 2017. Competition and niche separation of pelagic bacteria in freshwater habitats. *Environmental microbiology,* 19**,** 2133–2150.

Pianka, E. R. 1973. The structure of lizard communities. *Annual review of ecology and systematics***,** 53–74.

Pigott, C. & Pigott, M. 1963. Late-glacial and post-glacial deposits at Malham, Yorkshire. *New Phytologist,* 62**,** 317–334.

Pohlert, T. 2024. PMCMRplus: Calculate Pairwise Multiple Comparisons of Mean Rank Sums Extended.

Poponessi, S., Aleffi, M., Sabovljević, M. S. & Venanzoni, R. 2020. Bryophyte diversity hotspot: the Marmore Waterfalls Regional Park (Umbria, central Italy). *Italian Botanist,* 10**,** 33–45.

Porley, R. 2013. *England's rare mosses & liverworts: their history, ecology, and conservation,* Princeton, N.J, Princeton University Press.

Porley, R. & Hodgetts, N. G. 2005. *Mosses and liverworts,* London, Collins.

R Core Team 2024. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing.

Redfearn, P. L. 1957. *A study of the Bryophytic Vegetation of Limestone Outcrops in Florida (Doctoral dissertation).* The Florida State University.

Roberts, S. 2025a. Open Limestone Pavement.

Roberts, S. 2025b. Wooded Limestone Pavement.

Robinson, M. 2014. The ecodynamics of clearance in the British Neolithic. *Environmental Archaeology,* 19**,** 291–297.

Rodgers, J. L. 2018. *The effects of Livestock Grazing on Vegetation and Lepidopterans in Endangered Alvar Sites in Manitoba's Interlake (Masters thesis).* University of Winnipeg.

Rosén, E. Alvar vegetation of Öland—Changes, monitoring and restoration. Biology and Environment: Proceedings of the Royal Irish Academy, 2006. Royal Irish Academy, 387–399.

Sand-Jensen, K. & Hammer, K. J. 2012. Moss cushions facilitate water and nutrient supply for plant species on bare limestone pavements. *Oecologia,* 170**,** 305–312.

Schaefer, C. A. & Larson, D. W. 1997. Vegetation, environmental characteristics and ideas on the maintenance of alvars on the Bruce Peninsula, Canada. *Journal of Vegetation Science,* 8**,** 797–810.

Shannon, C. E. 1948. A mathematical theory of communication. *The Bell system technical journal,* 27**,** 379–423.

Silvertown, J. 2004. Plant coexistence and the niche. *Trends in Ecology & evolution,* 19**,** 605–611.

Silvertown, J., Dodd, M. & Gowing, D. 2001. Phylogeny and the niche structure of meadow plant communities. *Journal of Ecology,* 89**,** 428–435.

Silvertown, J. W. 1983. The distribution of plants in limestone pavement: tests of species interaction and niche separation against null hypotheses. *The Journal of Ecology***,** 819–828.

Slack, N. G., Reschke, C. & Gilman, B. 1988. Scorpidium turgescens Rediscovered in New York State. *The Bryologist,* 91**,** 217–218.

Slate, M. L., Antoninka, A., Bailey, L., Berdugo, M. B., Callaghan, D. A., Cárdenas, M., Chmielewski, M. W., Fenton, N. J., Holland-Moritz, H. & Hopkins, S. 2024. Impact of changing climate on bryophyte contributions to terrestrial water, carbon, and nitrogen cycles. *New Phytologist,* 242**,** 2411–2429.

Spitale, D. & Nascimbene, J. 2012. Spatial structure, rock type, and local environmental conditions drive moss and lichen distribution on calcareous boulders. *Ecological Research,* 27**,** 633–638.

Stevens, C. J. 2025. Large changes in vegetation composition seen over the last 50 years in British limestone pavements. *Functional Ecology,* 39**,** 128–139.

Tattersall, E. 17th December. personal communication. *RE: Interaction between canopy cover and location.* Figure to Roberts, S.

Tropicos.org. 2025. *Missouri Botanical Garden* [Online]. Available: https://tropicos.org [Accessed 2025].

Turetsky, M. R. 2003. The role of bryophytes in carbon and nitrogen cycling. *The bryologist,* 106**,** 395–409.
Tyler, T. 2002. Geographical distribution of allozyme variation in relation to post-glacial history in Carex digitata, a widespread European woodland sedge. *Journal of Biogeography,* 29**,** 919–930.
Tyler, T., Bengtsson, F., Dahlberg, C. J., Lönnell, N., Hallingbäck, T. & Reitalu, T. 2018. Determinants of bryophyte species composition and diversity on the Great Alvar of Öland, Sweden. *Journal of Bryology,* 40**,** 12–30.
Vanderpoorten, A. & Goffinet, B. 2009. *Introduction to Bryophytes,* Cambridge, Cambridge University Press.
Vincent, P. 1995. Limestone pavements in the British Isles: a review. *Geographical Journal***,** 265–274.
Vitt, D. H. & Slack, N. G. 1975. An analysis of the vegetation of Sphagnum-dominated kettle-hole bogs in relation to environmental gradients. *Canadian Journal of Botany,* 53**,** 332–359.
von Zeipel, H. & Eriksson, O. 2007. Fruit removal in the forest herb Actaea spicata depends on local context of fruits sharing the same dispersers. *International Journal of Plant Sciences,* 168**,** 855–860.
Walker, K. J. 2015. *Epipactis atrorubens* (Hoffm.) Besser. Dark-red Helleborine. Species Account. Botanical Society of Britain and Ireland. Available: https://bsbi.org/wp-content/uploads/dlm_uploads/Epipactis_atrorubens_species_account.pdf [Accessed 27 Jan 2025].
Ward, S. D. & Evans, D. F. 1976. Conservation assessment of British limestone pavements based on floristic criteria. *Biological Conservation,* 9**,** 217–233.
Watson, W. 1918. The bryophytes and lichens of calcareous soil. *Journal of ecology,* 6**,** 189–198.
Webb, S. 2013. Limestone Pavements. *In:* Waltham, T. & Lowe, D. (eds.) *Caves and Karst of the Yorkshire Dales.* Great Hucklow: British Cave Research Association, 93–110.
Webb, S. & Crowle, A. 2023. Definition of Favourable Conservation Status for Limestone Pavement. *Natural England*.
Wickham, H. 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York.
Williams, B., Parr, S., Moran, J., Dunford, B. & Conchúir, R. Ó. 2009. The Burren—Farming for the future of the fertile rock. *British Wildlife,* 21**,** 1.
Williams, P. W. 1966. Limestone pavements with special reference to western Ireland. *Transactions of the Institute of British Geographers***,** 155–172.
Willis, S. D. 2011. *The classification and management of limestone pavements-an endangered (Doctoral dissertation).* University of Liverpool, UK.
Wood, S. N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society,* 73**,** 3–36.
Yarranton, G. & Beasleigh, W. 1968. Towards a mathematical model of limestone pavement vegetation. I. Vegetation and microtopography. *Canadian Journal of Botany,* 46**,** 1591–1599.

Yarranton, G. & Beasleigh, W. 1969. Towards a mathematical model of limestone pavement vegetation. II. Microclimate, surface pH, and microtopography. *Canadian Journal of Botany,* 47**,** 959–974.
York, P. 2020. *Open Carboniferous Limestone pavement grike microclimates in Great Britain and Ireland: understanding the present to inform the future (Doctoral dissertation).* University of Chester, UK.
Young, C. C. 1997. *A test of the ecological specialization hypothesis and a structured metapopulation model in a saxicolous bryophyte community (Masters thesis).* State University of New York College of Environmental Science and Forestry.
Zamfir, M. 2000. Effects of Bryophytes and Lichens on Seedling Emergence of Alvar Plants: Evidence from Greenhouse Experiments. *Oikos,* 88**,** 603–611.
Zechmeister, H. 1995. Growth rates of five pleurocarpous moss species under various climatic conditions. *Journal of bryology,* 18**,** 455–468.
Zseni, A., Goldie, H. & rá ny-Kevei, I. B. 2003. Limestone pavements in Great Britain and the role of soil cover in their evolution. *Acta carsologica,* 32.