Large changes in vegetation composition seen over the last 50 years in British limestone pavements

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Data availability

Data available from the Lancaster University repository Pure: https://doi.org/10.17635/lancaster/researchdata/638

(Stevens, 2023)

Conflict of Interest

Carly Stevens is an Associate Editor of Functional Ecology, but took no part in the peer review and decision-making processes for this paper.

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Abstract

1. Limestone pavements contain a unique flora, dominated by ferns with a mix of herbaceous species more often found in woodlands, heathlands and grasslands. The crevices between the rocks are known as grikes, they provide a shaded habitat which, depending on pavement structure, can protect plants from grazing. Despite being of conservation importance and supporting a number of rare and scarce plant species there has been very little research into vegetation change in limestone pavements.
2. This study repeated a survey originally conducted between 1972 and 1975. The Ward and Evans survey visited 535 limestone pavement units spread across England, Scotland and Wales and recorded grike vegetation. This study was able to resurvey 516 of those pavements and repeat the survey using the original methods. Expansion of tree and shrub cover has been observed in some pavements but not previously quantified so tree cover was assessed using historic aerial photographs and satellite imagery.
3. On average species richness per pavement increased but there was a very wide range of change in species richness across individual pavement units ranging from a loss of 56 species to an increase of 38. Dissimilarity averaged 0.41. The area of pavement covered by trees or large shrubs increased by 62% between the two surveys but the number of pavements with zero tree cover also increased.
4. Breaking down pavement units into those with low (< 5 %), medium (5 – 30%) and high (> 30 %) current tree cover shows that species richness increased in open pavements but was reduced in pavements with high tree cover. Pavement units with high tree cover also showed higher dissimilarity and lower levels of indicators of disturbance. In pavements with high tree cover Ellenberg light (L) values were significantly lower than in open pavements.

Open pavements showed higher levels of competitive species (based on Grime CSR values) but no change difference in Ellenberg nutrient (N) values.

5. Vegetation in limestone pavements has changed considerably in the period between the two surveys with negative effects of high tree and shrub cover particularly problematic. There is an urgent need for investigation to support management decisions in this habitat.

Keywords: Alvar; limestone pavement; karst; tree cover; vascular plants; vegetation change

Introduction

Great Britain's limestone pavements are an internationally important habitat although they cover only approximately 28 km^2 (Mikolajczak et al., 2015). Limestone pavements (Natura 2000 classification 8240), also known as lapiaz, karren, and alvar, occur in a number of countries with some of the most extensive being in Ireland (320 km^2) and alpine pavements in Austria (525 km^2) (Mikolajczak et al., 2015). Other countries which have areas of limestone pavement include France, Italy, Switzerland, Sweden, Estonia and Canada. The majority of limestone pavements in Great Britain are located on the Carboniferous and Cambrian limestones of Northern England, with smaller areas of pavement located on the Carboniferous limestones of north and south Wales and Carboniferous and Cambrian limestones of central and north-west Scotland. Limestone pavements are Karst limestone features that developed during the Dinantian period by the movement of ice sheets. Initially mostly flat, dissolution by rainfall creates crevices in the exposed limestone resulting in a pattern of deep fissures (grikes) and stone slabs (clints). Limestone pavements can also form under soil which was then lost to erosion (Trudgill, 1983).

The grikes in limestone pavements provide a sheltered, shaded, humid habitat, somewhat protected from grazing, which results in a species rich flora that is distinct from surrounding grassland and heathland habitats (Silvertown, 1982, Ward and Evans, 1976). Although some species from surrounding grassland and heathland habitats can colonise, the flora of limestone pavements is dominated by ferns with frequent woodland species, creating a unique community assemblage. Limestone pavements support a number of plant species which are scarce in Great Britain and of high conservation value such as *Sesleria albicans*, *Actaea spicata, Dryas octopetala* and *Dryopteris submontana*.

Stone removal has been a considerable threat to the conservation of limestone pavements in Great Britain and other parts of the world. Stone removal from pavements has occurred over many hundreds of years and is evidenced by the stones found in many of the walls and buildings in the vicinity of limestone pavements. However, in the UK and Ireland particular damage came from the trend for the removal of the surface stone of pavements to form decorative features such as rockeries, gate posts and wall tops. The removal of clints results in irreversible damage to pavements as solution features do not reform (Sweeting, 1972). Following the Ward and Evans (1976) survey the introduction of limestone pavements protection orders under the 1981 Wildlife and Countryside Act prohibited the removal of stone without permission (Goldie, 1993) providing widespread protection of the habitat, and now a majority of sites are also protected as sites of special scientific interest and national nature reserves.

Land management is also a major threat to limestone pavements and a deeper understanding of optimal management for limestone pavements is needed in order to conserve them. Limestone pavements are commonly found set within grasslands or heathlands which presents a challenge in terms of managing a parcel of land; optimal management for the surrounding land may not be the same as optimal management for the pavement and so needs must be balanced. This is especially difficult when managing land with grazing animals. Pavements are commonly managed by grazing either sheep or cattle, cattle will commonly avoid entering the pavement but depending on the physical structure of the pavement sheep will often venture in to reach plants within the grikes. Grazing is a very important tool in the management of limestone pavements but needs to be carefully considered. Overgrazing can result in a loss of diversity, changes in species composition as grazing tolerant species come to dominate and intolerant species are lost (Rosén, 1982, Titlyanova et al., 1988) and an absence of vegetation emerging from the grikes and growing on clint tops. Undergrazing results in scrub encroachment which can also lead to loss of diversity and changes in species composition as light levels are reduced in the understory (van der Maarel, 2007).

There has been very little investigation into the potential impacts that global change might have on limestone pavements vegetation. York and Burek (2011) were interested in potential impacts of climate change and found that variation in temperatures in grikes became less pronounced with depth of the grike, suggesting that the vegetation of grikes may be somewhat buffered against climate impacts, as has been observed in forests (Zellweger et al., 2019). However, there have not been any studies that have directly manipulated climate in limestone pavements and no assessment of impacts on vegetation so it is difficult to assess likely impacts of a changing climate, especially when potential interactions with nutrient levels and management are considered. Elevated nutrient deposition may also play a role in the distribution of vegetation in limestone pavements. While calcareous grassland communities have been seen to be well buffered against acidifying effects of nitrogen deposition and some nutrients can be less available at high pH, these typically nutrient poor communities are sensitive to eutrophication which can lead to changes in species composition (Carroll et al., 2003, Diekmann et al., 2014). This suggests that limestone pavements may also be vulnerable to the impacts of nitrogen deposition.

Limestone pavements are of high conservation value and understanding current vegetation composition, the threats to the habitat and potential for restoration of damaged limestone pavements is vital if we are to improve habitat condition. While some areas of limestone pavement, such as the Swedish alvars, are well described (e.g. Rosén, 2006, Ott et al., 1996, Bengtsson et al., 1998), there have been no national assessments that have investigated vegetation change over multiple decades and there have been very few studies of British limestone pavements. This study aims to address this knowledge gap by repeating a national survey of all limestone pavements in Great Britain originally conducted between 1972 and 1975 to assess the conservation value of British limestone pavements (Ward and Evans, 1975). Given the importance of increased tree and scrub encroachment in pavements in other regions the analysis of vegetation change was combined with analysis of tree cover using current and historic aerial images. It was predicted that limestone pavements would have undergone extensive vegetation change since the 1970s. The data collected was used to address the following hypotheses:

1. Flora of limestone pavements is impacted by nutrient enrichment leading to increased occurrence of competitive and nitrogen loving species;
2. Reduced disturbance and grazing pressure in open pavements has resulted in increases in species richness but also an increase in competitive species;
3. Tree and large shrub cover has increased in many pavements which has led to large changes in species composition favouring shade tolerant species and reducing species richness.

Materials and Methods

1970s survey

The original Ward and Evans survey (Ward and Evans, 1976, Ward and Evans, 1975) took place between 1972 and 1975 with the aim of surveying all limestone pavements in Great Britain. Limestone pavements in Great Britain can vary greatly in their physical structure with clint sizes varying from a few centimetres in diameter to several meters, and grikes varying in depth from a few centimetres to several meters (Goldie 1995). Pavements also vary considerably in the degree of weathering with some pavements featuring smooth surfaces with large amounts of grikes, runnels (surface features created by water erosion, Goldie 1995) and solution cups (hollows created by corrosive weathering, Ivimey-Cook, 1965), whereas others have fewer grikes, such as the massive exposure found at Gait Barrows, Cumbria (Goldie 1995).

The original survey visited 535 pavement units grouped into 23 sites where open pavements were present (the 1976 paper reports 537 pavements but two units were included twice). This covers the vast majority of open pavements in Great Britain at the time although a few small areas were missed. Pavement units were identified using a combination of 1:10 000 scale monochrome aerial photographs taken between 1963 and 1973, and local knowledge. Pavement units varied considerably in size with intact areas ranging from less than 0.1 ha to over 60 ha. Sites also varied considerably in size with groupings covering continuous or closely located areas of pavement (e.g. Great Asby) as well as more widely spread regional groupings (e.g. Wales). Each pavement was visited by two expert surveyors (Stephen Ward and David Evans) who walked over the pavement unit compiling a list of species present in the grikes. All vascular plants were identified to the species level with the exception of *Hieracium* spp. which were only identified to the genus level. Only species in grikes that were considered deep were recorded, a deep grike was defined as one twice or more deep than it is wide. A V-shaped template was used to confirm the depth to width ratio of the grikes. The amount of time spent recording was more or less in proportion to the pavements size with around 30-45 minutes being spent surveying a moderate sized pavement (Ward and Evans, 1975). A moderate sized pavements was not defined by Ward and Evans so surveyor effort was estimated based on discussion with Stephen Ward. After survey of a unit, abundance was estimated on a three point scale:

1 = one or two to a few individuals. Extremely sparse on the pavement;

2 = locally abundant or widely scattered over the whole pavement but not abundant;

3 = abundant (Ward and Evans, 1976).

Recent survey

The recent survey took place between 2017 and 2022 with all surveying conducted by the author. The same methods were applied as in the original survey with the exception that with only one surveyor the time allowance was doubled. There were occasions when other surveyors assisted and in these cases the time allowance was adjusted accordingly and adjustments were made when scrub cover was high making it difficult to traverse the pavements. Training with Stephen Ward was undertaken at the start of the survey in an effort to try and make results as comparable as possible but it should be noted that the abundance estimates are somewhat subjective as was the estimate of the appropriate recorder effort. Of the pavements in the original survey 5 have been completely removed by quarrying and a further 3 have had their area reduced. These 3 pavements were excluded from this analysis because due to the recording method there was no way of accurately adjusting results to account for the reduction in area. A further 12 sites could not be revisited because access permission was refused. Consequently this analysis focusses on the 516 pavements for which complete data sets were collected in both time periods (Fig. 1), this means that results reported for the 1970s data differ slightly from those published in Ward and Evans (1976). A replicability table is provided in Table S1.

Remote sensing

Some of the original photographs used to identify sites were available but many had been lost over the years. Where images were available, they were scanned at 600dpi. Where images were not available searches were performed in the Historic England air photograph archive and if none were available there, in the National Collection for Aerial Photography for archive images from between 1960 and 1975. It was possible to obtain images from an appropriate time period for 472 pavement units in England. Unfortunately, archive images could not be obtained for pavements in Scotland, Wales and five English pavements. Where possible, images with a resolution of 1:10 000 or 1:10 500 were selected to allow easy identification of trees and shrubs but in a small number of cases images were 1:12 000. A total of 110 aerial photographs were used to cover the 472 pavement units analysed. All images were imported into ArcGIS Pro, georeferenced and pavements were digitised as accurately as possible by drawing around the clearly visible rock features. In some cases high tree cover meant pavements were not clearly visible so original maps from the Ward and Evans survey were used. For modern images ARCGIS base maps were used. These ranged from 2018 to 2023 and were available for all pavements. Trees and large shrubs were digitised within the pavements for both the historic images and modern ones. The tabulate intersection tool was used to calculate area of tree and large shrub cover within each pavement (henceforth called tree cover).

Data analysis

All data analysis was conducted in R (version 4.3.1, R, 2021). Pavement units were consistent between surveys so all analysis was conducted at this level. Species richness was calculated per unit and analysed using linear mixed effects models (lmer) with easting and northing at a 10 km resolution used as random effects. P values were determined using normal approximation. Jaccard dissimilarity was calculated between the two time periods for each pavement unit using the R package Vegan (Oksanen et al., 2022). Species data were heavily zero weighted so change in abundance for individual species was summed in four categories: absent from the unit in both surveys, no change in abundance score, abundance score increased, and abundance score decreased. For species with more than 100 records across both surveys combined a binomial sign test was then used to test whether species increased and decreased with the null hypothesis of no change being that there was an equal chance of an increase, decrease or no change with n being the number of sites where the species was recorded in at least one survey. Detrended correspondence analysis (DCA) was used to examine the vegetation from the two time periods together and separately. DCA was conducted using R package Vegan (Oksanen et al., 2022).

To address hypotheses 1 and 2 indicator values were used because it was not possible to collate consistent management data for sites. Ellenberg light (L) and nutrient (N) values were taken from Hill et al. (1999), Grimes competitor (C), stress-tolerator (S) and ruderal (R) scores from Pierce et al. (2016), and disturbance indicator values (disturbance severity whole community and grazing pressure) from Midolo et al. (2022). Scores were not cover weighted. Ellenberg L values were calculated using all species and with trees and large shrubs removed. Analysis of indicator values was conducted using linear mixed effects models (lmer) with easting and northing at a 10 km resolution used as random effects. P values were determined using normal approximation.

Regression analysis was used to examine the relationships between tree cover and change in tree cover and response variables. A reduced data set of 472 pavements units was analysed when 1970s tree cover or change in tree cover was analysed.

To assess the impact of tree cover on species richness pavements were classified according to recent tree cover as either low (< 5 % tree cover in recent data; open pavements), medium (5 – 30 %; scattered tree cover) or high (> 30 % tree cover; wooded). Differences between groups were assessed using linear mixed effects models as described above.

Results

Changes in the plant community

A total of 284 vascular species were recorded in the 1970s survey (Ward and Evans, 1976). The recent survey recorded a total of 313 species.

The species richness of individual pavement units ranged from 8 to 83 (mean 39.1, standard deviation 13.1) in the pavements from the 1970s used in this study. In the recent survey species richness had a larger range with between 4 and 106 species (mean 41.3, standard deviation 15.25). A species richness of 4 was recorded in 3 pavement units but these were not the same pavement where 8 species were recorded in the 1970s. Highest species richness was in the same pavement unit in both the 1970s and the recent survey, at Scar Close in Ingleborough National Nature Reserve.

Between the two surveys 188 pavements showed a reduction in species richness, 25 pavements stayed the same and 301 pavements had an increase in species richness. The changes ranged from a loss of 56 species to an increase of 38 species. Across the dataset as a whole richness increased significantly between the two surveys ($p<0.01$, Fig. 2).

Jaccard dissimilarity averaged 0.41 for the data set as a whole with a range of 0.13 to 0.95 however, a majority of units fell within the range 0.25-0.55. All sites showed variation between units with some pavements changing more than others but 8 of the 12 sites with highest dissimilarity values were found in Wales.

Analysing both datasets together in a DCA shows considerable overlap between the datasets with little change in mean axis scores. There was a very strong gradient on axis 1 (Fig. 3). Removing species that occur in less than 10% of plots to aid interpretation revels that the majority species at the species at the extreme right of the axis are trees or shrubs: *Taxus baccata, Rhamnus cathartica*, and *Rubus fruticosus* had the lowest scores. In contrast the species the left of the axis is dominated by species of open habitats*: Deschampsia cespitosa, Myosotis sylvatica*, and *Cardamine hirsuta* scored most highly. This indicates that the gradient in axis 1 is driven primarily by tree cover. While trees and shrubs recorded in the grikes do not entirely represent the extent of canopy closure because species growing outside grikes were not recorded they do provide a good indication. Examining the distribution of the sites highlights that pavements in Lancashire and Cumbria have been most impacted by tree and scrub invasion.

In the data set as a whole disturbance severity significantly decreased and grazing pressure increased between the two surveys ($p<0.001$, Fig. 4a,b). Ellenberg L values increased significantly when calculated with all species and with trees and large shrubs removed ($p<0.001$, Fig. 4c). Ellenberg N values were significantly reduced ($p>0.001$, Fig. 4d). For Grime's CSR scores the C score decreased significantly ($p<0.001$, Fig. 4e) and the S score increased significantly ($p<0.001$, Fig. 4f). There was no significant change in the R score ($p=0.77$).

Analysing change in the abundance of individual species that occurred in 100 pavement units or more showed 32 species increased significantly while 21 decreased significantly (Table S2).

Changes in tree area

The total area of limestone pavement mapped was 3157 ha. The area of the 472 pavement units for which historic images were available was 2140.56 ha, of this 145.82 ha was covered in trees in the 1970s, this increased to 236.43 ha in the recent data set. Tree cover ranged from 0 to 91.95 % in 1970 and 0 to 100 % in the recent data. The average change in tree cover was an increase of 5.79 % per pavement. Despite the increase in tree cover overall the number of pavements with zero trees increased from 283 in 1970 to 298 in the recent data set. There was no significant relationship between pavement area and change in tree cover ($p = 0.37$). High tree cover is currently most common in the limestone pavements of Cumbria and Lancashire and less so in other regions, as was increasing tree cover between the two time periods.

Changes in the plant community related to tree area

Examining the recent data showed a weak but significant relationship between tree cover and species richness ($p<0.001$, $r^2 = 0.05$; Fig. 5a). In the reduced dataset there was also a weak but significant negative relationship between change in tree cover and change in species richness ($p<0.001$, $r^2 = 0.15$; Figure 5b).

Change in species richness was significantly different between tree cover categories ($p>0.001$) with on average, positive changes observed in pavements with low current tree cover, little change with medium current tree cover and negative change with high current tree cover (Fig. 6). Current species richness was significantly lower in pavements with high tree cover than medium cover ($p<0.001$) but not low ($p=0.05$; Fig 7a) and dissimilarity significantly higher in pavements with high tree cover than either medium or low cover (both $p<0.01$; Fig. 7b). Disturbance severity increased as expected with significantly higher scores observed in pavements with low tree cover and lower scores in pavements with high tree cover ($p<0.001$; Fig. 7c). Scores for grazing intensity were significantly higher in pavements with medium and low tree cover ($p<0.05$) as compared to those with high cover. Ellenberg L value (with trees and large shrubs removed) was significantly lower ($p<0.05$) at high tree cover compared to low (Fig. 7d). There was no significant difference in Ellenberg N between the different levels of tree cover ($p=0.70$). Grime C scores were significantly higher in pavements with low and medium compared to high tree cover while S scores were significantly lower in low tree cover pavements ($p<0.01$; Fig. 7e, f). Grime R scores were significantly higher under high tree cover ($p<0.05$).

Discussion

There have been large changes in limestone pavement vegetation over the last 50 years which indicators suggest are strongly related to management. However, there is a wide variability in the results with change in species richness across individual pavement units ranging from a loss of 56 species to an increase of 38. In particular, the results highlight contrasting responses in pavements where tree and shrub cover are low compared to those where they are higher. Pavements where tree cover has increased considerably have commonly seen reductions in species richness and large changes in composition. Pavements that remain open are more likely to have seen increases in species richness although this may not necessarily be an increase in species characteristic of limestone pavements.

Vegetation change

There has been considerable change in species composition observed between the two surveys with dissimilarity in pavement species composition between the two time periods averaging 0.41. Usher *et al*. (1994) identified high species turnover within Scar Close, a pavement included in this study, and it is possible that high species turnover is typical of these highly heterogeneous habitats.

Unfortunately, despite the widespread occurrence of these habitats throughout Europe, I am not aware of any research detailing whether such dissimilarity is typical of limestone pavement vegetation change over decadal timescales. Species richness increased across the dataset as a whole. Changes in species composition mean that considering species richness alone is not an especially useful measure but it is important to understand the reasons for these changes in species composition if we are to conserve this habitat.

Examining changes in indicator values across the data set as a whole reveals some changes but high variability in the data indicates that pavements have changed in opposing ways. Tree cover increased significantly between two survey periods but at the same time a high proportion of pavements had zero tree cover in the recent survey. Tree cover was also significantly related to species richness. Consequently, it was decided to consider pavements with high, medium and low tree cover separately. This revealed contrasting changes in habit related to tree cover.

Pavement units with high tree cover had significantly fewer species than medium or low tree cover units and richness was reduced over time whereas it increased in open pavements. Pavement units with high tree cover also showed significantly higher dissimilarity. Five tree species or large shrubs showed significant increases in cover between the two survey periods (*Acer pseudoplatanus, Crataegus monogyna, Corylus avellana, Fraxinus excelsior* and *Sorbus aucuparia*). Pavements may also have seen increases in canopy cover and density from trees that were already present in the 1970s and have grown larger. When disturbance is low the canopy closes and light levels in the grikes may become too low to support many species, as reflected in the reduced Ellenberg L scores at high tree cover. The DCA analysis revealed the overwhelming importance of tree cover in this habitat with a very clear gradient on axis 1 related to tree cover. Sites were selected in the original survey as open pavements although examining contemporaneous aerial photographs shows that even then, some of the pavements were quite wooded. In the recent data the tree cover gradient is very strong with considerable impact on the species richness of grikes. As the canopy closes, light levels in the grikes may become too low to support many species. Personal observation suggested that bryophyte cover is typically very high in such situations and leaf litter accumulates in the grikes. In these situations, the grikes are often very species poor with some species moving to the clint tops if levels of disturbance are low enough. Reductions in species richness related to increasing canopy cover have also been observed in ancient woodlands (Depauw et al., 2020).

The increase in canopy cover appears to be driven by two factors, on one hand there have been reductions in disturbance as shown by the disturbance severity scores. The disturbance is most likely as a result of grazing but using the grazing indicator value, only the difference between high and low grazing pavements is significant. This may be because even in pavements that are not grazed by livestock there is still grazing from wild animals (typically deer and rabbits). Surprisingly given the lower disturbance scores ruderal species were high in this community. Land abandonment and removal of grazing animals is a problem in conservation management of many semi-natural habitats globally and in Eurasia has been commonly viewed as a threat to biodiversity (Queiroz et al., 2014). Undergrazing and secondary succession are specifically recognised as a threat to limestone pavement habitats (Mikolajczak et al., 2015, Pärtel et al., 1999, Rosén, 2006) and extensive efforts have been undertaken to remove shrubs and trees from alvar in both Sweden and Estonia (Rosén, 2006, Rosén and van der Maarel, 2000, Hänni, 2019). Although much of this work has focussed on grassland vegetation there has been some investigation in pavements and Rosén (2006) emphasises the need for hand cutting in limestone pavement. This means that removal of trees and shrubs is time consuming and expensive. As with many habitats of conservation importance (Rey Benayas et al., 2007), the current flora of limestone pavements has been formed and modified by grazing animals which means that a delicate balance between too much and too little grazing must be maintained if these habitats are to be kept in a certain state. Current tree cover is will clearly be influenced by tree cover in the 1970s but also depends on the cover of trees in the surrounding area as well as management of the pavement.

Another driver is afforestation and whilst not commonly observed, there were several sites that had been planted with trees. Two pavements had been planted with evergreen species before the first survey but trees had matured and canopy cover increased in the intervening time period. Some pavements showed evidence of deciduous tree planting, this was observed in several previously open pavements with planting undertaken in an effort to reach the 5-15% tree cover suggested in UK biodiversity action plan habitat condition reporting guidance for limestone pavements (Common Standards Monitoring (CSM) guidance - JNCC, 2009).

The pavements with low tree cover are a mixed set with some pavements that are heavily grazed and show clear signs of overgrazing while others currently have a low grazing intensity but where trees have yet to recolonise or grow sufficiently to give much canopy cover in aerial images. In Yorkshire, where many of the pavements with zero tree cover are located, tree cover in the wider environment is low and the lack of seed sources means that regeneration is likely to be slow. High levels of grazing can be associated with reduced species richness (Scimore et al., 2007) and competitive species, which may be less typical of pavement communities, were more abundant in these pavements. Some pavement units showed clear signs of overgrazing with very short vegetation and no vegetation emergent from the grikes. In such situations there is a clear need to reduce grazing levels.

Contrary to expectations, Ellenberg N scores were significantly reduced, although only by a small amount. Since atmospheric deposition of nitrogen has increased in the period between the two surveys (Fowler et al., 2004) this is most likely to be related to reduced use of fertilisers and reduced grazing levels and consequent nutrient inputs from grazing animals and supplemental feeding but unfortunately detailed data on management history of individual pavement units were not available to confirm this. Competitive species also over time while stress-tolerant species increased. Examining this in relation to tree cover shows significantly fewer stress-tolerators and more competitors in open pavements.

Of the 20 species which had a significant number of decreases in abundance 19 are classified by Ward and Evans (1975, 1976) as species which depending on the presence of limestone pavement for survival in open situations, some are rare in the UK (Stroh et al., 2023) and some are identified under CSM guidance as positive condition indicators (JNCC, 2009). In contrast, of the 31 species that had a significant number of increases in abundance 20 are classified as depending on the presence of limestone pavement for survival in open situations. While this classification is subjective (Ward and Evans, 1975) it provides some indication that some habitat specialists are declining. In order to identify the conditions and appropriate management to promote these species further autecological studies are needed together with more investigation into the impact of management practices over time. Species that have increased are a mix of habitat generalists and specialists. Some of the species that have increased are species that are common in Great Britain and some, such as *Arrhenatherum elatius, Cirsium arvense, Cirsium vulgare, Jacobaea vulgaris, Pteridium aquilinum* and *Urtica dioica* are identified as CSM negative condition indicators (JNCC, 2009). *P. aquilinum* has increased in a number of upland habitats across the UK including grasslands and heathlands (Stevens et al., 2016, Lowday and Marrs, 1992). It can be particularly problematic in limestone pavements because it creates a dense canopy, spreads by rhizomes (Marrs et al., 2000) along grikes and leaves behind recalcitrant litter which can prevent other species germinating (Marrs et al., 2000, Frankland, 1976). *A. pseudoplatanus*, is considered non-native in Great Britain (JNCC, 2009). Whilst its management in protected areas is controversial (Morecroft et al., 2009) mature *A. pseudoplatanus* produces a very dense canopy leading to noticeably impoverished patches of pavement below it. Some species typical of the habitat have increased, including the rare fern *D. submontana*. Further research is needed to identify the conditions that promote or reduce the occurrence of individual species. The increase in less typical species is a worrying trend that also warrants further investigation.

Habitat loss

A total of 8 out of 535 pavements were impacted by commercial quarrying between the 1970s survey and the recent survey. This is a relatively low rate of habitat destruction and indicates the success of current methods of protection. Stone removal was a considerable threat to limestone pavements prior to the 1981 Wildlife and Countryside Act (Goldie, 1993). Ward and Evans (1976) suggested that of the sites they surveyed, 97 % showed signs of damage. The Wildlife and Countryside Act introduced Limestone Pavement Protection Orders (LPOs). LPOs were made by local planning authorities and are a legal instruction to owners and occupiers of land that prohibits removal or disturbance of pavement. Putting LPOs in place took considerable research effort (Goldie, 1993) but the relatively small number of pavements quarried and the lack of incidences of fresh damage observed in the recent survey seem to indicate that they have been successful. All of the pavements that were either removed or reduced in area were impacted by commercial quarrying operations and this process would have been subject to planning approval. This is in contrast to earlier removal which was largely not subject to any planning consent and at times represented theft of stone (Goldie 1987).

Data limitations

There are always potential flaws in repeating a historic survey but the detailed maps produced from the original survey and the ease of finding such distinct landscape features as limestone pavements mean that accuracy of relocation was good. The use of the V-shaped template meant that the grikes recorded were consistent. Surveyor effort was difficult to assess, guidance given in the original survey was that 30-45 minutes was spent surveying a moderate sized pavement with the survey conducted by two expert surveyors (Ward and Evans, 1975). In the recent survey a majority of sites were surveyed by one surveyor with some help from assistants of variable botanical ability. Whilst the guidance given was used as a standard it is hard to know if the data is entirely consistent. There are other limitations with the data, the 1-3 scale used for assessing vegetation cover is a rather blunt tool and the element of subjectivity means it is hard to be certain whether change has taken place at an individual site. Training was undertaken with Stephen Ward prior to commencing the survey to try and ensure data was a consistent as possible but small or localised changes need to be interpreted with caution. The inconsistent size of pavement units also considerably limit the utility of the data. Pavement units varied enormously and while it is possible to compare data across time periods because pavement units were consistent it makes it difficult to compare pavement units and sites.

Conclusions

Limestone pavements have been under researched in the UK. This is the first academic study in almost 50 years to provide a national assessment of vegetation composition for any country globally. As hypothesised limestone pavement have indeed undergone extensive vegetation change in Great Britain. Many species typical of limestone pavements declined in abundance while species that increased were often not habitat specialists. Indicators showed that disturbance had decreased but indicators of grazing pressure were less clear. Contrary to expectation Ellenberg N values decreased slightly as did mean CSR competitor scores while stress tolerator scores increased slightly indicating that eutrophication has been reduced across the dataset as a whole. This is most likely to be related to reduced grazing pressures. While open pavements often increased in their species richness, pavements with increases in tree cover over time and high tree cover in the present day frequently have fewer species in them than in the 1970s.

There have been no published management trials in British limestone pavements. This lack of research into the most appropriate management for limestone pavements means there is a lack of evidence base for management and restoration decisions to be based upon, something which needs to be urgently addressed. There are many organisations making efforts to manage limestone pavements so a first step in building an evidence base to support management decisions and identify actions which will promote desirable species is to ensure that monitoring is put in place when management changes are made. This would ideally be complemented by management trials and autecological studies.

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Figures

Figure 1. Map of the 10 km squares in which the 516 limestone pavement sites surveyed in both the 1970s (1972-1975) and the recent survey (2017-2022) were found.

Figure 2. Species richness of 516 limestone pavement units recorded between 1972 and 1975 (1970s) and 2017 and 2022 (2020s). Letters indicate significant differences (p<0.05).

Figure 3. Detrended correspondence analysis for 516 sites recorded between 1972 and 1975 (blue filled circles) and recent data (black open circles). Note that there is considerably overlap between the axis scores of the dataset and so many of the sites points for the 1972-1975 data set are hidden by the recent data points. The ten highest and lowest scoring species on axis 1 are plotted, only species occurring in more than 10% of sites are included to aid interpretation although all were included in the ordination. Eigen values: axis 1 0.26, axis 2 0.16.

Figure 4. Indicator values for a) Disturbance severity, b) Grazing Pressure, c) Ellenberg light (L); d) Ellenberg nutrients (N); e) Grime competitors (C) and f) Grime stress tolerators (S) of 516 limestone pavement units for data collected between 1972 and 1975 (1970s) and 2017 and 2022 (2020s). Letters indicate significant differences (p<0.05).

Figure 5. a) The relationship between change in tree cover between tree cover (calculated as the difference between archived air photographs (1967 - 1973) and recent satellite images (2018 -2023)) and change in species richness (data collected 1972 - 1975 and 2017 – 2022), and b) the relationship between tree cover (calculated using images between 1967 and 1973) and species richness (surveyed between 2017 and 2022) for 516 limestone pavement units.

Figure 6. Change in species richness of 516 limestone pavement units recorded between 1972 and 1976 (1970s) and 2017 and 2022 (2020s) at low (< 5 %), medium (5 – 30 %) and high (> 30 %) recent tree cover. Letters indicate significant differences (p<0.001).

Figure 7. Difference between values for a) Species Richness, b) Dissimilarity, c) Disturbance severity; d) Ellenberg light (L); e) Grime competitors (C); and f) Grime stress tolerators (S) of 516 limestone pavement units with low (< 5 %), medium (5 – 30 %) and high (> 30 %) tree cover in the recent survey. Letters indicate significant differences (p<0.05).

Figure 1

Figure 2

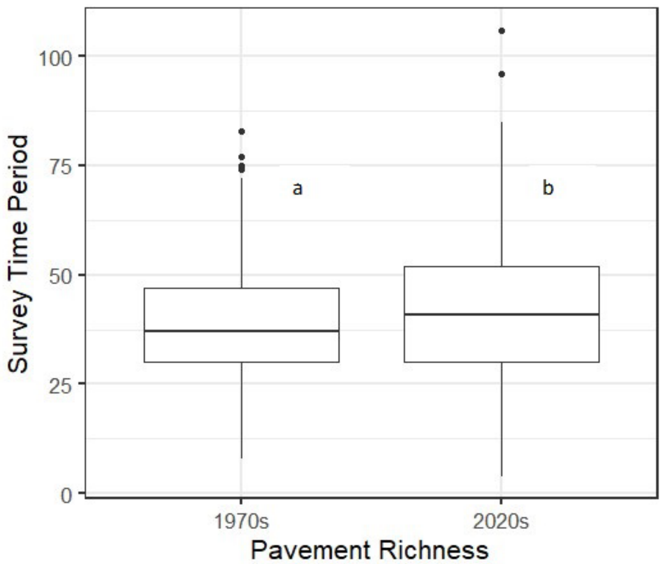
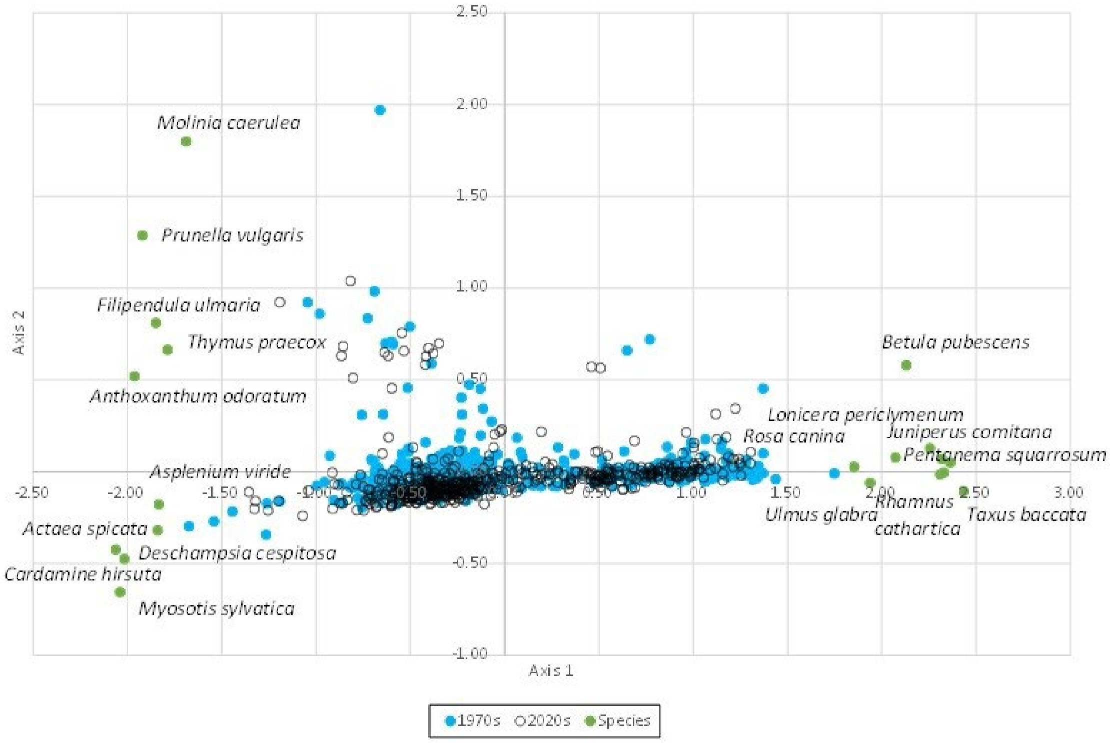
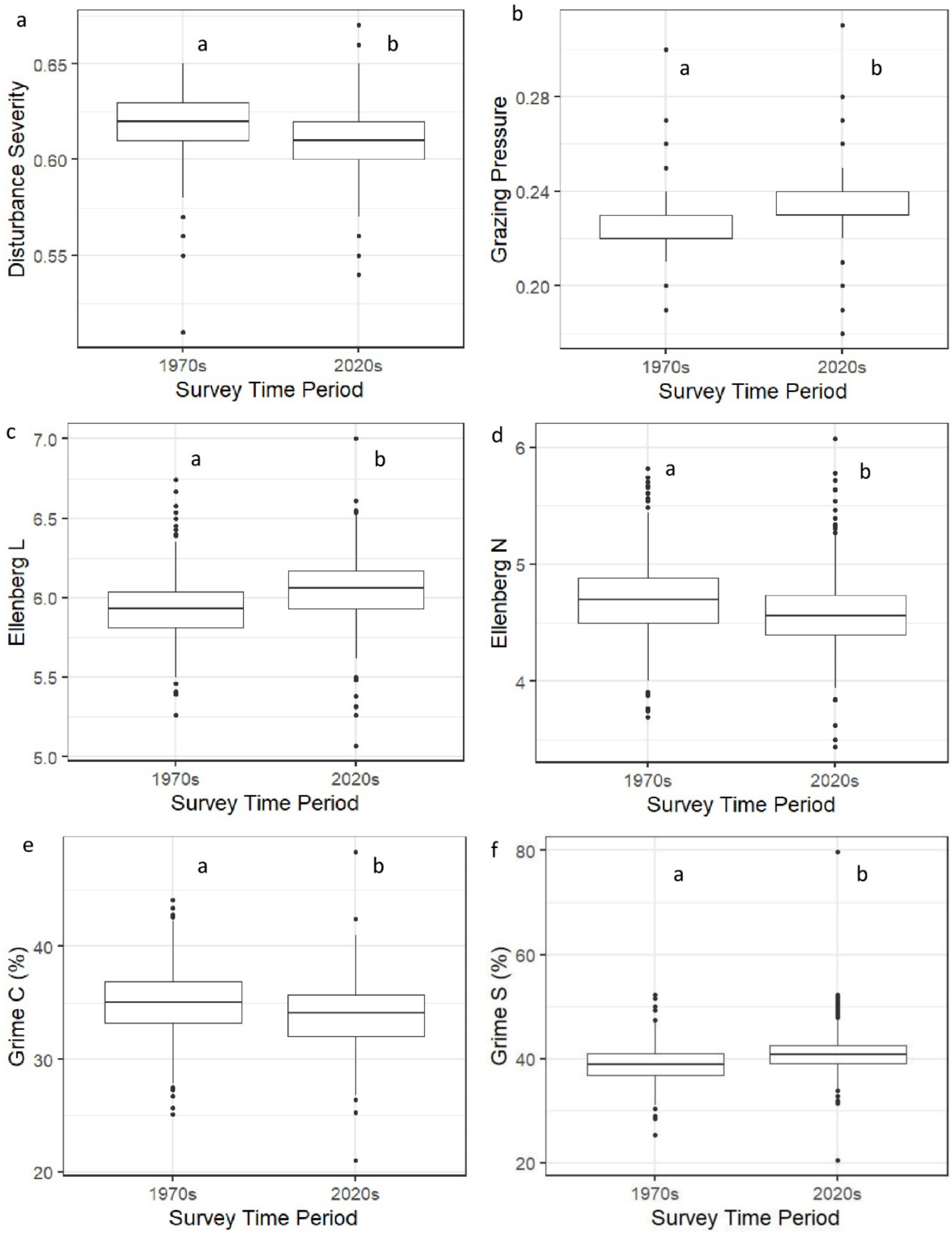


Figure 3



Molinia caerulea
Prunella vulgaris
Filipendula ulmaria
Thymus praecox
Anthoxanthum odoratum
Asplenium viride
Actaea spicata
Deschampsia cespitosa
Cardamine hirsuta
Myosotis sylvatica
Betula pubescens
Lonicera periclymenum
Rosa canina
Juniperus comitana
Pentanema squarrosum
Rhamnus cathartica
Ulmus glabra
Taxus baccata
Axis 1
Axis 2
1970s
2020s
Species

Figure 4



a
Disturbance Severity
0.55
0.60
0.65
a
b
1970s
2020s
Survey Time Period
b
Grazing Pressure
0.20
0.24
0.28
a
b
1970s
2020s
Survey Time Period
c
Ellenberg L
5.0
5.5
6.0
6.5
7.0
a
b
1970s
2020s
Survey Time Period
d
Ellenberg N
4
5
6
a
b
1970s
2020s
Survey Time Period
e
Grime C (%)
20
30
40
a
b
1970s
2020s
Survey Time Period
f
Grime S (%)
20
40
60
80
a
b
1970s
2020s
Survey Time Period

Figure 5

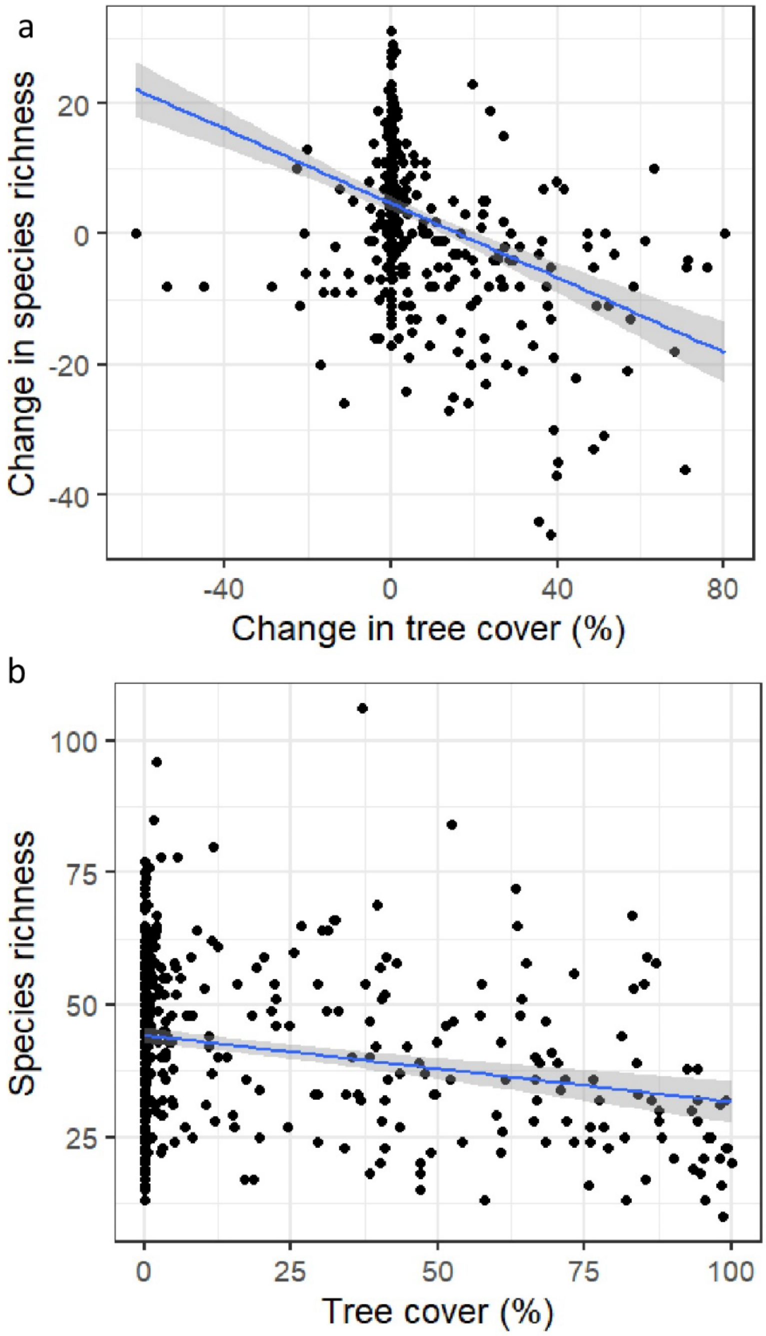
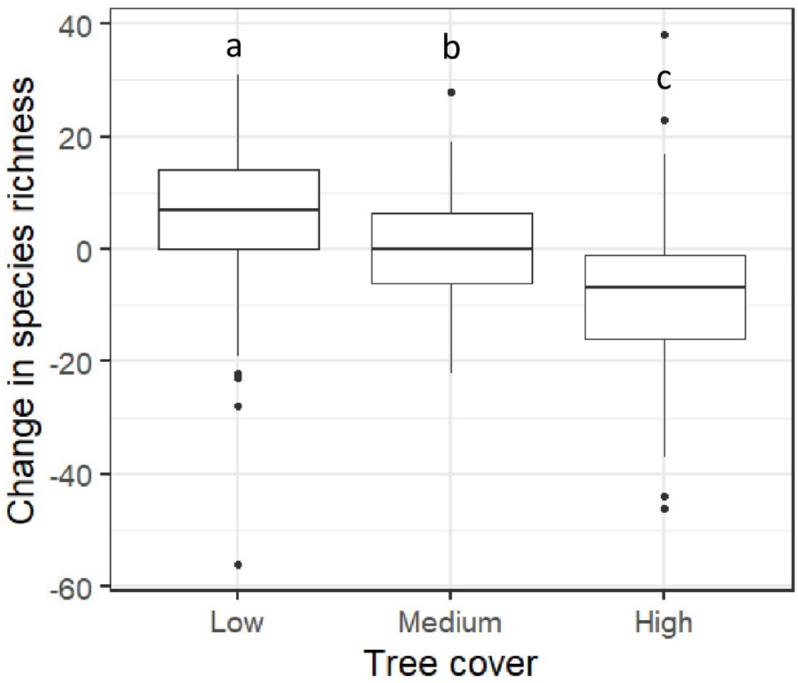
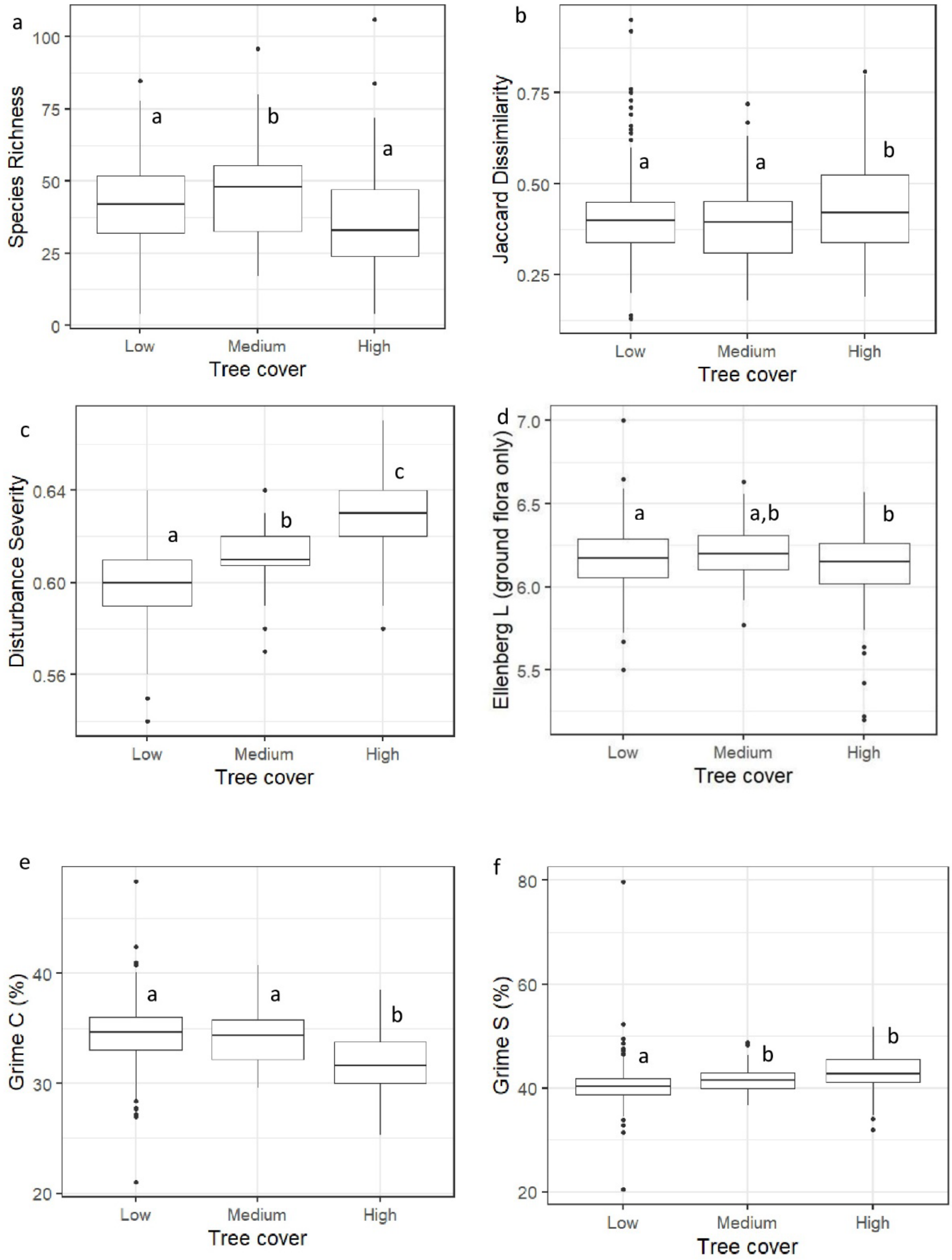

a
Change in species richness
20
0
-20
-40
-40
0
40
80
Change in tree cover (%)
b
Species richness
100
75
50
25
0
25
50
75
100
Tree cover (%)

Figure 6



a
b
c
Change in species richness
40
20
0
-20
-40
-60
Low
Medium
High
Tree cover

662 Figure 7



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