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Changes in surface active myriapod communities during the restoration of woodland to wood pasture: a long-term study

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Abstract. The myriapod communities of an area of woodland restored to wood pasture through tree felling was compared with a control site in dense woodland, using pitfall trapping over a 28-year period. 14 species of millipede and 13 of centipede were recorded. Numbers of individual species varied over time even within the control plot. There were significantly more centipede individuals and species and more millipede species in the control plot than the restoration area. NMDS ordination indicated three groupings for the millipedes in the restored area with the community changing following the initial restoration to a tight cluster but then further movement in later years. In contrast the control community showed little variation. 2015 showed the greatest change from other years, probably due to high abundance of two species of polydesmid millipede that year, in both plots. The results are discussed in comparison with other studies looking at the impact of the edge effect of forests. The community of the restored area has perhaps not changed as much as expected, which may indicate a high degree of resilience, although it may be acting more like a forest clearing than an edge.

Keywords. Millipedes, centipedes, habitat restoration, beech trees, forest edge.

INTRODUCTION

Burnham Beeches is a 383 ha nature reserve comprising beech dominated woodland (*Fagus sylvatica* L.) 40 km west of London. It is part of a Natura 2000 site (i.e. a site of European nature conservation importance), for Atlantic acidophilous beech forests (Natura 2000 code 9120). The main reason for the designation is its population of 400–500 year-old beech trees that were for centuries cut as pollards, producing a crop of wood every 15–20 years (Le Sueur 1931). The trees were set in wood pasture grazed by domestic livestock, probably a mixture of cattle, equines and pigs. The southern 220 ha of the nature reserve was common land which, although owned by the Lord of the Manor, gave local people rights to graze their livestock and cut the trees for fuel wood. Old descriptions and photographs indicate that the majority of the area was 'savannah-like' with scattered trees and some patches of scrub in a largely open environment. The soils are acidic with ground vegetation being similar to heathland, with *Calluna vulgaris* (L.) (ling/common heather) and grasses typical of acid soils.

In recent years, the idea that most of Europe, prior to human influence, was climax woodland with more or less continuous tree cover has been challenged. Recent research has indicated that it was more likely to have been dominated by a type of savannah with large herbivores driving the development of scrub and woodland and maintaining a greater proportion of open areas with scattered trees (Vera 2000). In medieval times, southern England had abundant areas of wood pasture but most were abandoned or destroyed in the early 20th century through loss to agriculture or building development, or through lack of grazing. These medieval wood pastures, although heavily managed, were perhaps arguably a more accurate reflection of the natural vegetation of the region than was previously thought.

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At one time almost all the beech and oak (*Quercus* sp.) trees within Burnham Beeches were managed as pollards, cut at regular intervals to produce a crop of wood which was probably largely used by local people for domestic fuel. Repeated cutting causes the trees to develop a knobbly area, around the point of cutting, developing decay pockets and water pools which provide micro habitats for many saproxylic invertebrates. Cutting also enables the trees to live longer than uncut trees so the older generation of pollards are around 500 years old. Over 60 red listed species have been recorded (Read 2010) on the reserve, almost all associated with these old trees. Tree management through pollarding ceased at Burnham Beeches around 200 years ago; grazing also declined so that by the 1920s this merely involved a few donkeys. In 1951 the nature conservation value of the area was recognised and the area was designated as being important for nature conservation in a UK context. However, by the 1980s the old trees had become swamped by younger secondary woodland, dominated by *Betula* spp. (birch) and *Ilex aquifolium* (L.) (holly), resulting from cessation of grazing, and were dying through lack of light. In addition, they had become very top heavy because of the lapse in their cutting cycle, resulting in trees splitting apart as the larger branches became too heavy for the ageing trunk beneath. Since then, substantial restoration work has been carried out to attempt to rescue the trees and to restore the wood pasture in which they stand. This has included tree clearance and the re-instatement of grazing using cattle, ponies and, in some years, pigs in the autumn. Wood pasture is increasingly being recognised as a distinct habitat in the UK and restoration is being carried out in a range of locations. However, this restoration has only recently started and documenting changes taking place is valuable to both assess the importance of the habitat and the implications of restoration. Substantial work has been carried out on the trees at Burnham Beeches (Read *et al.* 2010) and the preliminary impacts on ground vegetation and some ground active spiders has been reported (Read 2000). The impact of felling younger trees to give more light to ancient ones in terms of tree response and saproxylic species (those associated with decaying wood) of invertebrate was examined by Alexander *et al.* (2010) however little work has been published on the effects of similar management on surface-active invertebrates. Myriapods can provide an interesting insight to the changes taking place as a shaded woodland floor with abundant leaf litter, is replaced by a grassy sward with a much greater exposure to light. Millipedes being detritivores might be considered more likely to be impacted than the more predatory groups of centipedes, for example.

There are other studies that have documented myriapod communities in similar environments, including disturbance effects on forests due to tree clearance (Smith *et al.* 2017 and Stašiov & Svitok 2014) the latter in beech forests, studies of gradients between forested and open areas (Bogyó *et al.* 2015, De Smedt *et al.* 2016) and studies on the impact of forest fragmentation (Riutta *et al.* 2012). None of these situations are quite equivalent to wood pasture but are similar.

The current study reports on the results of part of a larger project looking at changes in the ground active invertebrates during restoration of wood pasture over a period of nearly 30 years. In general, most studies cover relatively short periods of time and typically use different sites at different stages of succession as a substitute for following long term changes (e.g. Bogyó *et al.* 2015)- The work of Tajovsky (2000), and Tajovsky *et al.* (2017) is notable for the long time scales of recording myriapod communities, even though not always continuous, one such study covered a time scale of 25 years (Tajovsky *et al.* 2017).

MATERIALS AND METHODS

Two areas were sampled. The restoration area was actively managed for nearly 30 years to restore wood pasture (through tree felling, re-instatement of grazing and periodic control of bracken and bramble). The tree clearance was carried out in two phases, winter 1991/92 and March 1994 during which the number of mature trees in the vegetation plot was reduced from 19 to 6 and shrub layer holly from 20% to a single bush. A control site nearby was also surveyed where no restoration had taken place and which remained densely vegetated with beech/holly woodland throughout the study (although at several times work in the vicinity may have made minor changes to the light levels).

Pitfall traps (plastic vending machine cups) 8 cm in diameter and 10 cm deep were installed, containing 50 ml of 4% formalin and a few drops of detergent, with wooden rain covers held about 3 cm above them on large nails. The quantity of fluid was sufficient to ensure captures remained in fluid except on a few occasions when the number of wood ants was very high. Ten traps were installed in each site in a 5 x 2 formation with traps 2 m apart, a format regularly used in the UK (Read 1987). Traps were emptied and re-set every two weeks during the season taking care to ensure that the lip of the cups were flush with the ground surface. Traps were first installed in the restored area in 1990 and in the control (unrestored area) in 1992 and run each year. Catches were sorted and the Myriapoda were identified to species level where possible and adults distinguished from immatures. Data presented here are for millipedes and centipedes for each year up to and including 2017. Although pitfall trapping has been used in previous studies (for example Stašiov & Svitok 2014), its validity as a method of comparing myriapod communities has been questioned and there are clear short comings (see for example Gerlach *et al.* 2009, Tuf 2015) but they are still regularly used in quantitative studies for example De Smedt *et al.* (2019) and in the UK Environmental Change Network (2020). Indeed, despite the considerable debate over the years regarding pitfall trapping as a suitable technique for sampling surface active invertebrates, the technique remains reasonably popular because it is relatively easy (and cheap) to operate and usually provides statistically viable results (Wheater *et al.* 2020). Myriapoda have long been sampled using pitfall traps (e.g. Van der Drift 1963) and the method was used here because of the need to trap in a way that drew least attention to members of the public and was feasible to run by volunteers, without taking up too much time and/or needing specific expertise to deploy.

Trapping usually took place between April and October/November but for operational reasons the trapping periods varied slightly between years, with two years when it started later (in early June in 1992 and in early May in 1996) and a further two years when it finished earlier (late September in 1993 and 1994). To include as much of the data as possible for analysis, the longest period of time for each year was used where the two trapping grids (i.e. restoration and control areas) were in agreement. As the number of days varied between years the analysis was carried out on numbers of myriapods per 100 trapping days.

Vegetation was also monitored annually around the pitfall traps. For the experimental area the plot was 30 x 30 m in size and was located just to one side of the traps. For the control, due to the shape of the woodland block, it was 20 x 45 m with the pitfall traps central to the plot. Each year 25 random quadrats, 0.25 m^2, were thrown (positions determined using random number tables) and percentage cover estimated for all species. A mean percentage cover figure was calculated for the whole plot per year and multiplied by the frequency to give a value that was arcsine transformed before ordination since the data were not normally distributed.

A notable feature of this part of Burnham Beeches is the high density of wood ant (*Formica rufa* L.) nests. This species forages on the ground and also in the tree canopies, which it reaches by walking along the ground using trails that are variable in location and extent. Thus, this species was found in high numbers in the pitfall traps at certain times and is generally very abundant on the surface across both areas where the traps were located. As wood ants are predatory and opportune generalists, their presence can have profound effects on the populations of other invertebrates (e.g. Fowler & MacGarvin 1985 and Punttila *et al.* 2004), including surface active species (e.g. Reznikova & Dorosheva 2004). The impact is usually negative, but some species are positively associated with wood ant abundance (for example the staphylinid beetle *Pella humeralis* (Gravenhorst)) and on others there may be no apparent impact.

Table 1. Species of millipede found in the two sites.

Millipedes	**Restored site** mean ± SE per year (percentage of years occurring: *n* = 28)	**Control site** mean ± SE per year (percentage of years occurring: *n* = 26)
Glomeris marginata (Villers, 1789)	6.8 ± 1.13 (82.1%)	19.9 ± 5.80 (96.2%)
Nanogona polydesmoides (Leach, 1814)	0.3 ± 0.17 (21.4%)	0.1 ± 0.04 (7.7%)
Chordeuma proximum Ribaut, 1913	1.2 ± 0.38 (57.1%)	6.8 ± 1.67 (96.2%)
Nemasoma varicorne C.L. Koch, 1847	0.02 ± 0.02(3.6%)	0 (0%)
Proteroiulus fuscus (Am Stein, 1857)	0.7 ± 0.19 (57.1%)	1.0 ± 0.22 (57.7%)
Tachypodoiulus niger (Leach, 1814)	8.2 ± 0.09 (100%)	11.7 ± 1.58 (100%)
Cylindroiulus britannicus (Verhoeff, 1891)	4.0 ± 1.63 (35.7%)	0.9 ± 0.36 (26.9%)
Cylindroiulus caeruleocinctus (Wood, 1864)	0.02 ± 0.02(3.6%)	0.02 ± 0.021 (3.8%)
Cylindroiulus parisiorum (Brolemann & Verhoeff, 1896)	0.07 ± 0.00 (7.1%)	0.02 ± 0.02 (3.8%)
Cylindroiulus punctatus (Leach, 1815)	5.1 ± 0.69 (100%)	4.1 ± 0.57 (100%)
Ophyiulus pilosus (Newport, 1842)	0.07 ± 0.03 (14.3%)	0.1 ± 0.05 (15.4%)
Polydesmus angustus Latzel, 1884	124.7 ± 20.00 (100%)	90.4 ± 20.08 (100%)
Polydesmus denticulatus C.L. Koch, 1847	33.4 ± 8.20 (89.3%)	94.5 ± 22.72 (100%)
Brachydesmus superus Latzel, 1884	0.07 ± 0.05 (7.1%)	0.3 ± 0.15 (19.2%)

Analysis comprised repeated measures ANOVA (by year) using Tukey-Kramer multiple comparison tests (Wheater & Cook 2000), using StatView v5.0, to explore potential differences between the sites on the basis of the numbers of individuals per 100 days trapping, the number of species, the proportion of immature animals compared to the number of adults (millipedes), and various measures of species diversity (Shannon *H'*, Simpson 1-*D*, Berger-Parker 1/*d*, and Evenness *J'* based on the Shannon index – Wheater & Cook 2015). The communities of millipedes and centipedes were ordinated separately using NMDS, with the Gower distance measure (Wheater *et al.* 2020), using PAST v3 (Hammer *et al.* 2001). Species turnover was measured as change in ordinational space between years, calculated as differences in ordinational space across the first three major ordination axes using an extension of the Pythagorean theorem. Correlations between the axes of major variation for myriapods and vegetation variables was completed using FCStats v2.1a (Wheater & Cook 2015, Wheater *et al.* 2020).

RESULTS

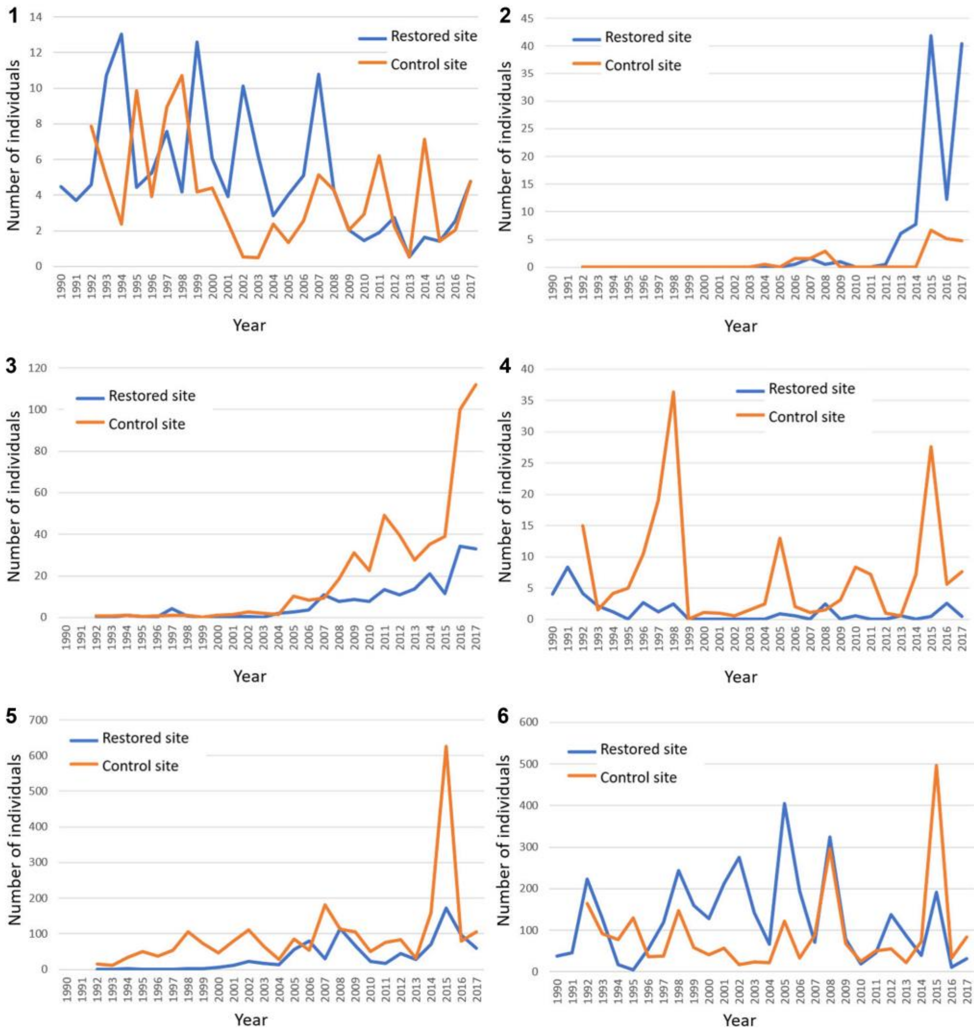
A total of 14 species of millipedes and 11 species of centipedes were found in the wood pasture restoration area compared to 13 species of millipedes and 12 species of centipedes in the control site (Tabs. 1–2). Figures 1–9 show the abundance of selected species which were caught in sufficient numbers to illustrate patterns of variation over time. Most of the species found were common British species with the most unusual in a UK context being the millipedes *Chordeuma proximum* and *Cylindroiulus parisorum* and the centipedes *Lithobius muticus* and *L. macilentus*. *Chordeuma proximum* has a strong southwest distribution in the UK and is an Atlantic species strongly associated with woodlands and may be associated with acid sandy soils (Lee 2006). The relatively high numbers caught, including juveniles, especially in late springs, indicate it is well established at Burnham Beeches. *Cylindroiulus parisorum* in contrast is a predominately south eastern species and rather less well recorded in the UK. Although there is some suggestion of an association with synanthropic habitats in continental Europe, where it is very sparsely distributed (Kime & Enghoff 2017), in the UK this species has been associated with decaying wood and loose bark (Lee 2006) so the finding in a nature reserve known for its decaying wood habitat is not unexpected. *Lithobius macilentus* has been found across the UK but the records are very patchy and it has not been found in the south west (Barber pers. comm.). The majority of the records are for woodland where it also appears to be most abundant (Barber & Keay 1988), it is only known from females in the British Isles and is the only British *Lithobius* apparently showing parthenogenesis (Barber pers. comm.). There were just 2 individuals caught during this project, both in the control plot. *Lithobius muticus* has a strong south eastern distribution in the UK and is a characteristic scrub and woodland species. It was regularly caught in the traps, especially in the restoration area.

Table 2. Species of centipede found in the two sites.

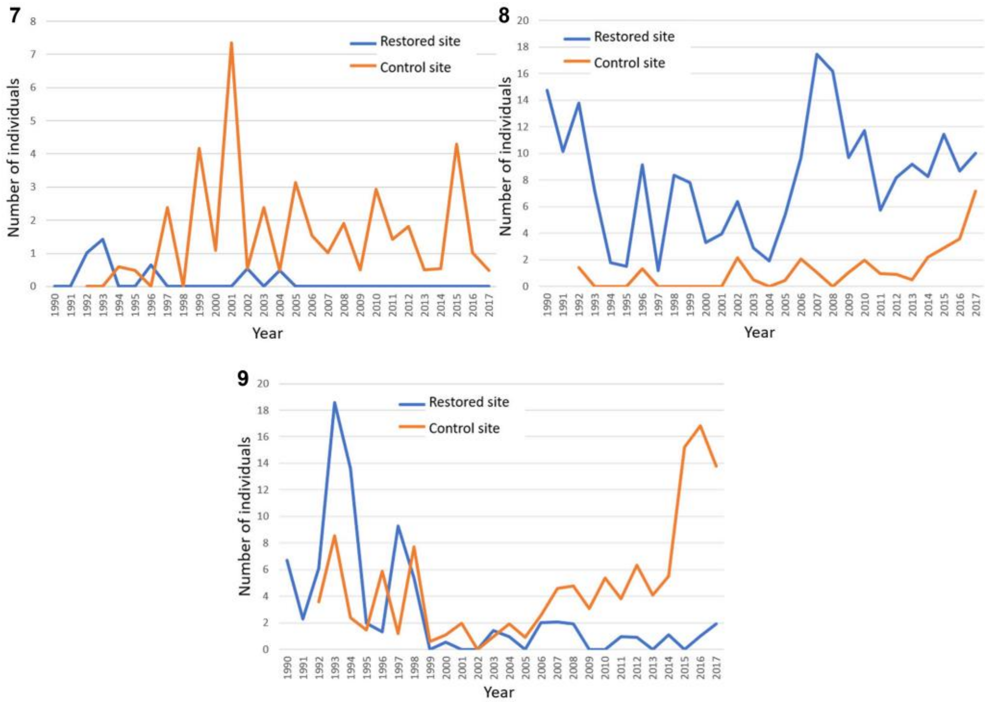
Centipedes	**Restored site** mean ± SE per year (percentage of years occurring: n = 28)	**Control site** mean ± SE per year (percentage of years occurring: n = 26)
Strigamia acuminata (Leach, 1814)	0.2 ± 0.07 (17.9%)	1.6 ± 0.33 (84.6%)
Strigamia crassipes (C.L. Koch, 1835)	0.7 ± 0.27 (46.4%)	1.9 ± 0.46 (61.5%)
Geophilus easoni Arthur *et al.*, 2001	1.0 ± 0.25 (67.9%)	1.9 ±0.42 (84.6%)
Geophilus flavus (De Geer, 1778)	0.1 ± 0.04 (21.4%)	0 (0%)
Geophilus insculptus Attems, 1895	0 (0%)	0.03 ± 0.03 (3.8%)
Geophiulus truncorum (Bergsoe & Meinert, 1886)	0.1 ± 0.05 (14.3%)	0.3 ±0.09 (34.6%)
Cryptops hortensis Donovan, 1810	0.2 ± 0.06 (25.0%)	0.4 ± 0.11 (38.5%)
Lithobius forficatus (Linnaeus, 1758)	8.0 ± 1.06 (100%)	15.0 ± 1.02 (100%)
Lithobius macilentus L. Koch, 1862	0 (0%)	0.1 ± 0.05 (11.5%)
Lithobius muticus C.L. Koch, 1847	8.0 ± 0.89 (100%)	1.2 ± 0.31 (61.5%)
Lithobius variegatus Leach, 1813	2.9 ± 0.90 (71.4%)	4.8 ± 0.88 (96.2%)
Lithobius crassipes L. Koch, 1862	0.3 ± 0.11 (28.6%)	0.6 ± 0.28 (26.9%)
Lithobius microps Meinert, 1868	0.04 ± 0.03 (7.1%)	0.03 ± 0.03 (3.8%)

The numbers of individuals in each species varied considerably with some only being found twice but other species being found in their hundreds. Numbers of *Cylindroiulus punctatus* declined over time in both plots whereas *Cylindroiulus britannicus* and *Glomeris marginata* increased over time (for *C. britannicus* from complete absence in the early years and *Glomeris marginata* from very low numbers to quite high). *Chordeuma proximum* shows a very spikey pattern and in some years it is much more abundant than others. The two larger polydesmid species were caught in very high numbers in 2015. Generally, *Polydesmus denticulatus* was relatively more abundant in the control plot and *P. angustus* in the restoration plot but both showed a spike in 2015 which was especially pronounced in the control plot.

Centipede species were also variable with some predominantly found in the control plot (like *Strigamia acuminata*), others (like *Lithobius muticus*) more abundant in the restoration plot. *Lithobius variegatus* was more abundant in the restoration plot in the early years but numbers declined over time while they increased in the control plot. Generally, there were more species in the control plots than the restoration areas.



Figures 1–6. Numbers of individuals in various myriapod species in restoration and control plots over time. 1 = *Cylindroiulus punctatus*; 2 = *Cylindroiulus britannicus*; 3 = *Glomeris marginata*; 4 = *Chordeuma proximum*; 5 = *Polydesmus denticulatus*; 6 = *Polydesmus angustus*.



Figures 7–9. Numbers of individuals in various myriapod species in restoration and control plots over time. 7 = *Strigamia acuminata*; 8 = *Lithobius muticus*; 9 = : *Lithobius variegatus*.

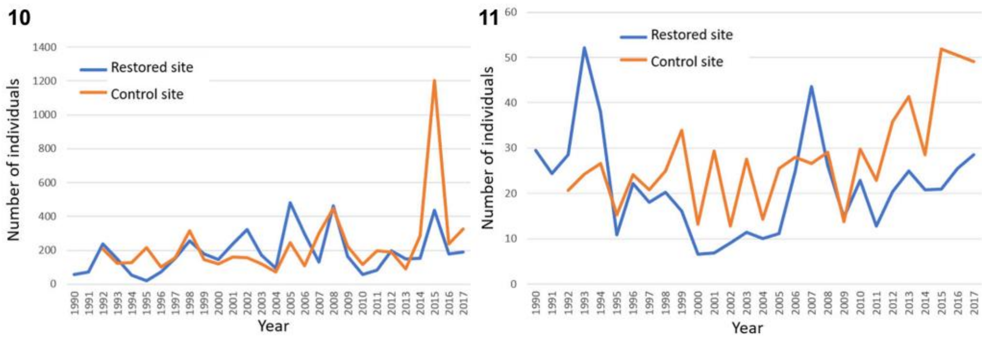
Table 3. Analysis of variance for millipede numbers and diversity (with year as a repeated measure).

Millipedes	$F_{1,25}$	P	**Comments**
Numbers of individuals per 100 trapping days	1.006	0.3254	No significant difference between sites
Number of species	4.475	0.0445	Control significantly higher than restored site
Proportion of immatures to matures	7.933	0.0093	Control significantly higher than restored site
Shannon index (*H'*)	0.393	0.5362	No significant difference between sites
Simpson index (1-*D*)	13.935	0.0010	Restored site significantly higher than control site
Berger-Parker index (1/*d*)	8.014	0.0090	Control significantly higher than restored site
Evenness (*J'*)	0.035	0.8535	No significant difference between sites

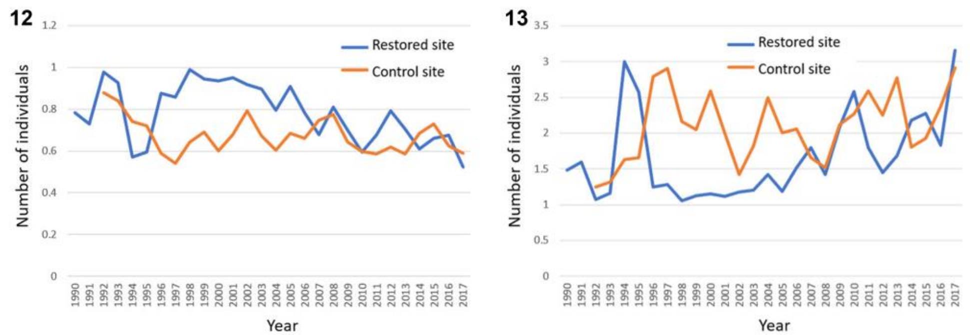
Comparison between the two sites (restored vs. control) showed that the numbers of individuals per 100 days trapped were not significant between the two areas for millipedes (Tab. 3) but showed significantly more centipedes in the control area than in the restored site (Tab. 4). Figure 10 illustrates the patterns found in terms of the number of millipedes per 100 trapping days in the two sites. Similar patterns can be seen at the two sites over time except for a more dramatic increase in 2015 for the control site. Figure 11 clearly shows that the number of centipedes per 100 trapping days is consistently lower in the restored site, the restored site has two major peaks (one at the beginning of the survey and one part way through), whilst the control is reasonably stable with an increase at the end. For both classes, the control area had significantly more species than the restored site (Tabs. 3–4). The proportion of immatures to adults was significantly higher in the control site for millipedes, but not for centipedes.

Table 4. Analysis of variance for centipede numbers and diversity (with year as a repeated measure).

Centipedes	$F_{1,25}$	***P***	**Comments**
Numbers of individuals per 100 trapping days	6.779	0.0153	Control significantly higher than restored site
Number of species	9.441	0.0051	Control significantly higher than restored site
Proportion of immatures to matures	2.093	0.1604	No significant difference between sites
Shannon index (*H'*)	0.384	0.5411	No significant difference between sites
Simpson index (1-*D*)	0.120	0.7324	No significant difference between sites
Berger-Parker index (1/*d*)	2.391	0.1346	No significant difference between sites
Evenness (*J'*)	0.074	0.7882	No significant difference between sites



Figures 10–11. Numbers of myriapods per 100 trapping days over time. 10 = millipedes; 11 = centipedes.



Figures 12–13. Indices over time for millipedes. 12 = Simpsons diversity index; 13 = Berger Parker Index.

No significant differences were found between the sites in terms of any of the diversity measures for centipedes. However, for millipedes, Simpson's index was significantly lower in the restored site, whilst Berger-Parker's index was higher in the control site. Figure 12 shows that the Simpson index for millipedes has remained more or less consistent over time for the control site, whereas for the restored site it has declined over time, becoming less diverse. Since this index is more influenced by the presence of common species, this implies that there are fewer common species in the restored site over time. The Berger-Parker index was also significantly different between sites and showed a clear increase over time for the restored site (Fig. 13). This suggests that species dominance has decreased over time, possibly related to the overall decline of several species including *C. punctatus* (Fig. 1) and *P. angustus* in the later few years (Fig. 6).

The NMDS biplots (Fig. 14) for millipedes show some separation along coordinate 1 (the axis of major variation) with the communities in the restored site for some early years lying to the left of the biplot, close to a large (fairly tight) cluster comprising the bulk of the data and the later years (2015–2017) being somewhat spread out to the right. This indicates that perhaps some changes did take place early on after restoration began, there was then a period of consolidation and then some larger changes occurred much later in the process. Although a similar spread of data can be seen on the biplot for the control site (with change occurring from bottom left to top right – Fig. 15), the data for the first 23 years are generally much more tightly clustered, implying a more consistent community structure over time. For the centipedes no obvious patterns emerged for either the restoration area or the control and similar groupings were found in the plots for the restoration and the control.

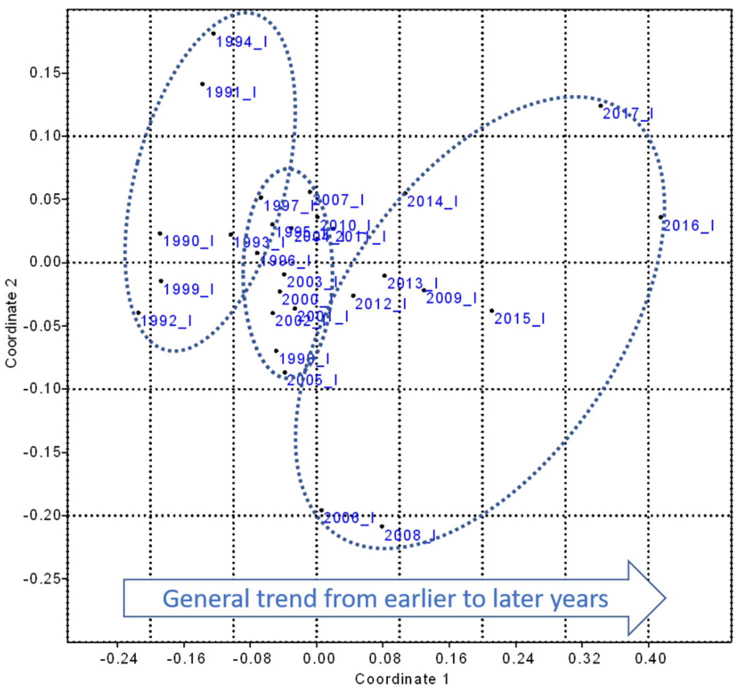


Figure 14. NMDS biplot of millipede communities over time for the restored site. Showing a general trend from early to later years along coordinate 1 (ellipses indicate groupings of early to later years).

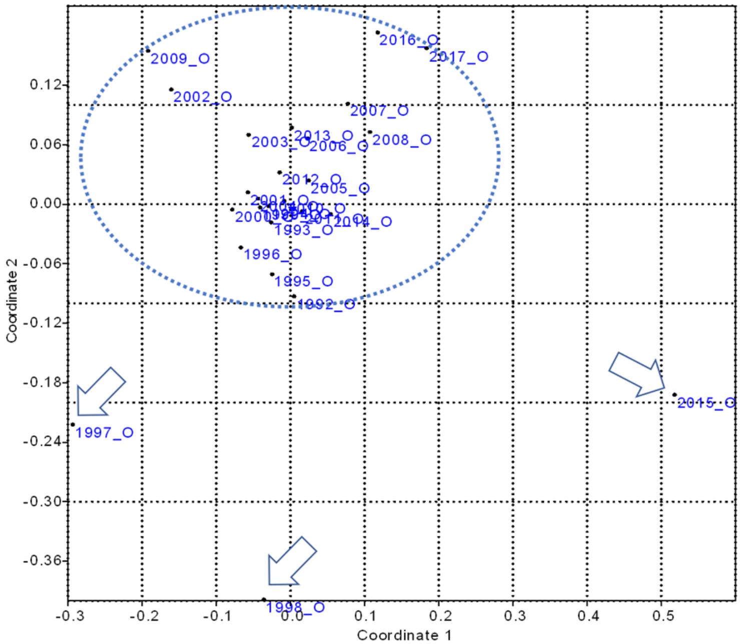


Figure 15. NMDS biplot of millipede communities over time for the control site. Showing a fairly tight grouping of years and three possible outliers (arrowed).

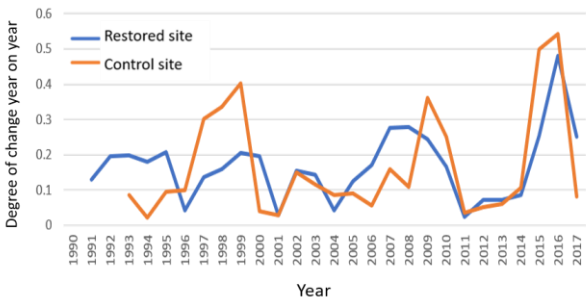


Figure 16. Degree of change in multidimensional space over time for millipedes. Indicating amount of community change.

Using change in multidimensional space as a measure of change in community structure between years, there were no differences between sites for either millipedes or centipedes. However, it can be seen for millipedes that the major change at both sites was in 2015 and 2016 (Fig. 16). If these dates are omitted from the analysis, the restored site can be seen to have a higher degree of change over time than the control site (repeated measures ANOVA $F_{1,24}$ = 11.392, P = 0.0029). For centipedes the amount of change between years is similar, although the patterns differ across the years with no discernible pattern.

The myriapod communities were then compared with the vegetation. Spearman Rank Correlations between the coordinate 1 scores from the ordination of the millipede and centipede communities and various measurements of the vegetation (number of plant species, individuals and diversity indices) were carried out. For the control plot there were no significant correlations, suggesting that the vegetation diversity is not a major influence on the myriapod communities. For the restoration plot the only significant correlations were found between the number of plant species and Shannon diversity, for both millipedes and centipedes (Tab. 5). Thus, the separation between the myriapod communities appear to be influenced by the number of species of plant including variation in the development of leaf litter (quantity and quality) providing resources such as food and shelter as well as influencing the microclimatic conditions.

Comparing the numbers of wood ants with the numbers of individuals and species of both centipedes and millipedes through Spearman Rank Correlation Coefficients revealed no significant relationships. Neither were there any significant results when compared with ordination coordinate 1.

Ordination (NMDS) of the vegetation data for the restored area shows no particular clusters of years and a change in community structure from left to right over time. The change in multidimensional space shows that between each year the rate of change is relatively low. In contrast, the plot for the control site shows a tight cluster of years with one major outlier (1999) and aside from this one year, the rate of change is also relatively low.

Table 5. Significant correlations between coordinate 1 scores for myriapod communities and vegetation in the restoration plot.

Factor	**Tied r_s**	***n***	**Tied *P***	**Direction of relationship**
Millipedes:				
Number of plant species	0.46397	26	0.01696	Positive
H' (Shannon) for plants	0.50632	26	0.00831	Positive
Centipedes:				
Number of plant species	0.46397	26	0.01696	Positive
H' (Shannon) for plants	0.50632	26	0.00931	Positive

DISCUSSION

Species found included a small number that can be considered interesting for the area. Despite the length of sampling time some species were only discovered in very low numbers (e.g. 2 individuals of *L. macilentus*). The number of centipede species found (13) compares with 10–21 found in previous studies from beech woodland in continental Europe (Stašiov & Svitok 2014), despite the limitations of pitfall trapping as a method and the relatively impoverished UK fauna. Although the UK has fewer species of millipede than other European countries at the same latitude, 14 species of millipedes were recorded which compares favourably with that of a forest edge in Belgium (De Smedt *et al.* 2016) where 10 species were found. Relative abundance of species were different however, in Belgium *Proteroiulus fuscus* was the most dominant and made up 33% of catch. This species was also found in the current study, but in low numbers.

Two species of centipede were only found in the control plot (*Geophilus insculptus* and *Lithobius macilentus*), but they both were encountered as very low numbers of individuals. *Geophilus flavus* was only found in the restoration plot and although at low numbers this was recorded in several years. This appears to be an eastern and northern species in the UK, is regularly encountered in disturbed places like urban and suburban locations and is found in grassland and pasture more frequently than woodland (Barber pers. comm.). Analysis of distribution records for preferred habitat in the UK found that *Geophilus insculptus* was equally likely to be found in the surface, leaf litter and subsurface layers and that *G. flavus* had a marked tendency to occur above ground (Barber & Keay 1988). The millipede *Nemasoma varicorne* was only found in the restoration area but again as just one individual. *N. varicorne* is not a species that would be expected to be found in pitfall traps regularly as it is very much an under-bark species on standing trees (see Lee 2006 for review of favoured tree species in the UK) but has also been recorded from pitfall traps (Kime 1997). The numbers of each species found in the two sampling areas over time were not evenly distributed and varied over time. Some showed clear differences between the control and restoration areas for example *Lithobius muticus* was consistently more abundant in the restoration area. Others showed changes over time within specific plots, for example *Cylindroiulus punctatus* became less abundant in the restoration plot over time, perhaps not surprising as this is a species living in decaying wood during the summer in France (Geoffroy 1981) and the quantity in this plot will have declined. Some species showed changes in abundance over time that appeared to be unrelated to restoration work being carried out. *Cylindroiulus britannicus* and *Glomeris marginata* were absent or almost absent at the beginning of the sampling period but now represent a substantial part of the millipede catch. *Chordeuma proximum* shows great variation between years within the control plot, which has not changed in other ways, and where the vegetation has remained very similar over time. The two main species of polydesmid millipede found also showed variation in numbers between the years, especially *P. angustus*. Captures in 2015 were notable with particularly large numbers of both species being trapped throughout the year.

The extreme variation in numbers found over time, not apparently always related to the restoration activity carried out, are interesting in highlighting apparently natural variation in myriapod activity over different years. The fact that the data for the last three years shows a similar spread to that found in the restored site, suggests that something other than the management implementation is impacting on the communities. The impact of trapping at the edges of the activity period for some species is also noteworthy. The traps may not be reflecting true abundance but are of course known to be dependent on the amount of activity and have strong bias for and against some species (Gerlach *et al.* 2009). The fact that some species became much more abundant over time would indicate that overtrapping is not having an obvious negative impact.

There were significant differences between total number of species found at the sites for both millipedes and centipedes, in both cases with the control being higher than the restoration area (i.e. the woodland had more species than an area perhaps equivalent to a forest edge, and the undisturbed habitat had more species than a disturbed one). Over time it might have been expected that a disturbed forest edge type habitat might have supported more species and this is what other work has found. For example, Stašiov & Svitok (2014) recorded a higher species richness of centipedes with increasing intensity of forestry thinning, although millipede species richness remained more or less the same. De Smedt *et al.* (2016) found that the species richness in oak woodland was lower in the centre of the forest than at edges and the activity density (measured by pitfall trapping) of millipedes was higher in the forest edges than the centre of deciduous forests across a range of latitudes and forest ages (De Smedt *et al.* 2019) although no relationship was found with centipedes. Tajovsky (2000) found that both the number of species and the density of millipedes increased in abandoned fields. Both peaked at between 3–6 years after abandonment, and then declined; it was suggested that the development of scrub caused temporary population increases. Bogyó *et al.* (2015) recorded significantly fewer millipede species in grassland compared to forests, although forest edges had even more than either.

High myriapod species richness has been recorded by Spitzer *et al.* (2008) in sparse stands

(30% canopy cover) of singled coppice woodland with low deer numbers, compared to areas of high deer numbers (which they equated to wood pasture) or dense woodland. Although the managed site in this study has the appearance of a forest edge it is still located within a larger block of woodland. Perhaps it has not yet gained species that would be typical of more open habitats, as they are less able to colonise, than a true forest edge.

In terms of numbers of individuals there was no significant difference between the sites for the millipedes but there were higher numbers of centipedes in the control plot. It might have been expected that the numbers of millipede, being decomposers, would be higher in the control site where there is more leaf litter but the results do not show this and indicate that there is sufficient food source for them. Perhaps the scrub and grassland plant species are compensating for the lower levels of tree leaf litter. Generalist predators may be more adaptable in the face of change; for example, spider numbers have been reported to increase as beech woodland canopy is opened up (Černecká *et al.* 2019). However, in this study centipedes seem to have declined in numbers. Perhaps those that are more active, like the lithobiomoph centipedes have been able to respond more rapidly to changing conditions than the generally slower moving millipedes. Alternatively, perhaps they are treating this area as a woodland clearing and are simply crossing it. *L. muticus* seems to be doing reasonably well in the restored area, perhaps it's more its preferred habitat than dense woodland.

In contrast other studies have shown significant differences. Bokor (1993) found double the abundance of centipedes in ecotones as in forest. De Smedt *et al.* (2016) found that the abundance of millipedes declined about 7 m inside the forest edge and Bogyó *et al*. (2015) recorded the highest abundance of millipedes at the forest edge. Again, these studies indicate that forest edges are better than dense forest in terms of number of individuals whereas in our study the open area could be acting more as a forest clearing than a true edge.

For millipedes the control plot has a significantly higher proportion of immatures to matures. This could be because there were more immatures or because there were fewer adults in this area. This former would make more sense, within the woodland the ground is covered in leaf litter which is likely to be a more suitable substrate for breeding than the more open grassland and scrub of the restored area.

Of the diversity indices calculated there was no relationship between the sites for the centipedes but for millipedes the restored site was significantly higher for Simpson (indicating an increase in the number of common species) and the control was higher for Berger-Parker (where a high value in the most frequently found species impacts negatively on the index), although no difference was found with the Shannon index or Evenness. This suggests that the restored area is dominated by a number of relatively common species. This perhaps is not surprising, with a relatively small number of species responding positively to perturbations during the restoration and habitat management work.

Stašiov & Svitok (2014) calculated evenness and found that the highest scores for centipedes were found in unthinned forest and for millipede in forests with moderate levels of thinning. Shannon for both groups was found to increase with increasing intensity of past thinning.

All previous studies have shown the importance of forest edges, ecotones and forestry thinning which appears to have positive impacts for both centipedes and millipedes. De Smedt *et al.* (2016) described ecotones and forest edges as being warmer and with deeper leaf litter, as well as being possibly higher in pH and nitrogen deposition which would favour decomposers. Bogyó *et al.* (2015) also states that they have a higher percentage of leaf cover and more deadwood. All of these factors suggest that they could be very good places for myriapods. In contrast, Ruitta *et al.* (2012) tested a hypothesis that decomposition would be slower at the forest edge and found that the soil was moister and decomposition of ash and oak was faster in the forest interior compared with the edge where decomposition and moisture was more limited.

The macrofauna accelerated decomposition regardless of moisture levels, but the authors felt that forest fragmentation was an important ecosystem process. De Smedt *et al.* (2018) showed that moisture content was a more important factor in the speed of good quality leaf litter breakdown than temperature indicating that moisture could be a constraint in more open habitats. Spitzer *et al.* (2008) concluded that areas where the tree cover had been cleared to 30% and left to regenerate, with low grazing pressure, were most important for species of conservation concern, which were referred to as 'relic species'. They recommended preserving highly heterogeneous and sparse canopy conditions and restoring such conditions in selected areas to benefit open woodland specialists. David (2009) concluded that habitat heterogeneity at a landscape scale seemed to be good for millipedes, even at the cost of fragmentation. While this may be true at a large scale, this study has questioned the validity of this statement at a small scale.

The present study appears to have supported the view that forest fragmentation has a negative impact on decomposer communities as the unmanaged control plot was better in terms of both species and numbers of centipedes and numbers of millipede species. Notwithstanding, aside from the physical characteristics, Tracz (2000) described ecotones as having two roles, as barriers and a transit zone and they clearly have a very important role to play as warm and sheltered places for certain species. The level of leaf litter accumulation will depend on the species of tree/shrub and the physical characteristics of the ground and this could be very variable, contributing to a patchy nature of the grass/scrub/tree mosaic.

Characterisation of communities through ordination indicated some changes in ordinal space over time for the millipedes in the restoration plot. There appears to be some change relatively soon after large scale changes to the vegetation and then a period of consolidation with little change, followed by more substantial changes in the later years. Examination of the change in more detail indicates that the main year of difference was 2015 (the change will be reflected twice for this unusual year, between 2014–15 and again 'back' from 2015–16). The ordination for the control plot also shows some changes in later years with 2015 a particularly different year to any others. 2015 is particularly notable for the 10-fold increase in captures of *Polydesmus angustus* and *Polydesmus denticulatus*, which were consistently high during the year, especially in the summer months. There are several possible reasons for this, of which climatic aspects are one. Peak adult activity of *P. denticulatus* is reported to be in June and July (Lee 2006) but while adults of *P. angustus* have been found at this time they are usually scarce over the summer (Lee 2006). Blower (1985) noted that *P. angustus* can be found in large numbers around cultivated land, with the subadults highly aggregated, and that it is a relatively fleet footed species. Other Polydesmids, notably species of the family Paradoxosomatidae have been reported to swarm in Nigeria (Lewis 1971) and Tasmania (Mesibov 2014). David (2012) measured the intrinsic rate of increase in laboratory populations of *P. angustus* subjected to seasonal conditions and calculated that a small group of 10 females at the start of a breeding season can potentially grow to over 3,000 females for the next year. It was considered that outbreaks of this species in favourable field conditions could be generated by a small number of fertilised females.

Relating the myriapod communities with the ground vegetation showed no significant relationships with the control plot, which is to be expected as this has not greatly changed over the years of study. However, the number of species of plant in the plots around the traps and their diversity, measured using the Shannon index, shows a positive correlation with coordinate 1 of the ordination of the millipede communities. This indicates that the number of plant species does have an impact on the millipede communities, with plant species being positively correlated along coordinate 1 of the ordination separating the millipede communities over time. A key feature of the restoration has been the increase in diversity of the ground vegetation which is a function of the grazing as well as tree clearance. Therefore, it is not surprising that the 'new' millipede communities in these restored areas are related to the change in vegetation. However, the movement in the millipede communities in recent years, both in the control as well as the restoration site, suggests that there is more than vegetation causing these changes. Perhaps, in addition to the alteration in management, we are seeing some impact of wider environmental changes including changing climate and broader management changes (such as clearing within dense woodland) on both communities.

Previous work has also indicated the importance of vegetation on myriapod communities. Bogyó *et al.* (2015) used DCCA to separate out three communities of grass, forest and forest edge and found that changes in millipede abundance was highly correlated with vegetation structure. Scheu (1996) found that while there was a continuous change in floral composition from arable fields to beech woodland it was moisture levels and leaf litter that were the key determinants explaining a substantial part of the variation in communities of millipedes using CCA. Neither moisture levels nor aspects of leaf litter were measured in the present study however they are potentially a major influence on invertebrates inhabiting the leaf litter zone. Poser (1990) found that, while there were more lithobiid centipedes and higher numbers of *Strigamia accuminata* in plots with augmented litter, there were more edaphic centipedes in areas without litter. Increased leaf litter depth as a result of heavy metal pollution was a driver for a study by Read & Martin (1990). A significant positive correlation was found between numbers of millipedes and litter depth. However, this seemed to be largely explained by *G. marginata*, numbers of which were positively correlated with litter depth and when this species was removed the results were not significant. De Smedt *et al.* (2016) found a strong decrease in numbers of *G. marginata* on a transect into woodland, the abundance of this species was different to other species being more abundant at the forest edge where it was suggested that the leaf litter might be of better quality due to the lower carbon to nitrogen ratio (although in this study it was not more abundant). It was also postulated that *G. marginata* was very desiccation tolerant so less restricted to the forest interior than other species.

CONCLUSIONS

Long-term studies of ground active invertebrates are relatively rare and this study has given some insight into communities, both where there has been active restoration work for habitat conservation and in a comparable woodland area that has not been actively managed. In the latter, plant and invertebrate communities generally changed very little over time, although some species did become more, or less, abundant and for a few species there were surprisingly big changes over time. This perhaps indicates a degree of turn-over which may be related to longer term climatic changes, but with just a single plot this is difficult to evaluate further.

The area restored to wood pasture, as might be expected, showed a higher degree of change, which in part does appear to be related to the changes in vegetation that has taken place in this area. Changes in the millipede communities, in particular, appear to have shifted in recent years, a relatively long time after the major part of the restoration work was carried out. While some of this may be due to external, possibly climatic changes, some species may have been advantaged or disadvantaged by the tree clearance, the impact of which has over-ridded more 'global' changes. It seems that 2015 was an exceptional year, when the abundance of a couple of common millipede species increased dramatically, including in the control site. The restored plot appears to have changed quite dramatically as a result of the restoration, from abundant leaf litter and decaying wood under tree canopy, to a grass and herb dominated sward with lower levels of patchily distributed leaf litter and decaying wood. It is therefore remarkable that the myriapod communities have proved so resilient.

The value of woodland vs. wood pasture as a habitat for myriapods requires further study and this was not an intended aim of the work. While the woodland control was consistently better than the restoration area for numbers of millipede and centipede species as well as overall numbers of centipedes, the community did not change as much as might have been expected. This either demonstrates a high degree of resilience as a remnant of the previous woodland, or that wood pasture retains sufficient pockets of woodland like habitat to support good populations of these groups, or that the current degree of restoration is producing clearings within woodland rather than effecting a more major change. The wood pasture restoration is intended to favour the saproxylic communities rather than the myriapod communities, but it is perhaps re-assuring that they have not been significantly negatively impacted as a result of the management work.

Long-term studies such as this one are also useful in revealing variation in species abundances over time in areas with no apparent change in management. The control site, over a nearly 30 year period, has shown large changes in abundances for a small number of species. These may show long-term trends or big variations between individual years. This indicates how much variation there can be between individual years and shows the importance of long-term studies such as this.

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