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A comparison of sampling methods and temporal patterns of arthropod abundance and diversity in a mature, temperate, Oak woodland

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ABSTRACT

Arthropods underpin fundamental ecological processes such as herbivory, pollination and nutrient cycling, and are often responsive to subtle changes in environmental conditions. Thus, changes in their abundance and phenology may be crucial indicators of system-wide responses to climate change.

The new Birmingham Institute for Forest Research (BIFoR) Free Air Carbon Dioxide Enrichment (FACE) facility provides a unique opportunity assess arthropod diversity and abundance in mature deciduous forest and the effect of sampling method and seasonality. This is an essential first step before attempting to measure the potential impacts of climate change, such as elevated CO_2, on arthropod populations. Two fundamental criteria are: i) diverse sampling methods in order to effectively assess diversity and in particular, differences between structural layers of the woodland system, e.g., ground, sub-canopy and canopy layers, ii) a temporal resolution that can identify seasonal patterns of change (phenology). This paper sets out the methodological approaches employed to achieve these objectives.

A total of 22,568 invertebrates from 108 families were sampled across 12 months of continuous sampling using a range of techniques from forest floor to canopy. Diptera were the most abundant order sampled and had the greatest number of families represented (45). Phenology patterns generally followed the anticipated seasonal cycle, with increasing abundance and diversity from spring to summer. Temperature was the best environmental predictor of abundance within Malaise and pitfall traps. Precipitation was not correlated with any monthly patterns of trap data. Yellow pan traps collected more arthropods than white or blue traps. Canopy beating yielded a greater diversity than that in the understory samples.

These data provide an important baseline from which to assess any future impacts of eCO_2 over the 10-year BIFoR FACE experiment, and highlight the importance of employing diverse sampling methods, temporal replication and measuring environmental factors over appropriate timescales.

1. Introduction

Arthropods play an integral role in terrestrial and freshwater ecosystem function and stability due to their high abundance, diversity and key contribution to ecosystem processes such as herbivory, pollination and nutrient cycling. However, many groups of arthropods are currently experiencing significant global declines (Biesmeijer et al., 2006; Conrad et al., 2006; Brooks et al., 2012; Hallmann et al., 2017 and Wagner, 2020), which has been linked to multiple drivers including habitat loss/fragmentation, pollution, agrochemicals, invasive species and changing climatic conditions (Lister and Garcia, 2018; Sánchez-Bayo and Wyckhuys, 2019; Wagner, 2020). Long-term monitoring of arthropod populations, therefore, is essential to build an accurate picture of ongoing trends in arthropod communities (Didham et al., 2020) and associated ecosystem health. This is particularly relevant when considering the timescales of which ecosystems respond to environmental changes, for example mature forest ecosystems may take several years to respond, therefore long-term monitoring is required to detect these changes. Due to their ectothermic physiology and short life cycles, arthropod populations are typically highly responsive to subtle

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changes in environmental conditions (Cornelissen, 2011). As a result, they are expected to be amongst the first group of organisms to respond to climate change and thus represent a useful indicator group (Ferris and Humphrey, 1999). In order to accurately measure these potential changes, it is essential that we gain an accurate understanding of current patterns of arthropod abundance and diversity across different ecosystems as a baseline (see Table 1).

Around 30% of the earths land surface, >42 million km^2, is covered by forests (Bonan, 2008). Forest ecosystems are, therefore, of global importance in terms of housing biodiversity, regulation of water cycling and carbon sequestration (Jenkins, 2002). Accordingly, understanding the implications of environmental change, such as increasing concentrations of atmospheric CO_2, on ecosystem processes within forests will be vital to elucidate the global impacts of climate change in the near future. The key role played by arthropods within forests means that in order to understand these impacts it is necessary to determine how they affect arthropod diversity, abundance and phenology, as well as the consequences of any changes on the ecosystem via feedback loops.

Mature forests have a high degree of structural diversity, particularly across their vertical profile, which is comprised of several key layers including soil/ground, leaf litter, field/shrub layer, understory and canopy. This structural diversity not only contributes to an overall high degree of biodiversity, but also the complexity of spatial and temporal (phenological) species distribution patterns (Schowalter and Ganio, 1998). Characterising this complexity necessitates the use multiple arthropod sampling techniques over entire seasonal timescales, however, this level of detail has been lacking from many previous forest climate change experiments. A recent exception is EucFACE (Facey et al., 2016), but it is important to note that Eucalyptus forest systems are not as diverse nor experience such extensive seasonal/phenological changes as encountered in temperate deciduous woodland.

Various sampling techniques are employed to monitor arthropod populations, each with their own advantages and limitations (Grootaert et al., 2010). Sampling techniques may be considered either 'active', whereby the sampler actively collects samples, e.g. by beating vegetation, or 'passive', which relies on the movement of the sampled organism into a collecting device, e.g. pitfall traps, Malaise traps and pan traps (Leather and Watt, 2005). Passive sampling methods can be further dived into attractive, where the target organisms are lured to the sampling device by light, colour, pheromones etc., or interception, which relies on chance for an individual to be sampled. The sampling period, being the time over which sampling occurs, also varies for different methods, from a few seconds for instantaneous sampling such as beating, to several weeks for continuous long-term trapping such as pitfall trapping. Different techniques can disproportionately favour certain taxa depending on life history, abundance and behaviour, and will therefore produce a different 'sample profile'. For example, pitfall trapping is an extensively utilised sampling method to capture epigeal beetles, spiders and ants, but tends to under-represent Hymenoptera and Diptera (Woodcock, 2005; Southwood and Henderson, 2009). The sample profile will also vary across different habitats within a woodland system, as well as seasonally and under different environmental conditions (Southwood and Henderson, 2009). Thus, quantification of trends in arthropod populations may be strongly influenced by both acute environmental conditions and sampling methodology.

Table 1
Total number of samples derived from each sampling method per month by array type.

Sampling method	Treatment arrays	Control arrays	Non-infrastructure control arrays	Total per month
Pitfall traps	2 × 3	2 × 3	2 × 3	18
Malaise traps	1 × 3	1 × 3		6
Pan traps	3 × 3	3 × 3	3 × 3	27
Understory beating	1 × 3	1 × 3		6
Canopy beating	1 × 3	1 × 3		6
Total	24	24	15	63

The structural complexity of mature woodlands means it is challenging to perform an accurate, detailed and representative assessment of the arthropod assemblages across the full profile of the ecosystem. Sampling techniques have typically been restricted to a single vertical stratum (Leather, 2005), with the canopy infrequently sampled due to practical difficulties of access. This means the canopy layer is often under-represented in biodiversity sampling, despite the functional importance of arboreal invertebrates (Schowalter, 1995). Importantly, it also prevents comparisons being made between habitat layers, which may well respond differently to climate change. In order to build a more complete overall profile of the biodiversity within a woodland system, and especially across all vertical strata, it is necessary to employ several sampling techniques simultaneously (Kitching et al., 2001; Leather and Watt, 2005).

Against this background, the current study assessed multiple different sampling methods to characterise the arthropod fauna of the Birmingham Institute for Forest Research Free-Air CO_2 Enrichment ('BIFoR FACE') facility across the full vertical profile of the woodland system and across a complete seasonal cycle. The purpose was to provide a baseline against which future changes in abundance, diversity or phenology of arthropods can be compared throughout the 10-year duration (minimum) of this unique climate-change experiment. Outputs from different sampling methods were compared to provide a characterisation of the sample profiles generated within this ecosystem and assess whether there was any sampling redundancy. We also interpreted arthropod trap data in relation to temperature and precipitation to identify other potential climatic drivers of arthropod abundance, diversity or phenology. An analysis of pan trap colour efficacy was made between the 3 most common flower colours in the local environment. Finally, a comparison of the abundance and diversity of arthropods from the canopy and understory was made via an assessment of sampling using a consistent sampling method.

2. Materials and methods

2.1. Experimental site

The study was conducted at the Birmingham Institute for Forest Research Free-Air CO_2 Enrichment ('BIFoR FACE') experimental facility, located in Staffordshire, UK (52°47′58″N, 2°18′15″W) as described in Hart et al. (2019). The site comprises 21 ha of mature, semi-natural broadleaved woodland (>200 years continuous tree cover), characterised by > 150-year-old 'standard' English Oaks, *Quercus robur*, and a previously coppiced common Hazel, *Corylus avellana*, understory. There are several other species of tree dispersed across the woodland including Sycamore, *Acer psuedoplatanus*, hawthorn, *Cretaegus monogyna*, and Ash, *Fraxinus excelsior*.

There are 9 experimental arrays across the site, comprising 6 infrastructure arrays of which 3 are CO_2 fumigated treatment arrays and 3 are non-fumigated control arrays. The remaining 3 arrays are non-infrastructure controls (Fig. 1). CO_2 enrichment commenced in April 2017 and will continue throughout the 10-year duration of the FACE experiment. Treatment arrays receive CO_2 fumigation to elevate the average concentration across the array to 150 ppm (~550 ppm total) above ambient (~400 ppm), measured in real time (Norby et al., 2016).

2.2. Arthropod sampling

Five sampling methods were selected to maximise sampling coverage whilst minimising physical impacts on the site and to avoid oversampling. Both active and passive sampling methods were employed for one full year from March 2017 to February 2018. Sampling was conducted in four key vertical strata of the forest: ground (0 m), field/shrub

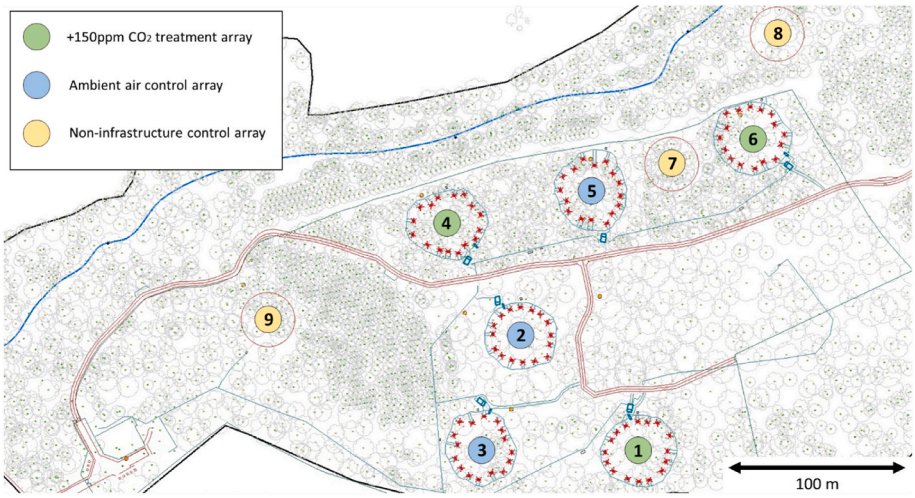

Fig. 1. The BIFoR FACE experimental site in Staffordshire, showing array locations and numbering. Arrays 1, 4 and 6 are infrastructure treatment, receiving +150 ppm CO2 above ambient. Arrays 2, 3 and 5 are infrastructure control, receiving ambient air. Arrays 7, 8 and 9 are non-infrastructure controls. Red marks within infrastructure arrays denote CO2 delivery pipe support towers.

(0–1 m), understory (1–4 m) and canopy (20–25 m), in the last week of each calendar month. Trap location within the arrays was generated randomly prior to set up. No trapping or sampling took place within the 2 m 'mixing' zone around the perimeter of the arrays.

Pitfall trapping. Pitfall traps are a standard and widespread sampling method for sampling epigeal arthropods such as beetles, spiders and ants (Southwood and Henderson, 2009). Two pitfall traps were installed in each experimental array (18 in total) which is consistent with other forest FACE experiments (Sanders et al., 2004; Facey et al., 2016). The traps consisted of a 570 ml plastic cup, (8 cm diameter and 10 cm depth), positioned so the rim was level with the soil surface. Pitfall traps had a two-week 'bedding in' period before any sampling took place to allow any increased catch rates derived from 'digging in' effects to subside (Greenslade, 1973). Traps were filled to about 1/3 with water with a drop of scentless detergent to break the surface tension, and covered by a tile held above the soil surface on metal legs to prevent rain and debris from falling in. The sampling period was 7 days, with traps collected in at approximately the same time of day as they were deployed. Between trapping periods, pitfalls were closed with a lid to prevent by-catch.

Malaise trapping. Malaise traps are an effective sampling method for capturing large quantities of flying insects such as Diptera and Hymenoptera. A Malaise trap (passive) (Watkins and Doncaster, UK) was deployed in each of the infrastructure treatment and control arrays (total 6) to sample insects flying through the field layer (0–1 m). The traps (main screen 180 cm × 160 cm) were operational over a 24-h sampling period from approximately 10:00am to 10:00am during which the collection bottle was attached, filled to 1/3 with water plus a drop of scentless detergent. During 'non-operational' intervals the collection bottle was removed, and the trap left open in situ.

Pan-trapping. Pan traps are an effective method for sampling flower-visiting arthropods that have been employed previously in FACE experiments (Hillstrom and Lindroth, 2008). The Pan traps consisted of a plastic bowl of 20 cm diameter and 10 cm depth, half-filled with water plus a drop of scentless detergent (as above), mounted on a crossbar approximately 1 m off the ground supported by a single post. Three colours of pan trap, spray painted yellow (~580 nm), blue (~475 nm) or white, were deployed in each experimental array (total 9). These colours represent the most frequent floral colours in the woodland. Pans were operational for 24 h.

Understory and Canopy beating. Beating is a standard method for sampling foliage and is often used to sample arboreal arthropods (Delvare et al., 1997). Understory (Common Hazel) and canopy (Oak) vegetation were both sampled by beating at a single location near the centre of each experimental array once a month (6 understory and 6 canopy). Insecticidal approaches, such as 'fogging', were not viable as these would have a large, lasting impact and affect subsequent sampling. To avoid damage to vegetation the foliage was agitated, instead of being struck with a stick, as conducted by Altermatt (2003) to sample canopy arthropods in a forest FACE experiment. Due to the logistical limitations of sampling in the canopy, a large plastic funnel (25 cm) was used instead of a traditional full-sized beating tray. An area of approximately 1 square metre was systematically agitated over the course of 30 s above the funnel connected to a collecting pot. *Quercus robur,* English Oak, was selected as the dominant canopy species and was sampled at a height of between 25 m and 30 m, at a point which was within reach from the central tower. *Corylus avellane,* Common Hazel, was selected as the dominant understory species and was beaten from ground level (1.5–2 m), directly below the point in the canopy where Oak beating occurred. Beating occurred during every month that the trees had photosynthetically active leaves (April–October).

Processing and identification of samples. Samples were collected in 70% ethanol for long term storage before identification. All arthropods in each sample were counted and identified (initially to order level) under a stereomicroscope (SMZ140; Motic, Spain). All pan trap and beating samples were identified to family. Coleoptera from pitfall samples were acknowledged as a key group and identified to family.

2.3. Meteorological data

2.3.1. Temperature

Mean air temperature during a given sampling period was calculated from hourly means measured by a Campbell Scientific 107 Thermistor and recorded on a Campbell Scientific CR300 series datalogger fitted to one of the towers of each FACE array at a height of the upper canopy (approximately 22 m). The time window for meteorological measurements related to beating sampling was set at 24 h from 00:00 to 23:59 of the day the sampling took place. The time windows for meteorological measurements related to Malaise and pan trapping were set at 48 h from 00:00 the day the traps were deployed to 23:59 the day samples were collected. The time windows for meteorological measurements related to pitfall trapping was set at 168 h (= 7 days) from 00:00 the day the traps were deployed to 23:59 the day samples were collected.

2.3.2. Precipitation

Mean throughfall precipitation was calculated for the site from measurements taken from 2 ARG100 tipping bucket Rain gauges in each

array and recorded on a Campbell Scientific CR300 series datalogger. Total throughfall was calculated for the same time windows as mean temperature.

2.4. Statistical analyses

All statistical analyses were performed in R, version 3.5.2 (R Core Team, 2015). The two pitfall trap samples taken from the same experimental array simultaneously were pooled to negate pseudoreplication.

2.4.1. Overall abundance

The effect of eCO_2, sampling method and month on arthropod abundance was tested with a generalised linear mixed model with negative binomial errors. The model was fitted with the 'glmmTMB' package (Brooks et al., 2017), with array as a random effect. The effect of eCO_2 was not considered further (SM1).

2.4.2. Meteorological analysis

The analyses of mean temperature, maximum temperature, minimum temperature and throughfall precipitation on arthropod abundance for each sampling method during the respective time windows were performed using a Generalised Linear Model with quasi-Poisson errors (Kuznetsova et al., 2017).

2.4.3. Pan trap colour analysis

Arthropod abundance across the three coloured pan traps was analysed using a generalised linear mixed-effect model with negative binomial error structure. The model was fitted with the 'glmmTMB' package (Brooks et al., 2017), with pan trap colour and month as fixed effects with a linked dispersion model and array as a random effect. The model was validated with the 'DHARMa' package (Hartig, 2022).

2.4.4. Canopy vs. understory comparison

Simpsons and Shannon-Wiener diversity indices were calculated at family level for understory and canopy beating samples. Species richness has been shown to strongly correlate with both genus and family numbers (Báldi, 2003). As a result, family can be used as a surrogate for species diversity for taxa difficult to identify past family level (Derraik et al., 2002). The analyses of arthropod abundance, Simpson's diversity and Shannon-Wiener diversity of canopy vs understory was performed with generalised linear mixed effect models. The models were fitted with the 'glmmTMB' package (Brooks et al., 2017), with location (Canopy vs understory) and month as fixed effects and array as a random effect. A negative binomial error structure was applied in the abundance model and gaussian error structures in the diversity models.

3. Results

3.1. Overall abundance

Over the 12-month sampling period a total of 22,568 arthropods were collected and identified, comprising 24 orders. Of these orders, 12 were within the class Insecta, 4 within Arachnida, 3 within Entognatha and 7 from other classes. Diptera were the most abundant order overall, with 10,869 individuals, and the most frequently sampled in pitfall traps (Ground layer), Malaise and pan traps (field/shrub layer) (Fig. 2a, b, c). Coleoptera and Hymenoptera were the second and third most sampled orders, with 2795 and 2643 individuals collected respectively. In total, 141 families were identified (SM2), with 65% of individuals belonging to just 6 families, specifically Staphylinidae (32.9%), Leoididae (4.5%) and Carabidae (8.1%) for the Coleoptera; Sciomyzidae (13.1%) and Chironomidae (3.0%) for the Diptera; and Platygastridae (3.4%) for the Hymenoptera. Araneae were the most frequently sampled group by canopy and understory beating (34.2%, Fig. 2d).

A total of 10,230 arthropods were sampled from the ground layer using pitfall traps (Fig. 3a), 9289 from Malaise traps (field/shrub layer), 2299 from pan traps (field/shrub layer) (Figs. 3c and 471 from canopy beating and 279 from understory beating (Fig. 3e). Sampling method had a significant effect on the overall abundance of arthropods sampled ($z = 13.049$, $p < 0.001$, Table 2).

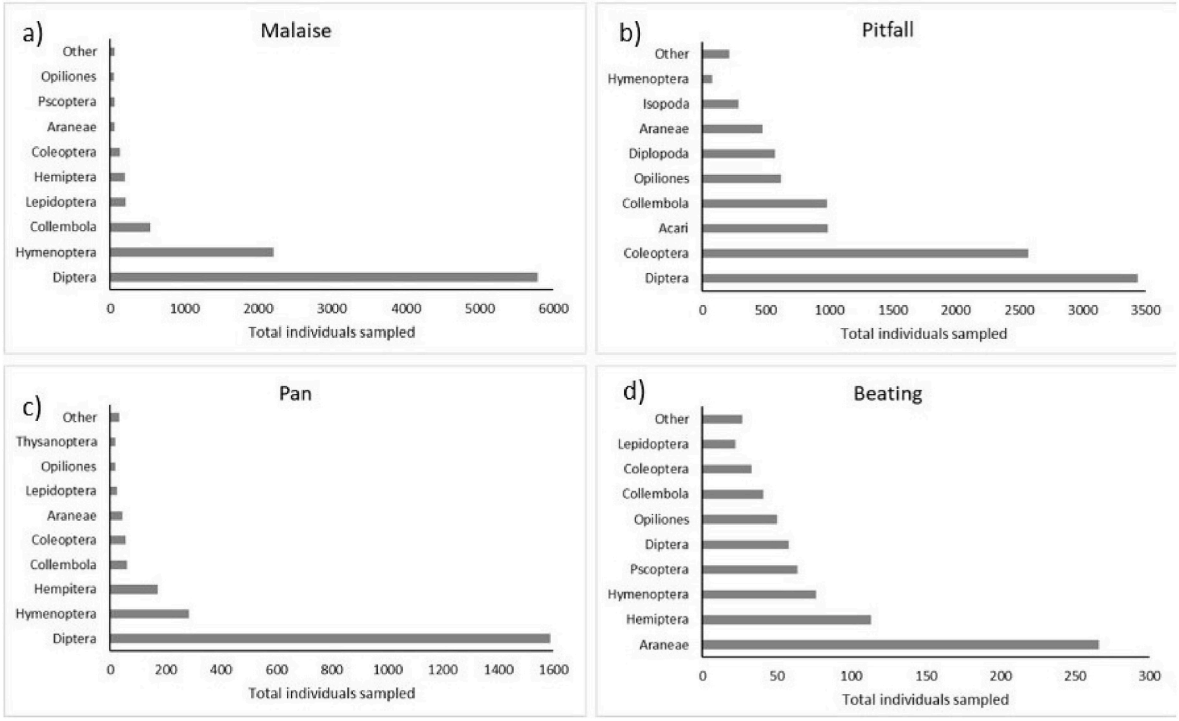

Fig. 2. Total number of arthropods from the 9 most frequently caught orders using the 4 sampling methods: Malaise (a), pitfall (b), pan trapping (c) and combined canopy and understory beating (d). Totals are cumulative across the complete 12-month sampling period (March 2017–February 2018).

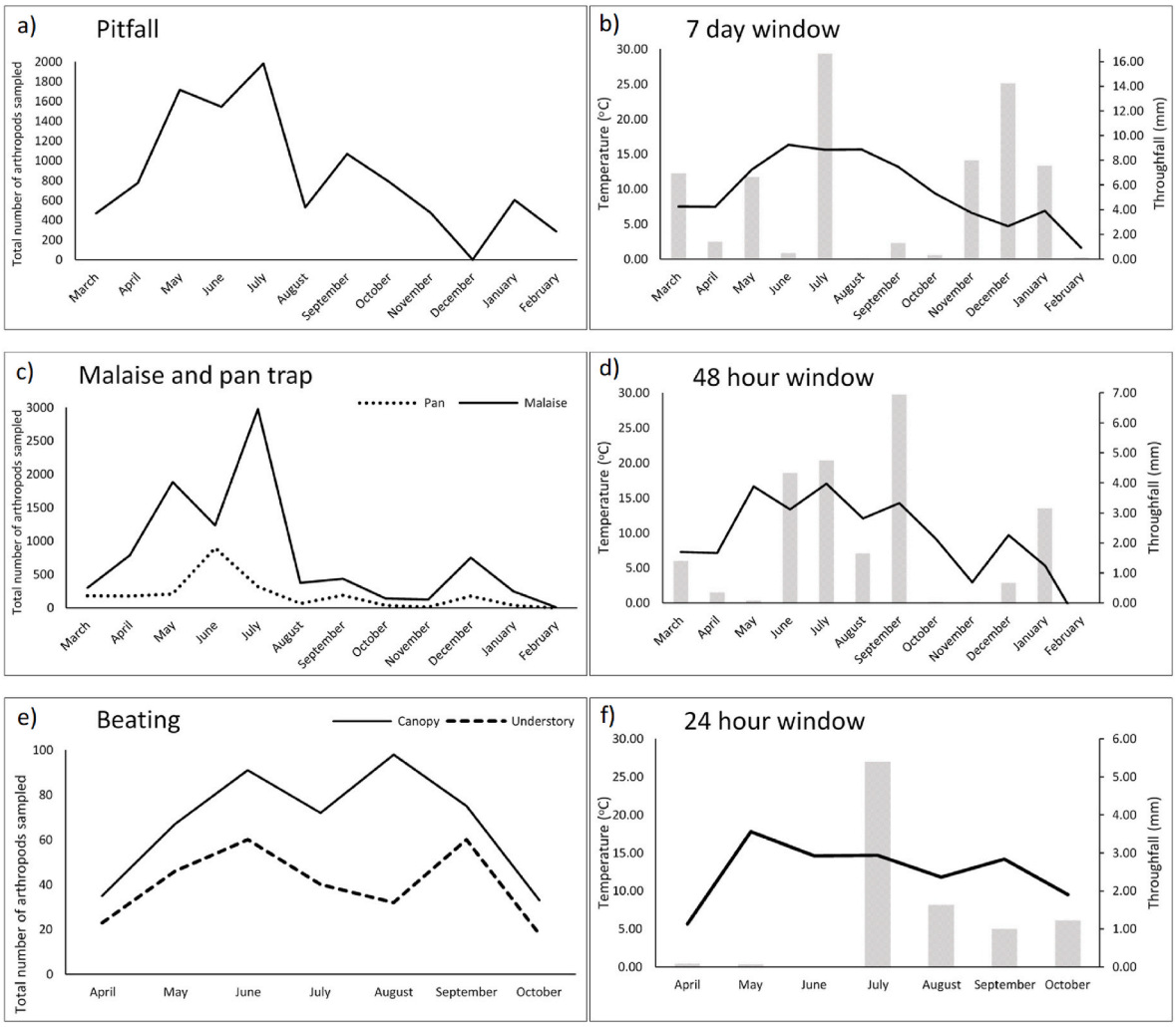

Fig. 3. Total number of arthropods sampled monthly by pitfall (a), pan and Malaise trapping (c) and canopy and understory beating (e) over the 12-month sampling period (March 2017–February 2018). Mean temperature and total throughfall precipitation during the associated time window, 7 days for pitfall (b), 48 h for pan and Malaise trapping (d) and 24 h for beating (f).

Table 2
Summary of results of the GLMM analysing overall arthropod abundance. Significance codes: $p < 0.001$***, $p < 0.05$*.

	Estimate	Std. Error	z-value	p-value
Conditional model:				
(Intercept)	*2.2732*	*0.1208*	*18.823*	*< 2e-16* ***
Understory	*−0.4387*	*0.1654*	*−2.652*	*0.008* **
Malaise	*2.7171*	*0.1557*	*17.447*	*< 2e-16* ***
Pan trap	*0.824*	*0.1431*	*5.756*	*8.6e-09* ***
Pitfall	*2.3927*	*0.138*	*17.336*	*< 2e-16* ***
Dispersion model:				
(Intercept)	*2.3212*	*0.5303*	*4.378*	*1.20e-05* ***
Month - August	*−2.139*	*0.5557*	*−3.849*	*0.000119* ***
Month - December	*−3.8416*	*0.6021*	*−6.381*	*1.76e-10* ***
Month - February	*−4.0165*	*0.5957*	*−6.743*	*1.55e-11* ***
Month - January	*−2.6043*	*0.5706*	*−4.564*	*5.02e-06* ***
Month - July	*−2.07*	*0.6697*	*−3.091*	*0.001995* **
Month - June	*−2.5018*	*0.6345*	*−3.943*	*8.05e-05* ***
Month - March	*−2.2808*	*0.5697*	*−4.003*	*6.24e-05* ***
Month - May	*−1.6068*	*0.684*	*−2.349*	*0.018814* *
Month - November	*−3.2119*	*0.5771*	*−5.565*	*2.62e-08* ***
Month - October	*−2.457*	*0.5491*	*−4.475*	*7.65e-06* ***
Month - September	*−1.2376*	*0.591*	*−2.094*	*0.036241* *

3.1.1. Temporal patterns of abundance: phenology and climate profiles

There was a clear phenological pattern of arthropod abundance, with total numbers (collected across all trapping methods) increasing each month from March 2017 to a peak of 5387 individuals in July 2017 (Fig. 3). Sampling month had a significant effect on the overall abundance of arthropods sampled ($F_{11,360} = 6.765$, $p < 0.001$). There was a significant decrease in the total number caught in August using all sampling methods except canopy beating, which experienced its highest overall catch during this month. Total abundance rebounded slightly in September followed by a consistent decline in abundance until November 2017. Pitfall traps collected more arthropods than any other method for every month between August 2017 to February 2018 except December 2017, when both Malaise and pan trap collections increased slightly (Fig. 3a vs. Fig. 3c). Mean December temperatures for the 7-day pitfall collection period were low (4.70 °C), compared to November (6.61 °C) and January (6.89 °C), while mean 48-h temperatures for Malaise and pan trapping periods were high (9.67 °C) compared to November (2.96 °C) and January (5.34 °C) (Fig. 3b and d).

Mean temperatures calculated for each 48-h Malaise trap collection period had a significant correlation with arthropod abundance using this method (Fig. 3c and d; $F_{1,5} = 2271.6$, $p < 0.001$). Mean temperatures for each 7-day pitfall trap collection period also had a significant correlation with numbers collected (Fig. 3a and b; $F_{1,5} = 2239.9$, $p < 0.003$). No correlations were found between temperature and abundance for pan

traps (Fig. 3c and d) or beating (Fig. 3e and f) methods, and throughfall precipitation did not correlate with arthropod abundance from any sampling method (Table 3).

3.1.2. Pan trap colour

Yellow pan traps consistently collected significantly more arthropods than either the blue or white traps for all months, with overall means of 14.6, 2.92 and 3.77 individuals respectively (Fig. 4a; $z = 9.563$, $p < 0.001$, Table 4). Blue traps were significantly greater than white across the year overall (Fig. 4a; $z = 2.270$, $p = 0.0232$). Sciomyzidae were the most abundant family sampled by pan traps (33.4%), of which 99.6% were caught in yellow traps (Fig. 4b).

3.1.3. Canopy vs understory

Arthropod abundance from canopy beating was significantly higher compared to the understory beating across the 12-month period (Fig. 3e; $z = -4.193$, $p < 0.001$, Table 5). This difference was greatest in August 2017 and driven mainly by Araneae and Braconidae. Family level diversity in the canopy was also greater than in the understory for all months, except September, for both Simpson's and Shannon-Wiener indices (Fig. 5a and b respectively). Simpsons and Shannon-Wiener diversity index scores of the canopy were also both significantly greater than understory ($z = 2.241$, $p = 0.025$ and $z = 3.143$, $p = 0.002$).

4. Discussion

This study provides a spatial and temporal characterisation of arthropod abundance and diversity across a mature Oak woodland, and importantly a site that will experience 10 years of +150 ppm CO_2 as part of the BIFoR FACE experiment (Hart et al., 2019). It also allows us to evaluate different sampling methods which will be fundamental for future studies determining mid-to long-term impacts of eCO_2 on arthropods in temperate forest ecosystems.

4.1. General arthropod abundance and diversity

The dominance of Diptera, Coleoptera and Hymenoptera across all sampling methods (these three orders comprised >72% of the total individuals sampled) suggests that these groups may be key drivers of ecological processes, however, these taxa are also highly diverse in both species and functional groups. Other forest FACE experiments also found similar sample composition at order level, suggesting that the sample obtained is both reasonably representative and comprehensive (Altermatt, 2003; Hillstrom and Lindroth, 2008; Stiling et al., 2010; Facey et al., 2016). It is, perhaps, unsurprising that Diptera were more abundant than any other order, given that flies have been found to dominate several other terrestrial ecosystems, e.g. in the Arctic (Schmidt et al., 2017). Similarly, at the family level we found that a relatively small number of families drove the overall abundance patterns observed, with 65% of individuals belonging to just 6 families (Staphylinidae, Sciomyzidae, Carabidae, Leoididae, Platygastridae and Chironomidae).

4.2. Comparison of sample profiles

The methods used in this study to sample each layer varied considerably, for example the duration of the sampling period or 'active' vs 'passive' sampling. Whilst this allows efficient sampling of each individual layer to build a picture of the overall arthropod community composition within a structurally complex system, it means it is not possible to directly compare layers based on numbers of individuals produced alone. The data presented in this study does, however, provide a useful characterisation of the sample profile produced by each sampling method in the context of a mature temperate Oak woodland.

Table 3
Summary of results of the GLM analysing mean temperature on overall abundance for each sampling method. Significance codes: $p < 0.001$***, $p < 0.05$*.

Explanatory variable	Estimate	Std. Error	t-value	p-value
Pitfall	0.1212	0.0313	3.871	0.0031
Beating	0.07069	0.03205	2.205	0.07856
Malaise	0.19875	0.04157	4.781	0.000745
Pan trap	0.13639	0.07032	1.940	0.0811

The ground layer was sampled by pitfall trapping, with samples dominated by Nematoceran Diptera and epigeal Coleoptera. Almost all of the Diptera sampled from this layer were adult Chironomidae or several other fly families that possess larvae that feed in leaf litter. While larvae themselves were rarely sampled, most likely due to either their limited motility or because larval stages inhabit freshwater habitats, adults were sampled in very large numbers. The most abundant beetle families were Staphylinidae and Carabidae. Whilst both these families are large and functionally diverse, the majority of species identified from samples in this study were predatory.

The Malaise trapping and pan trapping sampled from the field/shrub layer and consisted chiefly of Diptera and Hymenoptera. The two most abundant Dipteran families were Sciomyzidae, whose larvae are predators/parasites of Gastropoda, and Chironomidae whose larvae are abundant in freshwater habitats, tree holes, rotting vegetation as well as soil, and play an important role in detritus processing and trophic cycles (Armitage et al., 2012). The majority of the Hymenoptera sampled belonged to the family Platygastridae, which are typically egg parasitoids of Diptera, Coleoptera and Hemiptera (Buhl and Notton, 2009).

Araneae were by far the most abundant order from the canopy and understory beating, with a great abundance and diversity of spiders sampled from the canopy compared with any other layer. Spiders are exclusively predatory, with the majority of species sampled from the canopy belonging to hunting guilds which construct webs. It is likely, therefore, that in this habitat the canopy provides a greater source of prey and vegetation structure to construct webs, with more limited vegetation structure within the ground and field layers supporting fewer spider species (Oxbrough et al., 2005). Indeed, forest canopies are known the be important reservoirs of spider diversity in temperate forests, with the composition of assemblages differing between the canopy and understory (Larrivée and Buddle, 2009). The next most abundant families sampled via canopy and understory beating were Aphididae and Braconidae. Aphididae are phloem feeding herbivores which are often very abundant due to large, rapid population increases during certain stages of their lifecycle. Braconid wasps are the second most diverse family of parasitoid wasps, with an equally diverse host range, which includes many species of aphid. .

4.3. Phenology and climate data

Unsurprisingly, given the temperate location of the BIFoR FACE site, there was a clear, strong seasonal phenology in both abundance and diversity of arthropods within the woodland. These seasonal patterns highlight the importance of characterising phenology in two ways. First, temporal replication can ensure results are more representative of the system as a whole and not skewed by stochastic events (Southwood and Henderson, 2009). For example, during August the abundance of individuals sampled decreased by 80% relative to the previous month, before increasing again in September. This event would have provided a false characterisation of the site if sampling had occurred only in August. Second, the sampling interval of phenology sampling is crucial, and if not frequent enough can miss key phenological events (Southwood and Henderson, 2009). Optimisation of sampling intervals is, therefore, again a trade-off between precision and practicality.

Our study also highlights the importance of interrogating climate data within time periods relevant to the sampling methods employed, and not just using, for example, monthly or yearly means (e.g. Lister and Garcia, 2018). There are several instances where mean temperatures for the 48-h Malaise or pan trapping periods give a very different picture of

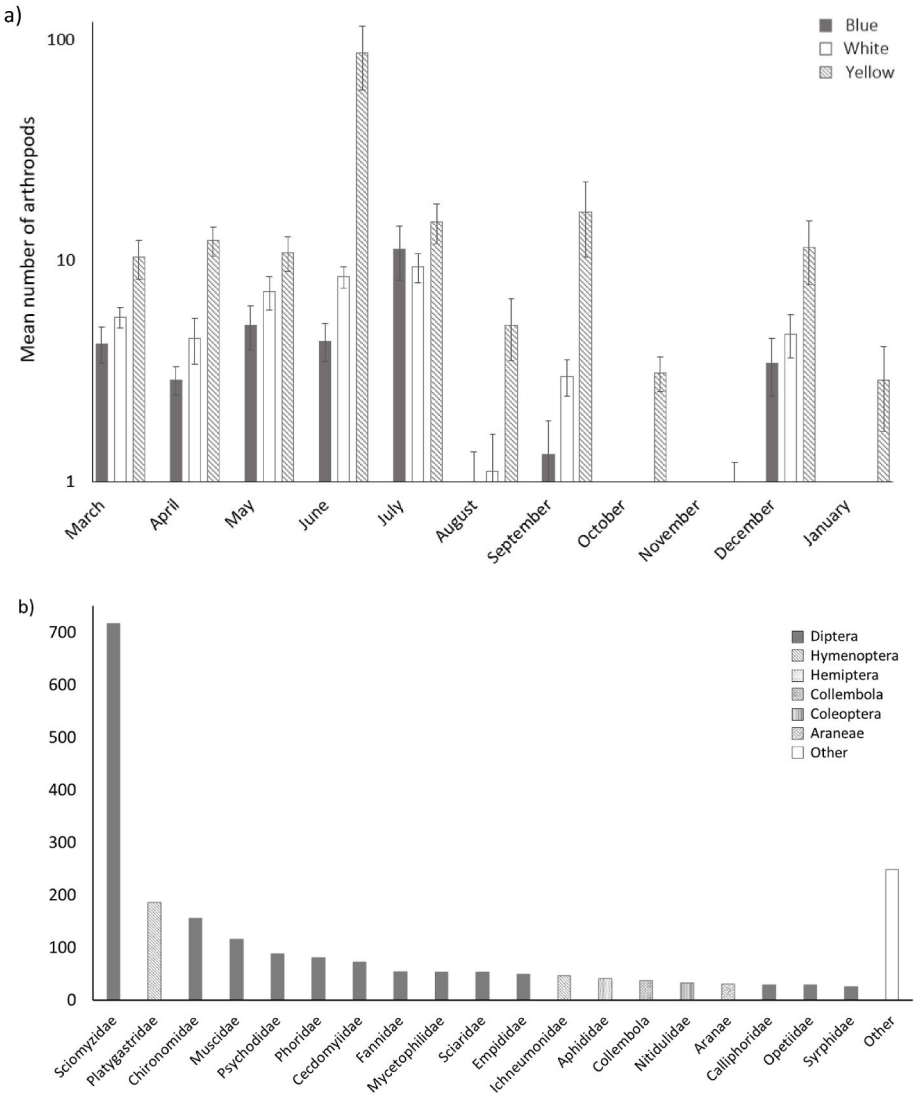

Fig. 4. (a) Median (± Interquartile range) number of arthropods sampled by blue, white and yellow pan traps each month across the 12-month sampling period (March 2017–February 2018). (b) Total number of arthropods from the 19 most frequently collected families in all pan trap samples. Totals are cumulative across all 3 colours and the complete 12-month sampling period (March 2017-Febraury 2018).

Table 4
Summary of results of the GLMM analysing pan trap colour. Significance codes: $p < 0.001$***, $p < 0.05$*.

	Estimate	Std. Error	z-value	*p-value*
Conditional model:				
(Intercept)	1.4993	0.1067	14.056	<2e-16 ***
Colour - White	0.2513	0.1107	2.27	0.0232 *
Colour - Yellow	1.059	0.1107	9.563	<2e-16 ***
Dispersion model:				
(Intercept)	1.0275	0.204	5.037	4.72e-07 ***
Month - August	−1.9659	0.3956	−4.969	6.73e-07 ***
Month - December	−0.252	0.4352	−0.579	0.5626
Month - February	−23.89	3714.19	−0.006	0.9949
Month - January	−2.8694	0.428	−6.704	2.03e-11 ***
Month - July	−0.4505	0.3972	−1.134	0.2567
Month - June	−1.792	0.3167	−5.659	1.52e-08 ***
Month - March	1.5754	0.8034	1.961	0.0499 *
Month - May	0.9689	0.6621	1.463	0.1434
Month - November	−3.4521	0.4665	−7.401	1.36e-13 ***
Month - October	−2.2922	0.3977	−5.763	8.24e-09 ***
Month - September	−0.9797	0.4017	−2.439	0.0147 *

climate conditions for a particular month than when looking at the 7-day mean temperatures for the pitfall trapping periods, e.g. December 2017 (Fig. 3). This is an important finding as it highlights that the duration of sampling period as well as the duration of environmental monitoring influence whether or how the relationship between then is interpreted.

The lack of a correlation between arthropod abundance, particularly flying insects which form the majority of arthropods sampled in this study, and precipitation is an interesting and unexpected result. This suggest that woodland systems may be more buffered against the effects of precipitation, perhaps due to the structural component of the trees/canopy. The next step is to characterise microclimate conditions relevant to the locations of these trapping methods, e.g. soil temperature and moisture availability for ground layer, shrub layer air temperature and above canopy precipitation. This resolution of microclimate data was not available for the first year of sampling at the FACE site, but is now in place for the remainder of the experiment.

The different sampling methods also reveal variation in phenological patterns across vertical layers within the woodland system, both in magnitude and direction. For example, in August the total number of arthropods sampled from the canopy increased from the preceding month whereas understory decreased (Fig. 3e). This temporal variation may be driven by actual shifts in arthropod abundance, climatic factors

Table 5
Summary of results of the GLMMs analysing beating in canopy and understory. Significance codes: p < 0.001***, p < 0.05*.

	Estimate	Std. Error	z-value	*p-value*
Abundance				
(Intercept)	1.8085	0.2065	8.759	<2e-16 ***
Understory	−0.5532	0.132	−4.193	2.76e-05 ***
Month - August	0.7609	0.2509	3.032	0.002428 **
Month - July	0.6502	0.2526	2.574	0.010051 *
Month - June	0.9659	0.2482	3.892	9.93e-05 ***
Month - May	0.6899	0.253	2.727	0.006390 **
Month - October	−0.1235	0.2742	−0.451	0.65234
Month - September	0.8646	0.2498	3.462	0.000537 ***
Simpson Diversity				
(Intercept)	2.4592	0.3312	7.425	1.13e-13 ***
Understory	−0.519	0.2316	−2.241	0.0250 *
Month - August	0.3851	0.4333	0.889	0.3741
Month - July	0.6533	0.4333	1.508	0.1316
Month - June	1.9657	0.4333	4.537	5.72e-06 ***
Month - May	0.5917	0.4333	1.366	0.1721
Month - October	−0.734	0.4333	−1.694	0.0903.
Month - September	0.2371	0.4333	0.547	0.5842
Shannon Diversity				
(Intercept)	−0.9763	0.13169	−7.414	1.23e-13 ***
Understory	0.28777	0.09156	3.143	0.001673 **
Month - August	−0.1544	0.1713	−0.901	0.36738
Month - July	−0.2756	0.1713	−1.609	0.1077
Month - June	−0.6598	0.1713	−3.852	0.000117 ***
Month - May	−0.2631	0.1713	−1.536	0.12461
Month - October	0.40353	0.1713	2.356	0.018485 *
Month - September	−0.1306	0.1713	−0.762	0.44587

or seasonal variation in sampling method efficacy. For example, movement behaviours such as flight, often vary seasonally in relation to life history and voltinism, which would affect sample frequencies for flight interception traps (Basset, 1991). This is well characterised by fluctuations in the number of Aphididae sampled, which exhibited low overall abundance but experienced two large peaks in May and September. These peaks were driven by an influx of alate aphids, which likely corresponds to the phenology of host alternation or dispersal flights (Dixon, 1977). Climate can also directly influence trap performance, for example if temperatures drop below insect thermal activity thresholds then the frequency and duration of movement is curtailed (Coleman et al., 2015). Equally, extended periods of precipitation will restrict flying insect movement in particular. Continuous sampling throughout the entire year is therefore important in order to allow subtle temporal changes in arthropod abundance and diversity to be measured in relation to seasonal climate patterns, whilst also allowing detection of shifts in phenology between years.

4.3.1. Pan trap colour

Pan traps are an effective method for sampling flower visiting insects within forested ecosystems, particularly when a range of colours are used (Campbell and Hanula, 2007). The dominance of Diptera and Hymenoptera in the pan trap samples highlights the relative importance of these groups as potential pollinators within the woodland ecosystem. In the present study this dominance is largely driven by flies in the Sciomyzidae, Chironomidae and Muscidae families and wasps in the Platygastridae family. These Dipteran families are mostly comprised of saprophages and the Hymenoptera families are all parasitoids. This is consistent with other studies which have also found that these feeding guilds dominate pan trap samples in temperate forests (Hillstrom and Lindroth, 2008).

The data from this study corroborates the evidence that the colour of pan traps is important in determining efficacy, with yellow pans consistently sampling the greatest number of individuals in this system. This is consistent with previous studies which demonstrate that high reflectance colours are more effective (Vrdoljak and Samways, 2012). As well as the physical properties of different colours, their effectiveness may also be influenced by the relative abundance of flowers of the same colour in the surrounding landscape. It has even been suggested that catch sizes might be inversely proportional to the availability of flowers of the same colour in bloom in the vicinity (Cane et al., 2000), representing a 'dilution effect'. There was a high abundance of blue and white flowers in bloom throughout the flowering period at this site, such as common hogweed, *Heracleum sphondylium,* and common bluebell, *Hyacinthoides non-scripta*, and the relative paucity of yellow flowers. This, coupled with the consistent greater number of arthropods samples by yellow pan traps potentially provides support to the dilution effect hypothesis.

Another interesting and important result was that there was a low overlap in the taxa caught by different pan trap colours. In some instances, entire families were sampled almost exclusively by one colour, for example Panorpidae in blue or Sciomyzidae in yellow pan traps. The different sample profiles produced by each colour means that obtaining an extensive and representative sample requires the use of a combination of colours (Campbell and Hanula, 2007).

4.3.2. Importance of the canopy

A large proportion of the biomass and biodiversity of a mature temperate woodland occurs within the canopy layer (Halle, 1995) and this layer is particularly important for a large number of arthropods (Ulyshen, 2011). In order to accurately sample the habitat, it is, therefore, vital to include all layers across the vertical profile, including the canopy. Despite this, many studies of woodland biodiversity omit or have limited representation of the canopy layer due to inherent difficulties associated with sampling many metres off the ground. This is particularly true for temperate forests, where much less attention has been paid to canopy arthropods than for tropical forests (Ulyshen, 2011).

Studies have found mixed results in regard to patterns of abundance and diversity of arthropods across the vertical layers of temperate forests, with the canopy supporting higher diversity (e.g. Sobek et al., 2009), equal diversity (e.g. Stork and Grimbacher, 2006), or lower diversity (e.g. Hirao et al., 2009) in different situations. In the current study, the overall number of individuals sampled by canopy beating was considerably smaller than the numbers in the pitfall, Malaise and pan trap samples. This, however, likely reflects differences in sampling method (equipment used and sampling duration) rather than any true abundance gradient. Direct comparisons of abundance can only really be made between samples taken by the same sampling method, which does allow us to compare understory and canopy diversity at the BIFoR FACE site. We found that overall abundance and diversity of arthropods in the canopy was consistently greater than the understory, with the greater abundance of Araneae and Braconidae in the canopy driving this overall pattern. This is consistent with findings in similar forest ecosystems for spiders (Larrivée and Buddle, 2009), but not for parasitic wasps (Pucci, 2008). This is an important result in the characterisations of the particular patterns of diversity within temperate deciduous woodland. There are a number of variables which may be driving this difference, including height, structural differences, tree species, phenology and microclimate. Furthermore, the extent of interconnectivity between the canopy and other layers remains unclear. A high degree of connectivity could influence the sample profile due to movement of arthropods into and out of the canopy, meaning that the timing and conditions of sampling is particularly important.

4.4. Future impacts of eCO_2

This study also found no significant effect of eCO_2 on the abundance, diversity or phenology of arthropods over the course of the first 12 months of this 10-year experiment (Supplementary material 1). This result is unsurprising as it is expected that a highly complex, mature system such as this would take longer than 12 months to respond in a way that would be detectable in broad scale changes to arthropod

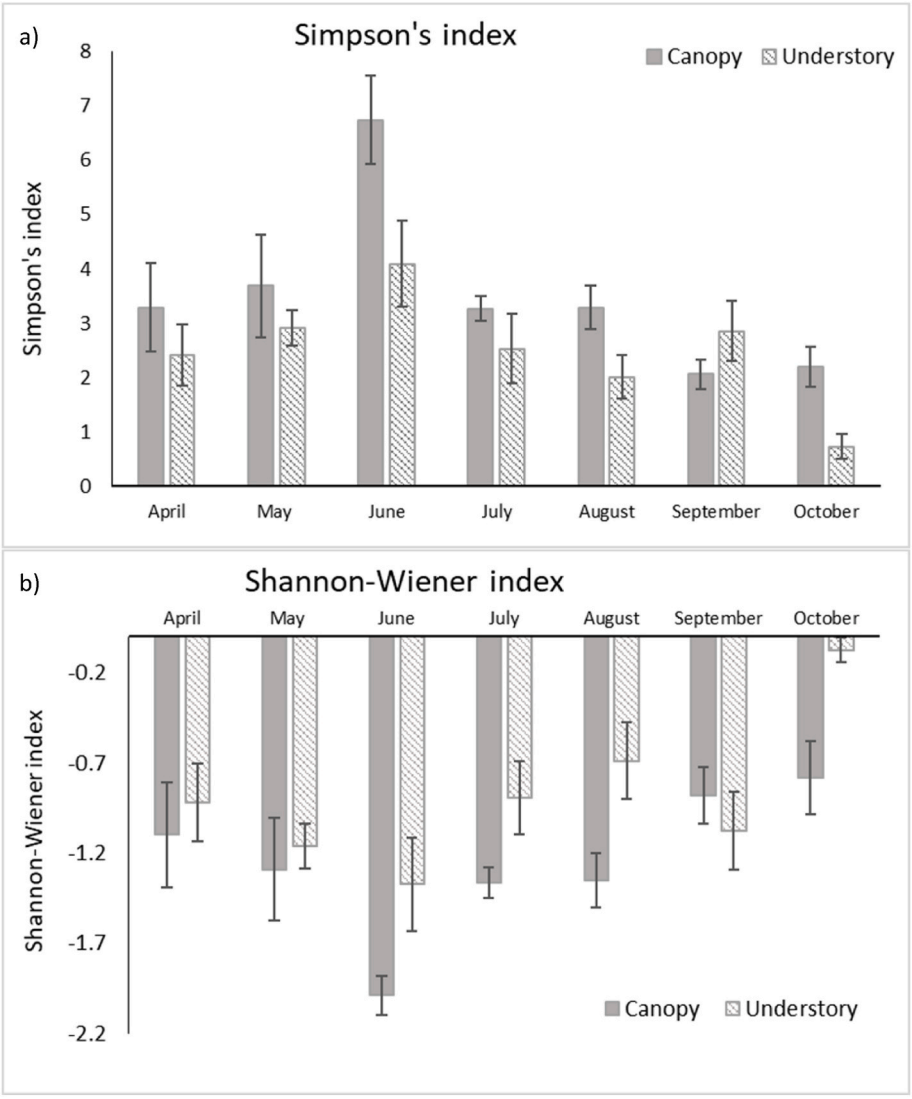

Fig. 5. Mean (± S. E.) Simpson's diversity index (a) and Shannon-Wiener diversity index (b) for canopy vs understory beating samples across the 7-month period (April to October 2017).

abundance and diversity. Despite this, the characterisation of the fauna provides an important baseline to allow the detection of future changes in response the eCO_2. Long-term monitoring of the experiment is ongoing, and the impact of eCO_2 can only be fairly assessed after multiple years of treatment.

5. Conclusions

This study has provided an evaluation of the sampling methods required to characterise arthropod biodiversity, abundance and phenology within spatially and temporally complex woodland systems. The comparison of sampling methods demonstrates that a combination of approaches is required to produce a comprehensive and representative sample of the whole ecosystem. There is no indication of sampling redundancy, as omission of any sampling method would result in the absence of one or more important functional groups. The variability in environmental conditions suggests that these variables should be measured with suitably defined spatial and temporal parameters relevant to the organisms to which they are to be related. The data supports the hypothesis that high reflectance colours are superior for pan trapping, but low species overlap between colours suggests that simultaneous deployment of a range of colours is required for more comprehensive pan trap sampling. Finally, the different layers of the woodland have been shown to produce significantly different samples, therefore a complete sampling programme across vertical layers of this woodland is required to adequately detect this structural diversity. In particular, this study suggests that the canopy is a key layer within a mature woodland ecosystem that may exhibit different patterns of faunal abundance and diversity compared to other habitat layers. Monitoring of arthropod populations continues at the BIFoR FACE site, which can be compared against this baseline to discern any potential impacts of eCO_2 on arthropod communities.

CRediT authorship contribution statement

Liam M. Crowley: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft. **Katharine Ivison:** Investigation. **Abigail Enston:** Investigation. **Dion Garrett:** Investigation, Formal analysis, Writing – review & editing. **Jon P. Sadler:** Methodology, Formal analysis, Writing – review & editing, Supervision. **Jeremy Pritchard:** Supervision. **A. Robert MacKenzie:** Supervision, Funding acquisition. **Scott A.L. Hayward:** Conceptualization, Methodology, Writing – review & editing, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.actao.2022.103873.

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