2015

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Harvey, K. (2015) 'Factors influencing canopy invertebrates in Britain', The Plymouth Student Scientist, 8(1), p. 123-157.
http://hdl.handle.net/10026.1/14088

The Plymouth Student Scientist
University of Plymouth

Factors influencing canopy invertebrates in Britain

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Abstract

Canopy research is becoming increasingly important as the extent of woodland habitats decreases and becomes more fragmented. Invertebrates are a diverse group of canopy fauna which are commonly used as bio-indicators to assess the health of woodland. However, current knowledge and understanding of invertebrate abundance and diversity in temperate forest canopies is limited and usually based on individual preliminary studies. In this study, data from six individual studies across eight locations, two in Scotland and six in the south-west of England were analysed to determine differences between tree species: oak (*Quercus robur*), scots pine (*Pinus sylvestris*) and beech (*Fagus sylvatica*); trapping methods: pitfall, fan and bubble; and regional variation in invertebrate abundance and diversity. After data were collated, sub-samples were selected to run statistical analyses to minimise variation of trapping method, region, season, and tree species. Invertebrates in oak were found to be more diverse and abundant compared to scots pine. Too few samples were conducted in beech trees for a fair comparison. Fan traps proved to be the most effective trapping methods as samples contained the greatest number and diversity of invertebrates. However, consideration of the objective of the sampling needs to be taken into account; if bark-dwelling invertebrates were the subject of investigation then bubble wrap traps would be the most suitable method. No definitive conclusion could be drawn from the regional analysis as tree species could not be kept consistent, oak was only sampled in the south-west of England and scots pine in Scotland. This study highlights the need for consistency and a rigorous and systematic sampling method in order to compare invertebrate communities in a highly dynamic environment.

Introduction

The forest biome

Forest biomes cover approximately 31% of the world's total land area, four billion hectares (FAO, 2011) and are considered one of the most threatened habitats (Ozanne *et al*. 2003). The global rate of decline in forest area is slowing, with 5.2 million hectares per annum lost in 2000-2010, compared to 8.3 million hectares per annum in the previous decade. This slowing can be attributed to the ceasing of deforestation in temperate forests and the expansion of forest cover, mostly plantations across Europe (FAO, 2011).

4,500 years ago most of Britain was wooded with species such as birch, pine, oak, hazel, lime and elm (Read and Frater, 1999; Rackham, 2001). Today only 13% of the area is wooded (Forestry Commission, 2013), due to clearance for fuel, farming and raw materials (Ozanne *et al*. 1999). Of this woodland, 68% comprises non-native, commercial plantations (Maleque, Maetc & Ishhii, 2009), which accounts for sitka spruce, *Picea sitchensis*, now being the most common tree in Britain (Read and Frater, 1999). In Scotland, plantations dominate the landscape leaving fragments of the original sessile oak and scots pine woods, alternatively known as the Atlantic Oakwoods and Caledonian Pinewoods, which are both priority habitats in Britain (*92/43/EEC*). In southern Britain, mixed lowland broadleaved woodlands of oak and ash with localised fragments of beech and hornbeam are dominant (UK NEA, 2011). The British woodlands are considered to be neglected, under-planted and fragmented, suffering from heavy grazing by sheep and deer (UK NEA, 2011; Moseley, Ray & Bruce, 2006).

The canopy environment and its invertebrate community

The canopy can be defined as 'the aggregate of all crowns in a forest stand' (Ozanne *et al*. 2003). It has high heterogeneity, both vertically and horizontally, creating a wide variety of niches (Maleque, Maetc & Ishhii, 2009). This is a contributing factor as to why it supports 40% of extant species globally, 10% of which are specialists to the canopy environment (Ozanne *et al*. 2003). In addition to biodiversity, the canopy is important for its ecosystem services, for example, its role in capturing carbon from the atmosphere, reducing the effects of anthropogenic activity on the earth's climate (Walsh, 2012). The canopy can be described as the 'engine room' of the forest ecosystem. It influences the productivity of the forest, being the main area of photosynthesis, locking energy in its leaves which provide food for herbivores and then in turn for predators (Lowman & Wittman, 1996). Also, when leaves fall from the canopy, they provide nutrients for the forest floor and are important for the recycling of nutrients within the ecosystem (Deady, 2009).

In 1983, Erwin described the forest canopy as the 'last biological frontier', implying there is a significant gap in our knowledge and understanding of the canopy environment. Accordingly, Ozanne *et al*. (2003) recently reiterated that the canopy remains one of the world's least-known habitats. In recent years, research into canopy biology – 'the study of mobile and sessile organisms and the processes that link them into an ecological community' - has increased (Lowman & Wittman, 1996). Reasons for this could be due to the improvement and diversification of methods to access the canopy environment (Deady, 2009; Barker & Pinard, 2001). There are a plethora of techniques to access the canopy, each with their own advantages and disadvantages to consider when conducting sampling. The increased awareness of the threat facing the canopy environment and its biological importance escalated the need to establish ecological fundamentals of the canopy environment, its processes and biotic community (Deady, 2009; Barker & Pinard, 2001; Lowman & Wittman, 1995, 1996). Canopy dwelling organisms are increasingly being used as bioindicators to assess the health of a forest community and to predict the changes within the community in relation to climate change and fragmentation (Deady, 2009; Kremen *et al.* 1993).

Wilson (1987) estimated there to be over 30 million species of invertebrates globally, although revised figures now suggest between 2-6 million (Ozanne *et al.* 2003), of which 1,065,000 have been described (Gaston & Spicer, 1998). Of those invertebrates living in forest biomes, up to 50% of invertebrates are found in the canopy and between 7-13% of them are canopy specialists (Ozanne, 2005). This abundance could be due to the fact that canopy invertebrates require very small niches, allowing a large population to be supported in a relatively small area (Wilson, 1987). Terrestrial arthropods have been described as “the little things that run the world”, (Wilson, 1987); they have a significant role in the provision of ecosystem services (Prather *et al*. 2013). Humans would not last more than a few months if invertebrates were to disappear (Wilson, 1987). Invertebrates are a direct food source for many species, whilst also indirectly influencing food availability, through herbivory, for other heterotrophs (Walsh, 2012). Invertebrates play a crucial role in the decomposition of organic material, ensuring the recycling of nutrients (Prather *et al*. 2013). This can occur in the canopy in the suspended organic matter and substrate. They also act as pollinators; the economic value of pollination services provided by insects in the US was estimated to be $12 billion per annum (Ozanne *et al.* 2003).

Invertebrates are useful as bioindicators, primarily because they are so diverse and specialised to certain environments and are therefore sensitive to change (Kremen *et al.* 1993; Ferris & Humphrey, 1999). Invertebrates are easy to sample. They have large populations, so only a small area needs sampling; and this can be easily repeated. Invertebrates are relatively easy to identify (Kremen, *et al.* 1993; Ferris & Humphrey, 1999). If identification is not possible in the field, there are fewer societal and ecological constraints associated with taking a specimen for further study (Kremen *et al*. 1993). Overall, these attributes make invertebrates reasonably cost effective to sample (Ferris & Humphrey, 1999). Beetles (Coleoptera) are a particularly diverse and well documented group of invertebrates, which are frequently used as indicator species. An example of an invertebrate used to determine the state or changes in a woodland is the family Carabidae (ground beetles). Their presence indicates an influence of an open habitat and their abundance tends to increase with increased fragmentation of a woodland (Maleque, Maetc & Ishhii, 2009). Another example is the Cerambycidae (longhorn beetles) the larvae of this family depend on wood and the adults are phytophagous (plant feeders) and pollinators (Maleque, Maetc & Ishhii, 2009). These beetles are regarded as oak specialists and their abundance is greater in mature oak woodlands (Maleque, Maetc & Ishhii, 2009).

Factors influencing invertebrate communities

The canopy environment is very dynamic with high spatial and temporal variation. Numerous micro-climates created by the variation of humidity, solar radiation, exposure to desiccation and temperature. Invertebrates can be sensitive to micro-environmental changes within the canopy as well as within and between forests. In a study by Golden and Crist (1999) significant differences were found in invertebrate communities between 1 hectare plots.

Tree species

Significant factors influencing canopy invertebrate populations are the species of tree, its maturity and abundance within the woodland. Southwood in 1961 studied various trees found in Britain and investigated the number of invertebrates associated with each species (Table 1). Oaks were found to have the greatest diversity of invertebrates compared to any other species (Southwood, 1961; Ozanne 1999; Hill, Roberts & Stork. 1989). Southwood (1961) proposed that the number of invertebrates associated with a tree species depends on the length of time a species has been in Britain. Oak is considered native (Table 1) and, because it has a long history in Britain, invertebrates have had a long period of time to adapt to the trees' available niches. This could be a contributing factor as to why it has the largest number of invertebrates associated with it (Table 1).

Table 1: The number of insects associated with common British trees and their history in Britain (adapted from Southwood, 1961).

Tree	History in Britain since Pleistocene	Number of associated insects
Oak *(Quercus)*	Native	284
Willow *(Salix)*	Native	266
Birch *(Betula)*	Native	229
Hawthorn *(Crataegus)*	Native	149
Poplar *(Populus)*	Native	97
Apple *(Malus)*	Native and introduced	93
Pine *(Pinus)*	Native	91
Alder *(Alnus)*	Native	90
Elm *(Ulmus)*	Native	82
Hazel *(Corylus)*	Native	73
Beech *(Fagus)*	Native	64
Ash *(Fraxinus)*	Native	41
Spruce *(Picea)*	Native in interglacial Reintroduced *c*.1500	37
Lime *(Tilia)*	Native and introduced native	31
Hornbeam *(Carpinus)*	Native	28
Larch *(Larix)*	Introduced 1629	17
Fir *(Abies)*	Native in interglacial Reintroduced *c*. 1600	16
Holly *(Ilex)*	Native	7

In 1999, Ozanne conducted a study comparing the invertebrate communities in conifer and broadleaf species in Britain. Ozanne concluded that the two tree assemblages have very different communities. The broadleaved species: oak, birch, hazel and sycamore, supported the greatest diversity of invertebrates; however, the coniferous species had the greatest density of invertebrates. A possible reason for this difference between coniferous and broadleaved species could be difference in structural diversity. Mature oak has a greater architectural diversity (Ohsawa, 2007) compared to scots pine, which is relatively simple (Kuuluvinen *et al*. 1998).

In addition to the tree species, the maturity of the tree influences the number of invertebrates it can support. Older trees tend to have greater architectural diversity (Ozanne, 1999) as in-canopy deadwood, bores and hollows develop which create more niches and conditions which more invertebrates can inhabit.

Woodland characteristics
As with an individual tree, a mature woodland will have greater structural diversity. Greater variation of tree species, tree age classes, abundance of deadwood, patches of clearings, all which offer a wider variety of niches for invertebrates to colonise (Maleque, Maetc & Ishhii, 2009). Ozanne (1999) highlighted the importance of forest density in influencing the invertebrate community. A denser forest structure, more likely found in a coniferous plantation, provides more stable climatic conditions and a greater leaf-area, which are a more favourable environment for generalist invertebrate species. Therefore, the importance of a conifer plantation should not be overlooked as it can support a greater density of invertebrates.

Fragmentation and isolation
Fragmentation or insularisation (creation of insulated habitats) creates an edge effect, which can be defined as the 'biotic and abiotic contrasts between adjacent habitats' (Foggo *et al*. 2001). This effect can result in changes in the abiotic conditions, for instance: greater exposure, solar radiation, temperature and temperature fluctuations as distance towards the edge decreases (Murica, 1995). These changing conditions affect the biotic community, directly influencing abundance and distribution of species and this affects predator-prey interactions (Murica, 1995). Invertebrate abundance declines rapidly at the extreme edge of the forest habitat (Ozanne *et al*. 1997).

Much of the areas of forest in Britain are fragmented with tracks or clearings through woodlands rendering them completely void of core conditions (Ozanne *et al.* 1997). Hedgerows are argued to be ecological corridors creating landscape connectivity, allowing species to migrate between woodland patches; however, they would have to be 50m in width to create the core conditions to allow core species to migrate (Ozanne *et al.* 1997).

Also, within these hedgerows are isolated mature trees, situated in hedgerows or grassland habitat (Allen, 2008). Such trees are called 'keystone' species because they support high biodiversity relative to their size (Gibbons *et al*. 2008). Mature trees have a large range of niches created from characteristics such as bore holes and hollows (Allen, 2008). Such species could be seen as a low cost approach to maintain or increase the diversity of an agricultural environment (Dunn, 2000). The keystone trees support different invertebrates dependent on the matrix in which they are situated; for example, if the tree is located in a heathland the invertebrate community is strongly influenced by heathland invertebrates (Ozanne *et al*. 1999).

Management practices
Clear-cutting a forested area decreases the invertebrate diversity; forest specialist species are replaced by open habitat species, like the Carabid beetle (Maleque, Maetc & Ishhii, 2009). Thinning of forests has proved to encourage a mixture of open habitat and forest species (Maleque, Maetc & Ishhii, 2009). Patches of open and closed canopy encourages a diverse ground flora community which can support open habitat invertebrates, like the Lepidoptera. For example, the pearl-bordered fritillary butterfly relies on violets (*Viola spp*) as its food source and these do not tolerant dense shade.

Coppicing is a traditional method of exploiting woodland resources and a management technique used in Britain (Burchett & Burchett, 2011). A study by Hill, Roberts and Stork (1989) suggested that coppiced birch, *Betula pendula,* woodland supported the greatest abundance and diversity of invertebrates, in comparison to chestnut. In addition, the age class of the coppiced trees did not have a significant effect on species diversity or abundance. Also, the species of coppiced understorey had an impact on the invertebrate abundance. Under an oak canopy, coppiced hornbeam, *Carpinus betulus,* supported the greatest density of invertebrates, followed by: hazel, *Corylus avellana*, then sweet chestnut, *Castanea, sativa*. This would suggest that in coppice management birch and hornbeam could be encouraged in regards to maintaining invertebrate diversity, (Hill, Roberts & Stork 1989).

Deer populations have been increasing in Britain for 200 years (Fuller & Gill, 2001). Excluding deer from woodlands can benefit invertebrate communities (Lindsay & Cunningham, 2009). Heavy deer grazing prevents a diverse field layer and saplings from establishing (Rackham, 2001) which would create a greater range of niches for invertebrates to inhabit.

In-canopy temporal and spatial variation
An additional factor to note which influences canopy invertebrate communities is the time of year (Southwood *et al*. 2004). Overall, fewer invertebrates are found during autumn and winter and greater numbers in early summer (Richardson *et al*. 1997; Golden & Crist, 1999). Southwood *et al*. (2004) conducted a year round study on invertebrates in a woodland in Oxfordshire. The phytophagous invertebrates were grouped into the following four functional guilds: chewing, sucking, leaf mining and gall forming insects. A peak in the abundance of chewing insects was noticed in May, this could relate to the increase in fresh growth, young leaves being more palatable (Southwood *et al*. 2004). Subsequent to the peak in chewing insects were peaks in sucking insects followed by leaf miners and gall formers later in the year (Southwood *et al*. 2004).

From a sampling objective, the aspect of a tree needs to be considered as invertebrate communities, abundance and composition, vary. In a study by Stork *et al*. (2001) a greater number of beetles, Coleoptera, were collected on the south side compared to the north side of the tree.

Canopy invertebrate sampling techniques
Sampling of invertebrate communities needs to account for their high biodiversity and the variation in their spatial and temporal distribution (Ozanne, 2005). Therefore

consideration needs to be given to the location of samples within the canopy and the time of year of sampling. Methods to trap invertebrates are varied, each method has a certain bias towards a particular community of invertebrate and its practical advantages and disadvantages (Ozanne, 2005). In order to gain a fully representative sample of invertebrates a combination of methods need to be deployed (Gray, 2011; Ozanne, 2005).

Fan or vortex traps are designed to actively draw invertebrates into a collection chamber by a motorised fan powered by a 12 volt battery (Figure 1). These traps can be deployed using a 'Jameson big shot' to establish a pulley system. To place the traps with greater accuracy, a specialist with a Basic Canopy Access Proficiency qualification can be employed to manually manoeuvre them into position. The fan trap is a relatively new method for sampling canopy invertebrates, however, it has proven to be most effective with great sensitivity to the diversity of invertebrates (Gray, 2011). One drawback highlighted in a study by Gray (2011) is that fan traps fail to capture invertebrates of low abundance /rare species and they favour flying invertebrates which may therefore be over represented in a sample.

Figure 1: Photograph of fan trap installed in oak canopy (Burchett, n.d.)

Pitfall traps can be deployed by the same means as the fan traps (Gray, 2011). Pitfall traps were originally used to sample ground invertebrates, in the canopy they are suspended in contact with a branch and the four corners the platform can be anchored to suitable points (Figure 2). Pitfall traps are a passive sampling technique, invertebrates simply fall into the collecting container therefore sampling would need to occur for a suitably long period. These traps are relatively easy to deploy and retrieve, and cheap requiring no external power or specialised equipment (Ozanne, 2005; Carrel, 2002). It is suggested that pitfall traps function better in broadleaved trees compared to pine (Carl *et al.* 2004). Pitfall traps are not comprehensive samples tending to be dominated by Coleoptera, Diptera and Hymenoptera – largely flying inverts (Ozanne, 2005).

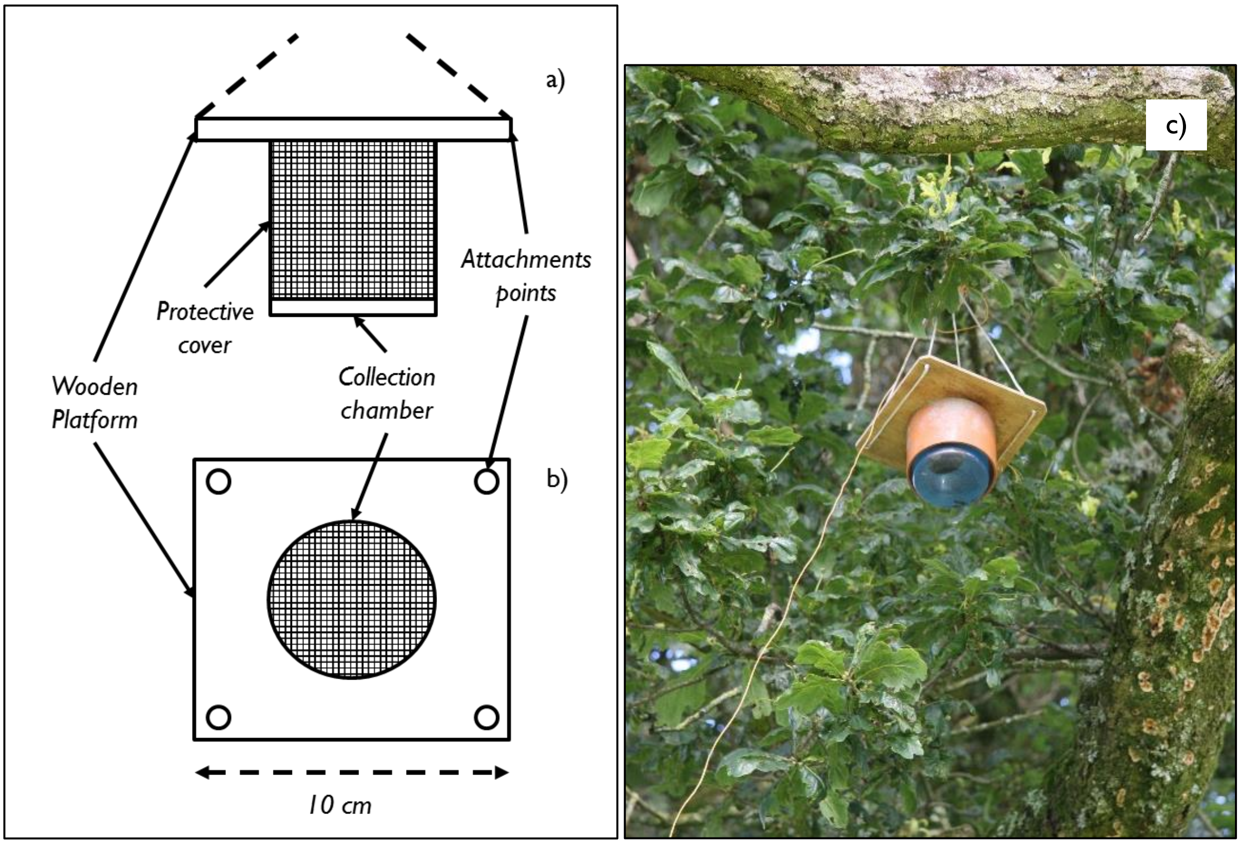

Figure 2: Schematic of a pitfall trap: a) Cross-sectional view, b) Aerial view, c) Photograph of pitfall trap installed in oak canopy (Burchett, n.d.)

Chemical knockdown is argued to be the most comprehensive and effective method for sampling canopy invertebrates (Ozanne, 2005). A chemical, usually a natural pyethrin or synthetic pyethroid, is used to temporarily paralyse the invertebrates. A fogging or misting machine is hoisted into the canopy to disperse the chemical. The invertebrates then drop out of the canopy into a collecting trap or sheet (Ozanne, 2005).The effectiveness of this technique is hindered by wind or rain which impede the chemical dispersal (Ozanne, 2005). However, chemical knockdown is not fully comprehensive as it is argued to favour slow moving invertebrates and under-estimate the populations of flying invertebrates (Gray, 2011). Also, bark and epiphyte dwelling or leaf spinning invertebrates are unlikely to be collected by this technique (Ozanne, 2005). Compared to fan and pitfall traps, chemical knockdown is the most expensive sampling method, however, unlike the fore mentioned techniques, time taken to conduct the sampling occurs in a matter of hours compared to days (Ozanne, 2005; Gray, 2011).

Bubble wrap traps (Figure 3) is the only method designed to sample bark-dwelling and poor dispersing non-flying invertebrates. Bubble wrap is laid on the trunk, bubble side to the trunk, covering an area 0.5-1m from the ground (Walsh, 2012). A black bin bag is then placed over the top of the bubble wrap to create a dark environment and all is secured around the trunk using string (Walsh, 2012). Samples are then collected after a few days using a pooter (Figure 3b).

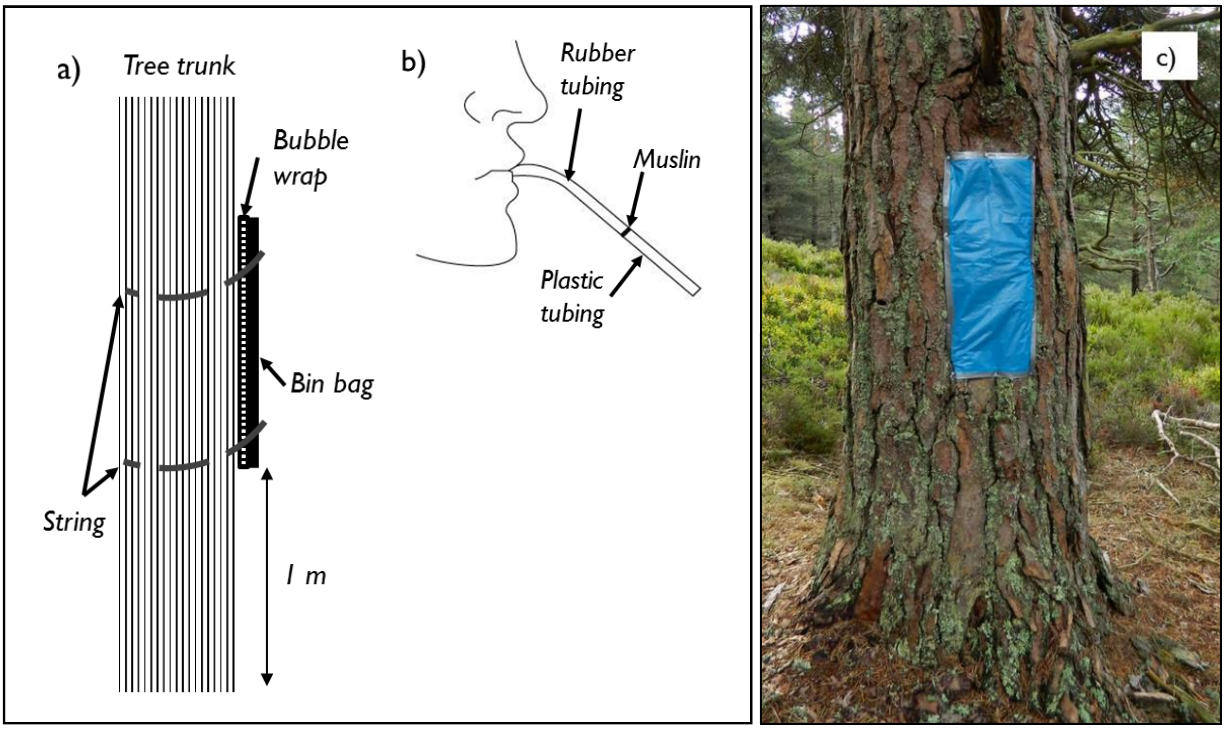

Figure 3: Schematic of a bubble wrap trap: a) Cross-sectional view, b) pooter, c) Photograph of bubble wrap trap installed on scots pine (Jovanovic, 2013.)

The majority of studies investigating canopy invertebrates are preliminary, and only conducted at one time of year and in one location. There is a need to combine studies to detect overall trends and regional differences in communities and verify preliminary observations.

The aims of this study are to:

1. Compare differences in invertebrate communities between oak (*Quercus robur* L.), scots pine (*Pinus sylvestris* L.) and beech (*Fagus sylvatica* L.)
2. Compare the effectiveness of pitfall, bubble wrap and fan traps in sampling invertebrate communities
3. Identify regional differences in oak canopy invertebrate communities between the south-west of England and Scotland

Methodology

Sampling sites

Data were collated from six studies conducted across Britain between 2007 and 2013 by Dr Stephen Burchett and a number of under-graduate and post-graduate students. In total, 8 locations were studied: two in Scotland, and six in the south-west of England (Figure 4). In total three tree species were sampled, oak (*Q. robur*), beech (*F. sylivatica*) and scots pine (*P. sylvestris*). A range of trapping techniques were used including pitfall, bubble wrap and fan traps. The habitat in which the tree being sampled was situated in varies. This is due to different aims of each individual study, for example, one was to compare the canopy invertebrate communities in trees in open grassland with those in a closed canopy; another compared communities in grazed and none-grazed woodland canopies. A summary of each study and their details can be found in Table 2.

Figure 4: Location of sampling sites (Google Maps, 2014)

Table 2: Summary of study details, (Natural England, 2014; British Geological Survey, 2014; Met Office, n.d.)

Collector	Region	Location	Season	Tree	Trap	Habitat	Geology	Altitude	Regional Climate (Annual average 1971-2000)			
									Temp-erature (°C)	Rain-fall (mm)	Sun-shine (hours)	Days of sleet/ snow falling
Castle, R., 2012	Devon, South west	Mount Edge-cumbe (SX 452523)	Winter	Oak (*Q. robur*) and beech (*F. sylvatica*)	Bubble wrap	Ornamental parkland, mixed broadleaf woodland	Staddon Formation- sandstone, siltstone and mudstone	116m	10.5-12	900-1200	1650-1850	0-10
Giles, C., & Kelf, R., 2013	Devon, South west	Yarner Wood, (SX 780787)	Summer	Oak (*Q. robur*)	Fan, pitfall, bubble wrap	North Atlantic oak woodland	Ashton Mudstone Member and Crackington Formation (undifferentiated) – Metamudstone and Metasandstone	198m	10-12	900-1200	1600-1650	0-15
Gray, N., 2011	Devon and Cornwall, South West	Bradmores Wood (SX 820726) Dartington Woods (SX 801633) Mount Edge-cumbe (SX 452523)	Summer	Oak (*Q. robur*)	Fan, pitfall, chemical knock-down	Neglected coppice mixed broadleaf woodland Ornamental parkland, mixed broadleaf woodland	Bradmores /Dartington woods: Gurrington Slate Formation Mt Edgecumbe: Staddon Formation- sandstone, siltstone and mudstone	Bradmores Wood: 83m Dartington Woods: 40m Mt Edge-cumbe: 116m	10-12	900-1200	1600-1850	0-15

Marks, N., 2007	Devon, South west	Bradmores Wood (SX 820726) Seale Hayne Farm (SX 828730) Yelland Cross Farm (SX 741623)	Late spring/ summer	Oak *(Q. robur)*	Pitfall	Neglected coppice mixed broadleaf woodland or field margins in conventional hedgerows and organic hedgerows, and open grassland	Seale-Hayne Farm/ Bradmores wood: Gurrington Slate Formation Yelland Cross Farm: Upper Devonian Slates	Bradmores Wood: 83m Seale-Hayne Farm: 79m Yelland Cross Farm: 173m	10-12	900-1200	1600-1650	0-15
Searle, D., & Sutton, L., 2012	Glen Moriston, west Scotland	Dundreggan Estate (NH 327145)	Summer	Scots Pine *(P. sylvestris)*	Fan, pitfall, bubble wrap	Remnant Caledonian forest of scots pine and ancient North Atlantic oakwood	Psammite	154m	5-7.5	1200 - 1700	700-1100	40-80
Jovan-ovic, N., 2013.	Aberdeen shire, east Scotland	Glen Tanar Estate (NO 454934)	Summer	Scots Pine *(P. sylvestris)*	Bubble wrap	Remnant Caledonian forest of scots pine	Granite, Biotite	330m	4.5-7	900-1500	1100-1300	50-130

Collation of data

Invertebrates were identified to at least family level. When all the data from the individually conducted studies were collated into a single database, replicates were combined and discrepancies, such as spelling of invertebrate families, amended. Once data were resolved to family level and uniformed, the total number of families per sample and total number of individuals per sample were calculated. Overall, 152 families and 6,713 individuals were recorded (Table 3 below).

Table 3: Summary of invertebrate families and individuals of each Order recorded in study

Order	Number of families	Number of individuals
Acari	1	6
Araneae	13	98
Coleoptera	31	569
Dermaptera	1	52
Diptera	38	2586
Entomobrymorpha	2	782
Gastropoda (class)	5	21
Hemiptera	13	287
Homoptera	1	2
Hymenoptera	24	1822
Isopoda	3	344
Julida	2	4
Lepidoptera	5	31
Lithobiomorpha	1	20
Megaloptera	1	1
Neuroptera	3	11
Opiliones	1	28
Poduromorpha	1	16
Psocoptera	2	9
Sarcoptiformes	1	11
Symphypleona	1	11
Trichoptera	1	1
Trombidiformes	1	1
Total	**152**	**6713**

Data Analysis

Entire dataset
A Non-metric Multi-dimensional Scaling (NDMS) ordination plot was created in Primer v6, as a preliminary analysis to identify similar clusters within the complete dataset.

An analysis of similarity (ANOSIM) was then carried out based on a Bray-Curtis similarity matrix. ANOSIM tests for the null hypothesis (H_0) that there is no assemblage differences between groups of samples specified by the levels of a single factor, in this case - tree species (Clarke & Gorley, 2006). If the actual R-statistic is outside of the null hypothesis R-statistic range (in this case: -0.03 – 0.04), then the groups are different. On the other hand, if the actual R-statistic was within the H_0 range, then the groups are similar. The significance level (%) determines if the difference/similarity is significant (Clarke & Gorley, 2006).

Sub-samples
The high variation within the dataset could distort the outcomes of analyses, e.g. the varying number of samples collected using different traps or in different tree species, and the different seasons in which the study was conducted. Therefore, to reduce variation the only samples included in the analyses were collected during the summer months and sub-samples were randomly selected to conduct further analysis. The influence of tree species was analysed using a sub-sample of 34 oak and 34 scots pine samples, each group studied using 17 pitfall and 17 bubble wrap traps. The trapping analysis, included 13 samples of each trapping method, focusing exclusively on oak canopies. Unfortunately, tree species could not be kept constant in the regional analysis because no oak samples were collected in Scotland. However, the sub-sample included 34 samples collected in the south-west of England and 34 samples collected in Scotland, each group included invertebrate samples captured using 17 pitfall traps and 17 bubble wrap traps.

To select the appropriate tests, the sub-samples were analysed to test whether the data followed a normal distribution. An Anderson-Darling test was conducted in Minitab v16 as part of a ‘graphical summary’ of the sub-samples (Dytham, 2011). All were found to have non-normal distributions (p-value <0.05), therefore non-parametric tests, the Mann-Whitney test and Kruskal-Wallis test, would need to be used in further analyses (Dytham, 2011).

The Mann-Whitney test was conducted in Minitab v16 on sub-samples with oak and scots pine tree species. It is the non-parametric equivalent of *t*-test, and tests for the null hypothesis that there is no significant difference between the medium of the two sets of data (Dytham, 2011). The Kruskal-Wallis test was used to analyse sub-samples which had more than two sets of data i.e. trapping methods: bubble wrap, pitfall and fan traps. It is the non-parametric equivalent of a one-way ANOVA (analysis of variance) (Dytham, 2011). It tests for the null hypothesis that all samples are taken from populations with the same median (Dytham, 2011).

Sub-samples were then run through a one-way SIMPER (similarity percentage) analysis in Primer v6. This quantifies the contribution of each family as a percentage of the sub-sample group (Clarke & Gorley, 2006).

Results

Influence of tree species on invertebrates

Tree species was expected to be the factor with the greatest influence on canopy invertebrate communities therefore an initial NMDS-ordination analysis was conducted on the entire dataset (Figure 5a).

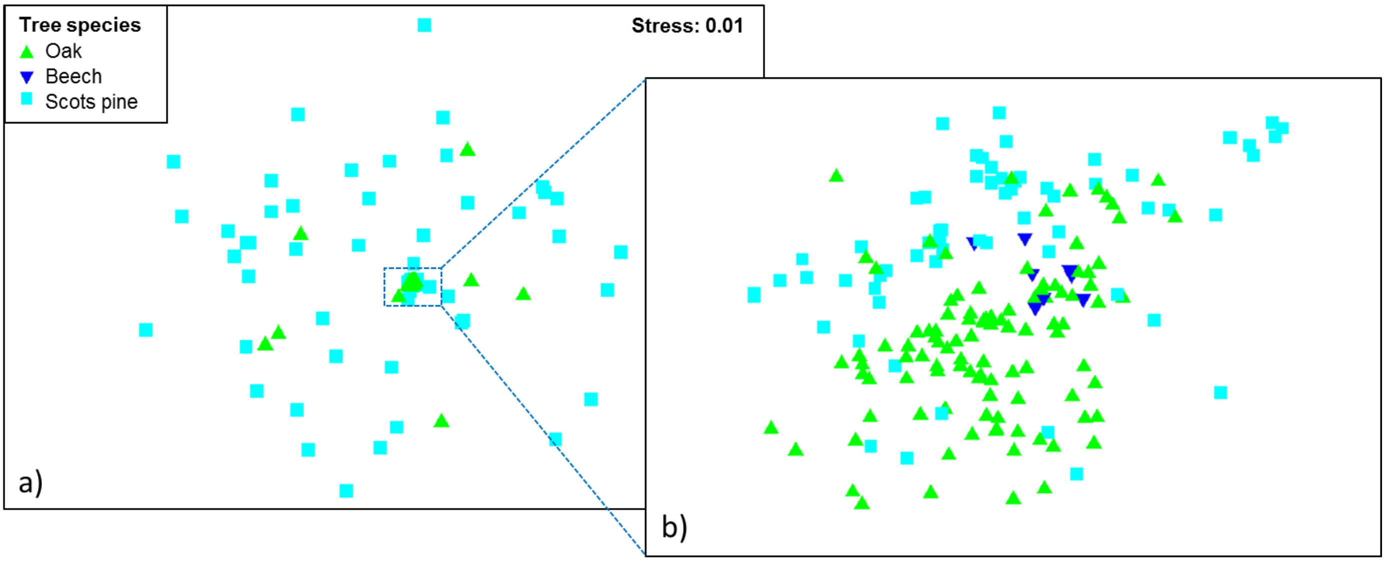

Figure 5: a) Non-metric Multi-dimensional Scaling plot based on Bray-Curtis similarity matrix after data was transformed. (Stress <0.05 gives an excellent representation with no misinterpretation), b) Zoomed to central cluster.

The NMDS-ordination plot suggested that samples of invertebrates from oak and beech were similar as they were indistinguishably clustered in the centre of the NDMS-ordination plot. Even when zoomed into the central cluster (Figure 5b), there were no obvious groupings of invertebrate samples relating to tree species. Between oak and scots pine there appeared to be high variation and no clear clusters between groups of tree species.

The analysis of similarity (ANOSIM) conducted on the entire dataset indicated that there was a difference between invertebrates recorded in different tree species (actual R-statistic 0.139 > H_0 range -0.03 - 0.04) (see Table 5). The significance level, 0.001, was less than 0.05, therefore the null hypothesis, that there are no assemblage differences between groups of samples specified by tree species, was rejected. Invertebrates in oak and scots pine trees were found to be significantly different (R-statistic 0.156>0.04, significance level 0.001>0.05).

When comparing beech with scots pine, there appeared to be a greater similarity between the two species compared to samples collected in a single tree species (R-statistic -0.004 with the H_0 range). However, this result was not statistically significant (significance level 0.517>0.05). Invertebrates samples in oak and beech were similar (R-statistic 0.003 is with H_0 range), but this again was not significant (significance level 0.468>0.05). A suggestion why no significant result was obtained when comparing beech samples to scots pine or oak could be due to the fewer samples collected in the beech trees (8 samples) compared to scots pine (120) and oak (116) included in the study.

Figure 6 suggests that oak trees support a greater diversity compared to scots pine because a greater number of families were recorded. Following a Mann-Whitney test this difference was statistically significant (p-value 0.0192<0.05).

Similarly to diversity, oak appeared to support a greater abundance of invertebrates compared to scots pine (Figure 7). The number of individuals recorded in oak and scots pine was statistically significantly different (p-value 0.0281<0.05).

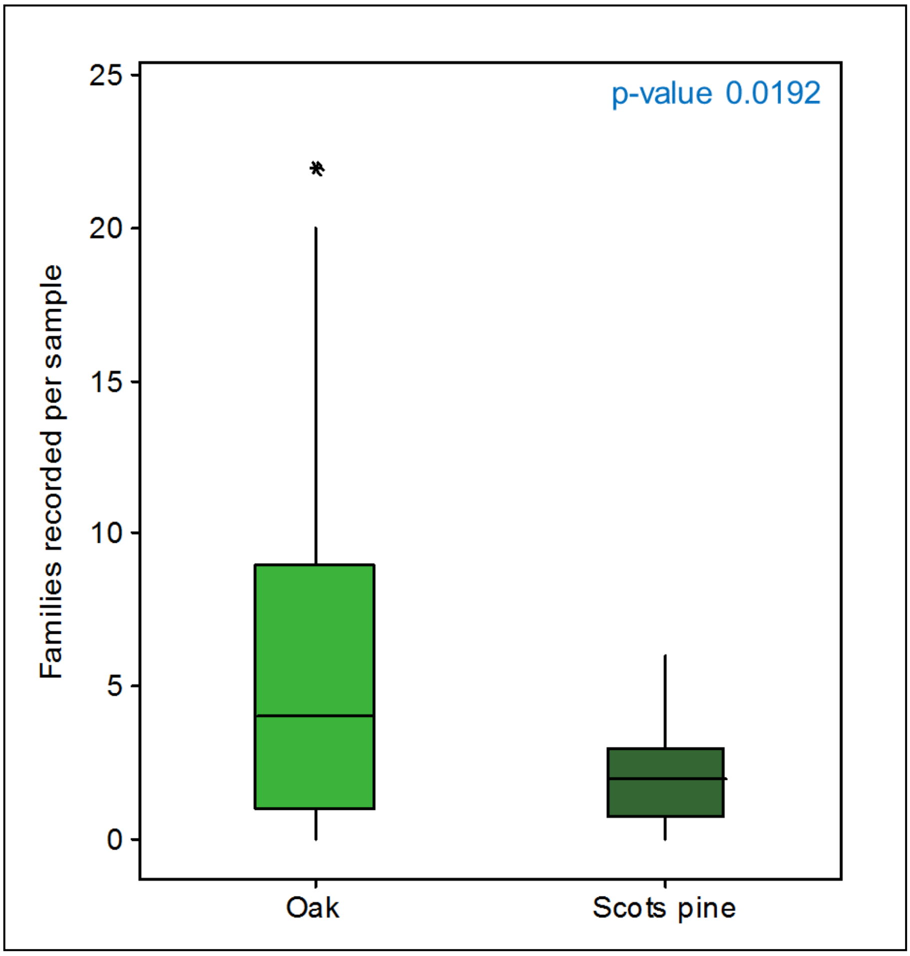

Figure 6: Number of invertebrate families recorded per sample (* indicates outliers). A non-parametric Mann-Whitney test was conducted to determine significant difference. (Sub-sample included 34 oak and 34 scots pine samples, each with collected using 17 pitfall and 17 bubble wrap traps).

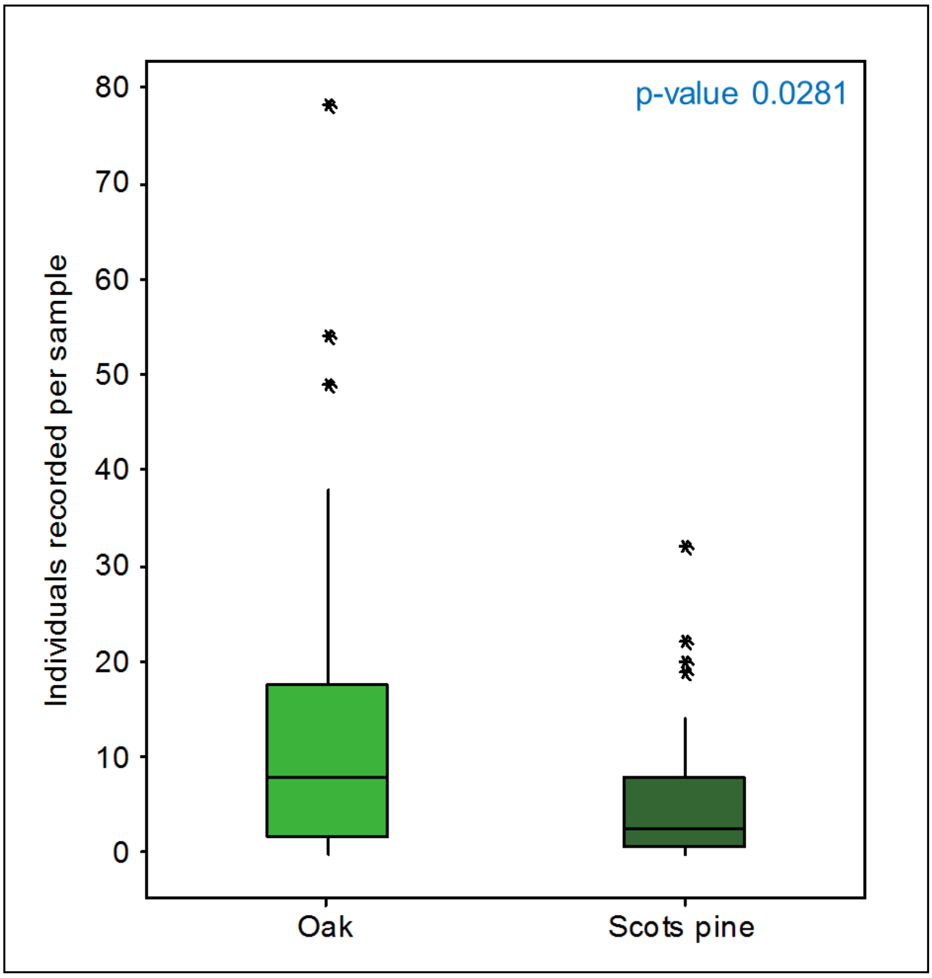

Figure 7: Number of individuals recorded per sample (* indicates outliers). A non-parametric Mann-Whitney test was conducted to determine significant difference. (Sub-sample included 34 oak and 34 scots pine samples, each with collected using 17 pitfall and 17 bubble wrap traps).

Figure 8 also indicates that oak supports a greater diversity than scots pine. Of the samples collected in oak, thirteen families contributed to 90% of the sub-samples whereas only five families contributed to 90% in scots pine. Scots pine samples were dominated by Ceratopogonidae and Formicidae, oak had a greater evenness of family contribution. Formicidae, Cecidomyiidae, and Aphididae were found in both tree species and could be argued to be generalist species. Bibionidae, Cicadellidae, Cynipidae, Dolichopodidae, Linyphiidae, Lithobiidae, Miridae, Phoridae, Porcelliondae and Sciaridae were only found in oak trees; these could be families' specialists to oak. Likewise, Ceratopogonidae and Chironomidae were only found in scots pine.

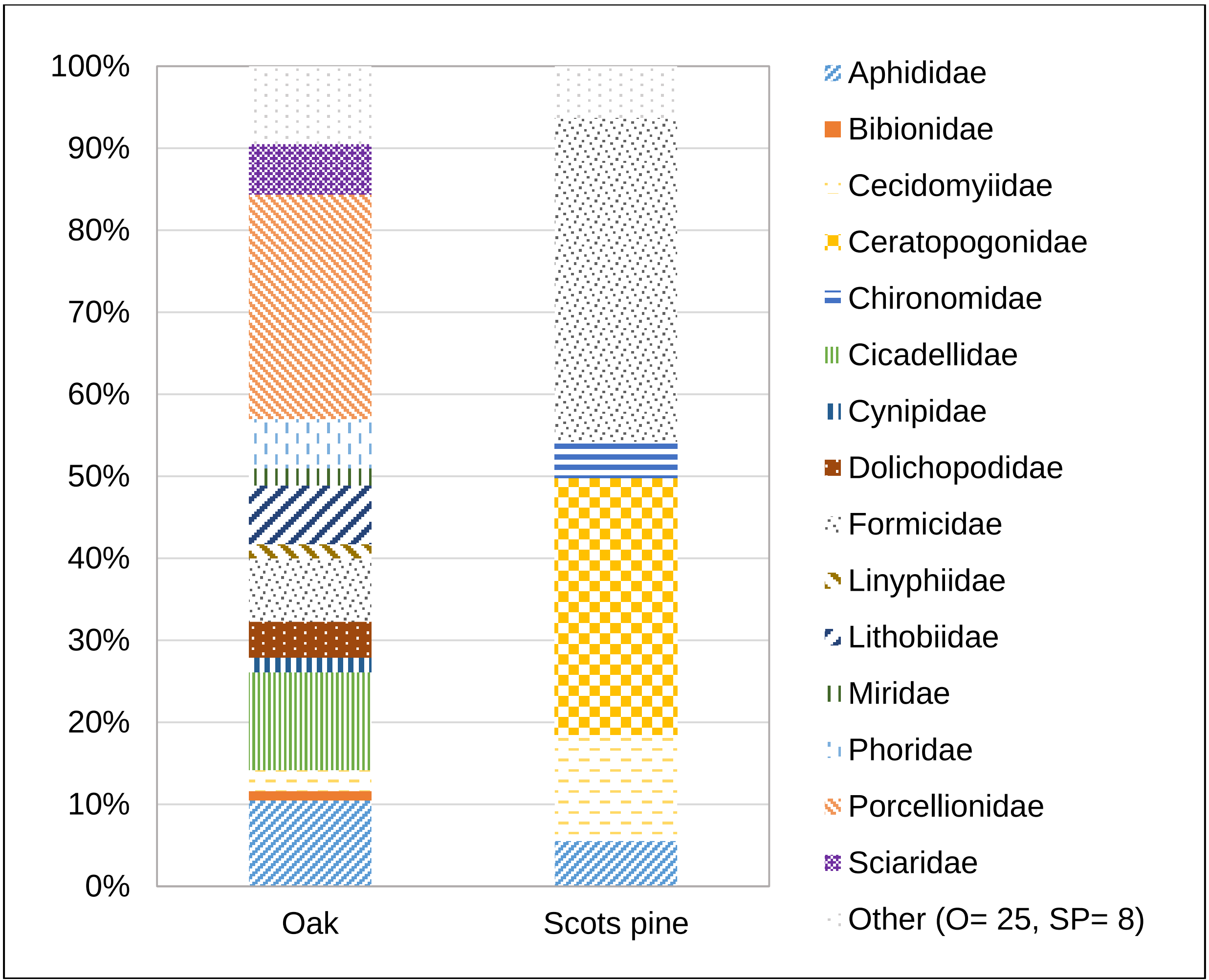

Figure 8: Contribution of invertebrate families to samples of oak and scots pine. (Conducted on a sub-sample including 34 oak and 34 scots pine, randomly selected, each group including 17 pitfall and 17 bubble traps. Families contributing to less than 90% of all families recorded were excluded, categorised as "Other". Similarity percentage (SIMPER) analysis conducted in Primer).

Effectiveness of trapping method

There was great variation between the number of families caught by each trapping method (Figure 9). There was a significant difference in the number of families caught by the three trapping methods (p-value $0.000<0.05$). Fan traps appeared to be most effective at trapping a greater range of families compared to pitfall and bubble wrap traps. Bubble wrap traps caught, on average, twice as many families compared to pitfall traps, nine and four respectively.

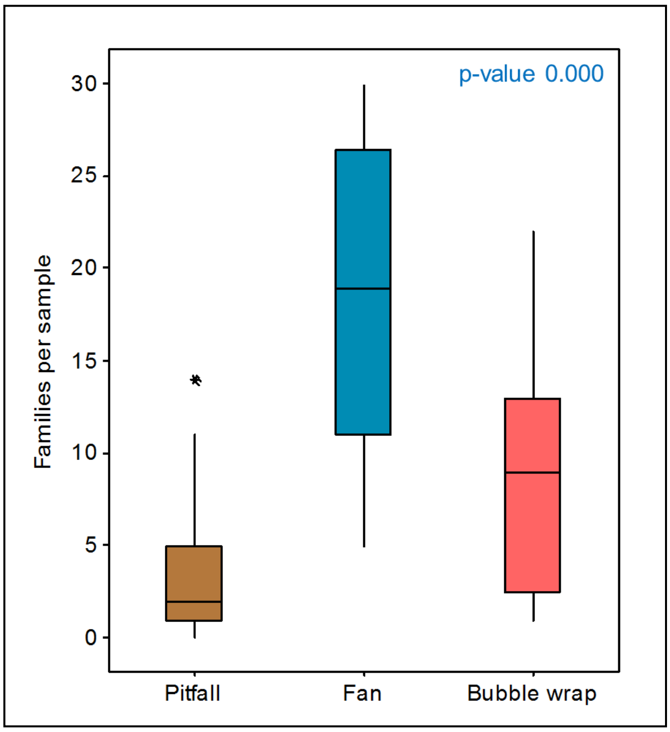

Figure 9: Number of invertebrate families caught in oak canopies using pitfall, fan and bubble wrap traps (* indicates outliers). A non-parametric Kruskal-Wallis test was conducted to determine significant differences. (Conducted on a sub-sample of 39 samples randomly selected to represent 13 samples of each trapping method).

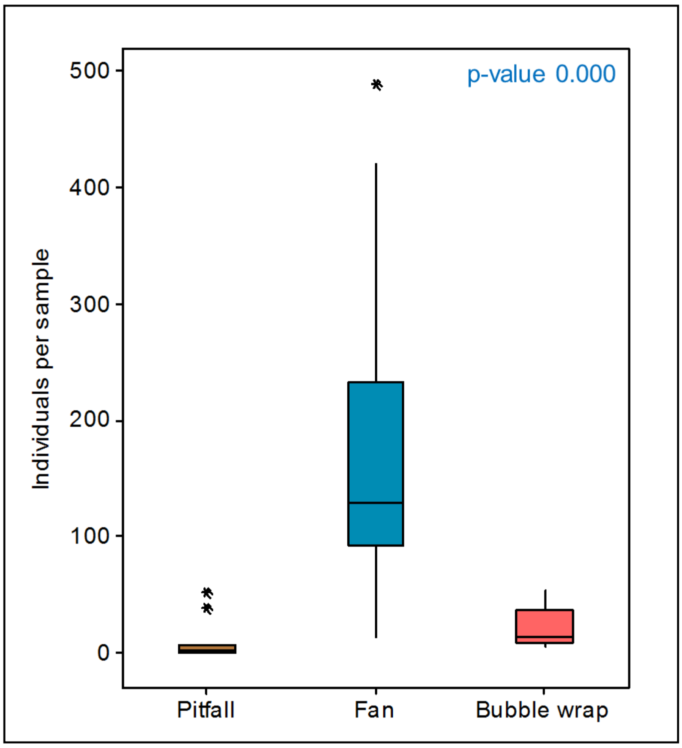

Figure 10: Number of individuals caught in oak canopies using pitfall, fan and bubble wrap traps (* indicates outliers). A non-parametric Kruskal-Wallis test was conducted to determine significant differences. (Conducted on a sub-sample of 39 samples randomly selected to represent 13 samples of each trapping method).

The number of individuals caught by each trap varied hugely from 0 to 400 (Figure 10). There was a significant difference in the abundance of invertebrates caught by each trapping method (p-value 0.000<0.05). As seen when comparing the diversity of families caught by the various trapping methods, fan traps caught the greatest abundance of invertebrates whereas fan and bubble wrap traps caught considerably fewer invertebrates.

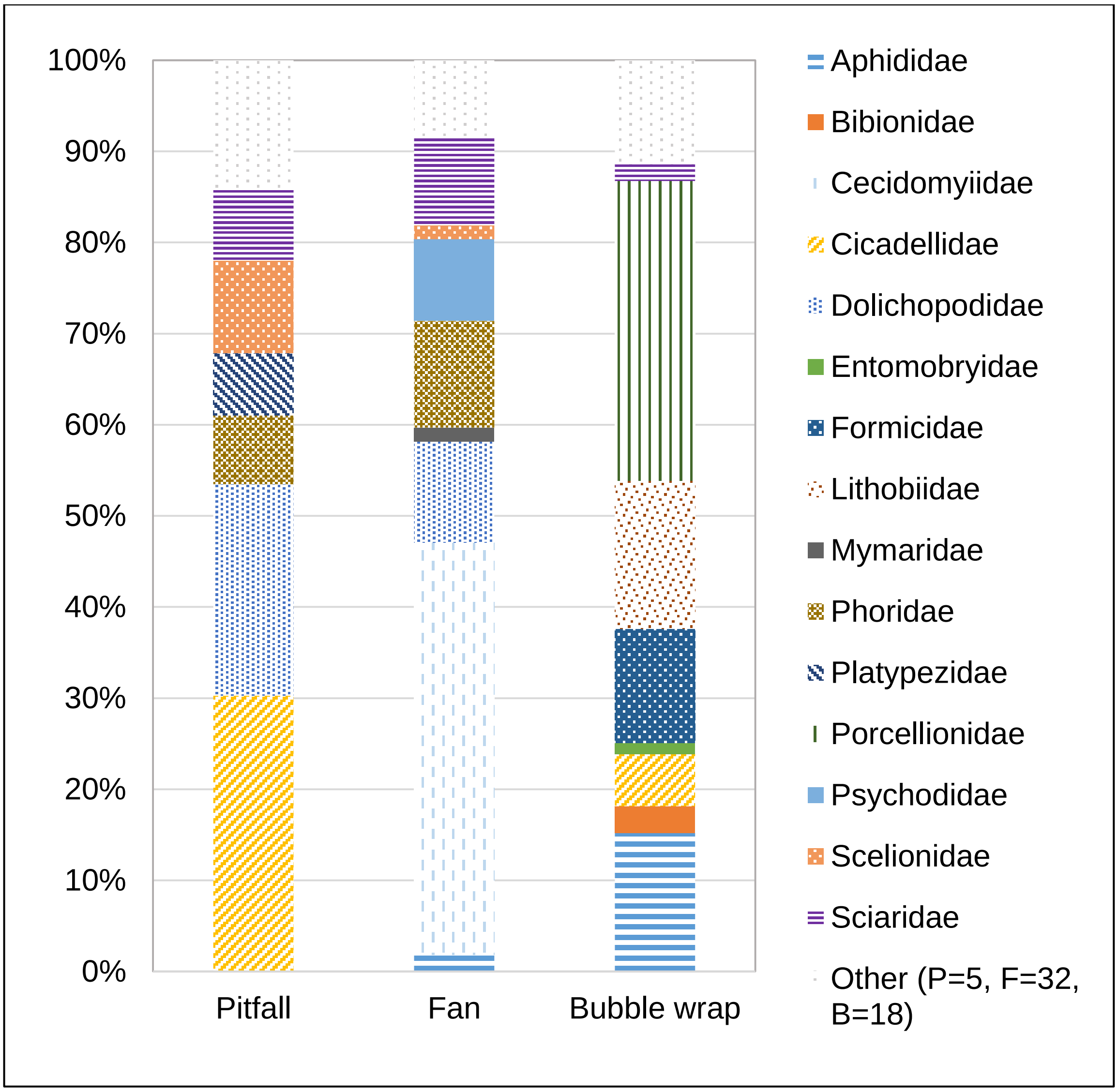

Figure 11: Contribution of invertebrate families to each trapping method used to sample oak canopies. (Each trapping method includes 13 samples randomly selected from main dataset. Families contributing to less than 90% of all families recorded excluded, categorised as "Other". Similarity percentage (SIMPER) analysis conducted in Primer).

When comparing the total number of invertebrate families caught by each trapping method (Figure 9) to the contribution of each family (Figure 11) there appeared to be a discrepancy. In Figure 9, pitfall and bubble wrap appeared be more effective relative to fan traps. However, Figure 11 shows that both bubble wrap traps and fan caught 8 families, while pitfall traps only 6 which contributed to 90% of the sub-sample. This discrepancy was due to the families which contributed a very small fraction to each sub-sample group being excluded from the SIMPER analysis, and categorised as "Other". Fan traps may have caught a greater diversity of families, however, the contribution of the majority of them was minimal. Cecidomyiidae dominated samples caught using fan traps, accounting for 45% of all families caught. Bubble wrap samples were dominated by Porcellionidae accounting for almost 30% of all families. The majority of families caught in pitfall traps were Cicadellidae and Dolichopodidae, combined accounting for over 50% of families.

Only species from the Sciaridae family were caught by all traps. Few families were caught by more than one trapping method, Aphididae, Cicadellidae, Dolichopodidae, Phoridae, Psychodidae and Scelionidae.

Regional variation in canopy invertebrates

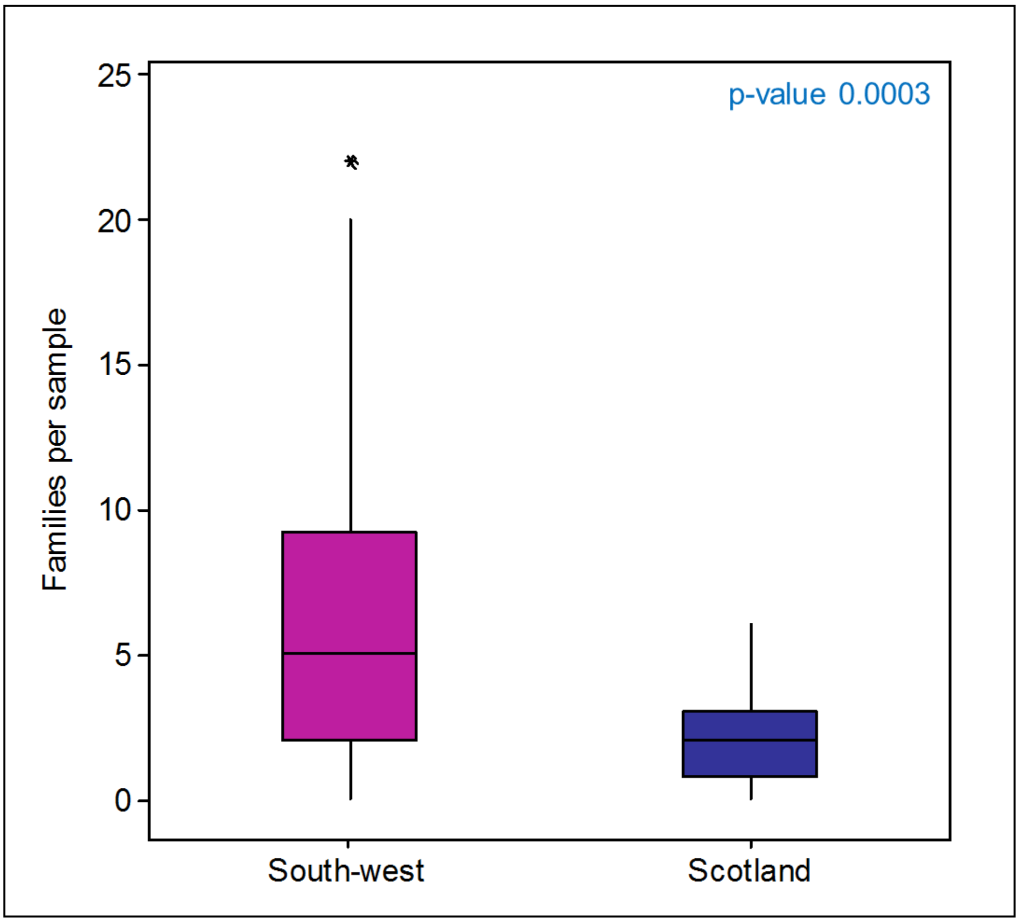

Figure 12: Number of families recorded in the south-west and Scotland (* indicates outliers). A non-parametric Mann-Whitney test was conducted to determine significant difference. (Sub-sample included 34 oak in the south-west and 34 scots pine in Scotland samples, each with collected using 17 pitfall and 17 bubble wrap traps).

The diversity of invertebrates in the south-west of England was much greater compared to Scotland (Figure 12), on average five families were recorded in samples collected in the south-west of England and only two in Scotland. This difference was statistically significant (p-value 0.0003<0.05).

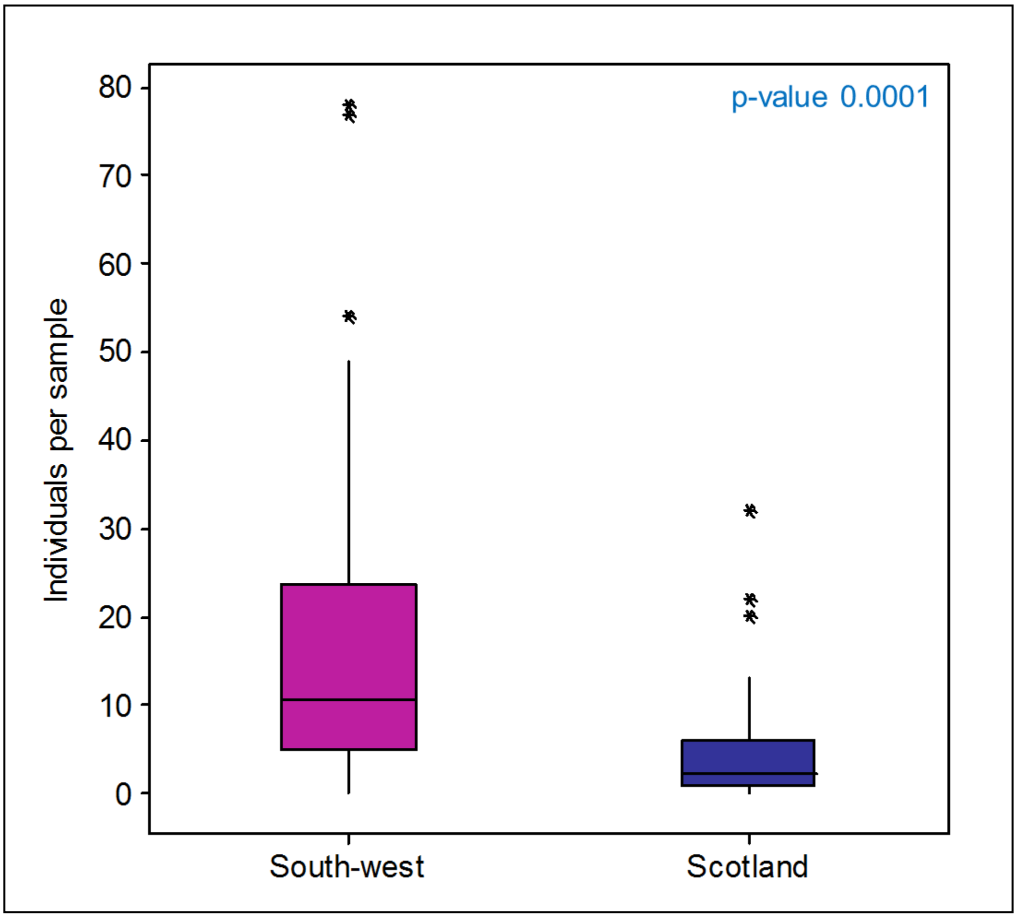

Figure 13: Number of individuals recorded in the south-west and Scotland (* indicates outliers). A non-parametric Mann-Whitney was test conducted to determine significant difference. (Sub-sample included 34 oak in the south-west and 34 scots pine in Scotland samples, each with collected using 17 pitfall and 17 bubble wrap traps).

Significantly more individuals were recorded in south-west of England compared to Scotland (p-value 0.0001<0.05). The average abundance of canopy invertebrates was five times greater in the south-west England than as recorded in Scotland (Figure 13).

Figure 14 indicates that the diversity of invertebrates is substantially greater in the south-west of England in comparison to Scotland. Four families contributed to 90% of all families recorded in Scotland, over 85% is accounted for by Formicidae and Staphylinindae. These two families were also the only families found in both regions. In the south-west of England, 12 families contributed to 90% of all families recorded. The most dominant families, Formicidae and Sciaridae, did not account for more than 20%, suggesting the south-west of England supported a greater evenness of families.

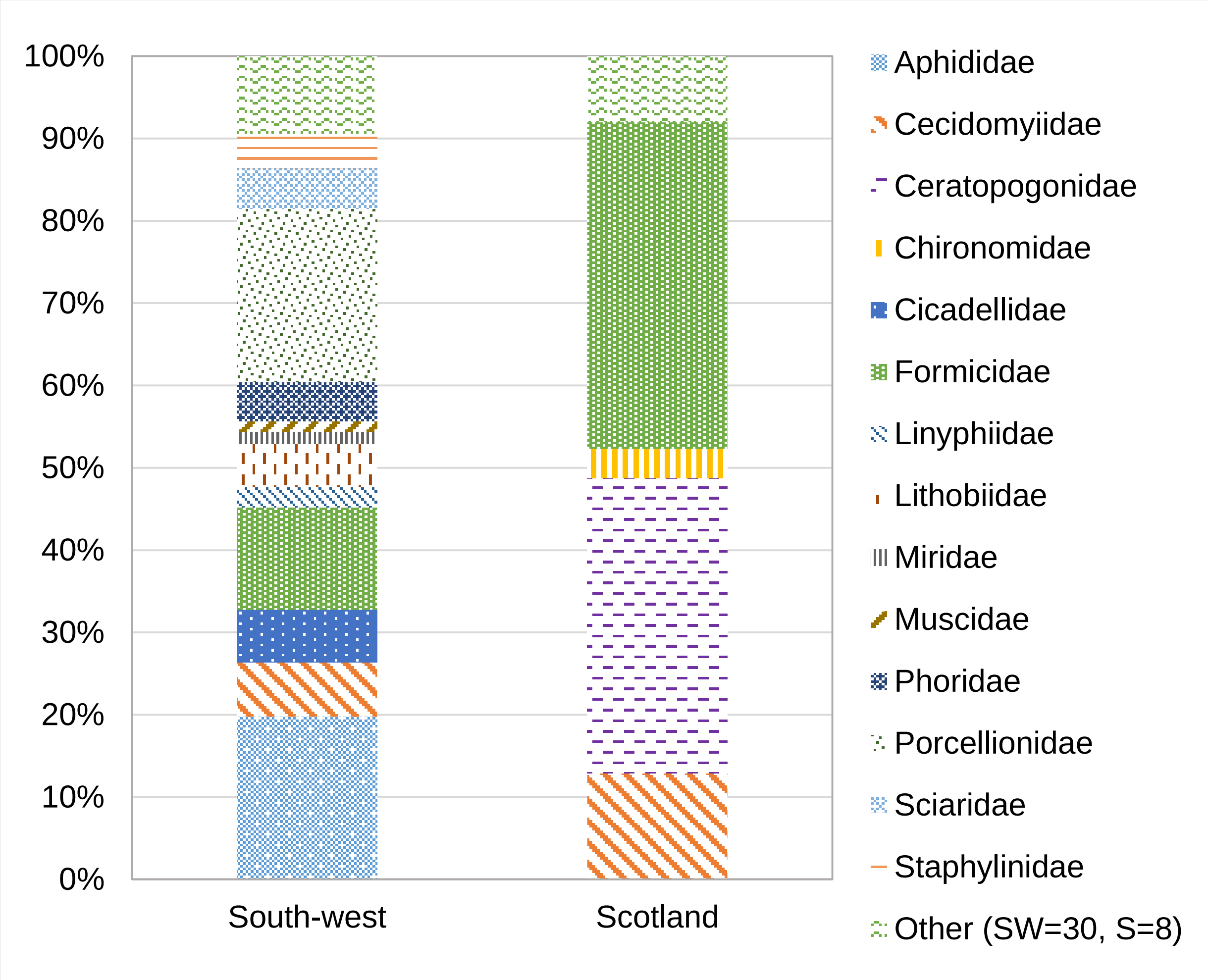

Figure 14: Contribution of invertebrate families to samples collected in the south-west and Scotland. (Conducted on a sub-sample including 34 oak in the south-west and 34 scots pine in Scotland, randomly selected, each group including 17 pitfall and 17 bubble traps. Families contributing to less than 90% of all families recorded were excluded, categorised as "Other". Similarity percentage (SIMPER) analysis conducted in Primer).

Discussion

Influence of tree species and the forest ecosystem

A clear difference between canopy invertebrate communities in oak and scots pine was evident in both analyses. Oak trees supported significantly more individuals and number of families compared to scots pine. Also, oak trees appeared to support a greater evenness of families as samples were not dominated by one family, whereas scots pine samples were dominated by Formicidae and Ceratopogonidae. Similarly, oak samples had a larger number of invertebrate families in the "Other" category accounting for 10% of the total contribution of families, compared to scots pine. These families may only be present in low abundance, therefore it could be argued the oak trees support a higher number of rarer invertebrate families compared to scots pine. These results agree with the hypothesis that deciduous tree species support a greater diversity of invertebrates (Southwood, 1961; Kennedy & Southwood, 1984; Ozanne, 1999; Ohsawa, 2007; Allen, 2008; Fuller, Oliver & Leather, 2008).

A reason why oak trees were able to support a greater diversity of families could be due to their greater structural complexity (Ohsawa, 2007) compared to scots pine trees, which are considered to have a relatively simple structure, especially those grown in a commercial plantation (Kuuluvinen, *et al.* 1998). However, naturally developed scots pine forests have shown to have complex small-scale structural heterogeneity (Kuuluvainen, *et al.* 1998). The greater the structural complexity, the greater the number of potential niches that are available for species to colonise.
An alternative explanation for the diversity in oak is that deciduous species are more appealing to phytophagous invertebrates because they are more palatable (Ober & Haynes, 2008). Deciduous foliage contains higher concentrations of nitrogen, which is a limiting nutrient for many phytophagous invertebrates, therefore deciduous trees offer a higher quality food resource compared to coniferous trees (Ober & Haynes, 2008). Also, coniferous foliage contains higher levels of resins and lignin, secondary defence compounds to discourage herbivory, which again makes deciduous species more appealing (Ober & Haynes, 2008). The greater number of phytophages in turn attracts other invertebrates, such as predatory Coleoptera.

Southwood (1961), and subsequently Kennedy and Southwood (1984), produced a paper quantifying the number of invertebrates associated with specific tree species. Kennedy and Southwood (1984) suggested the length of time a species has been in Britain influences the number of invertebrates associated with it. The argument was based on the principle that species richness will rise (at a slow rate) as a function of both area and time. In Britain, area is constant, therefore colonisation of host tree depends on the length of time the invertebrates have been exposed to the host tree, in other words, the length of time the tree species has been in Britain (Kennedy & Southwood, 1984). Oak (*Q. robur*) and scots pine are both considered native and to have been present in Britain since the Pleistocene (Southwood, 1961, Table 1).

Kennedy and Southwood (1984) suggested that the abundance or range of the host species was the most significant factor determining the diversity of invertebrates associated with a tree species. A larger range would include a wider range of habitats and therefore a greater variety of potential niches. Today, oak and scots pine have a similar range across Britain, extending from the south-west of England to the northern points of Scotland (Figure 15). However, given the location of the sites included in this study, oak is more abundant in the south-west of England compared to scots pine and the reverse in Aberdeenshire and central Scotland (Figure 4). This would indicate that the number of invertebrates associated with oak would be higher in the south-west of England compared to Scotland, and more invertebrates would be associated with scots pine in Scotland compared to those found in the south-west of England.

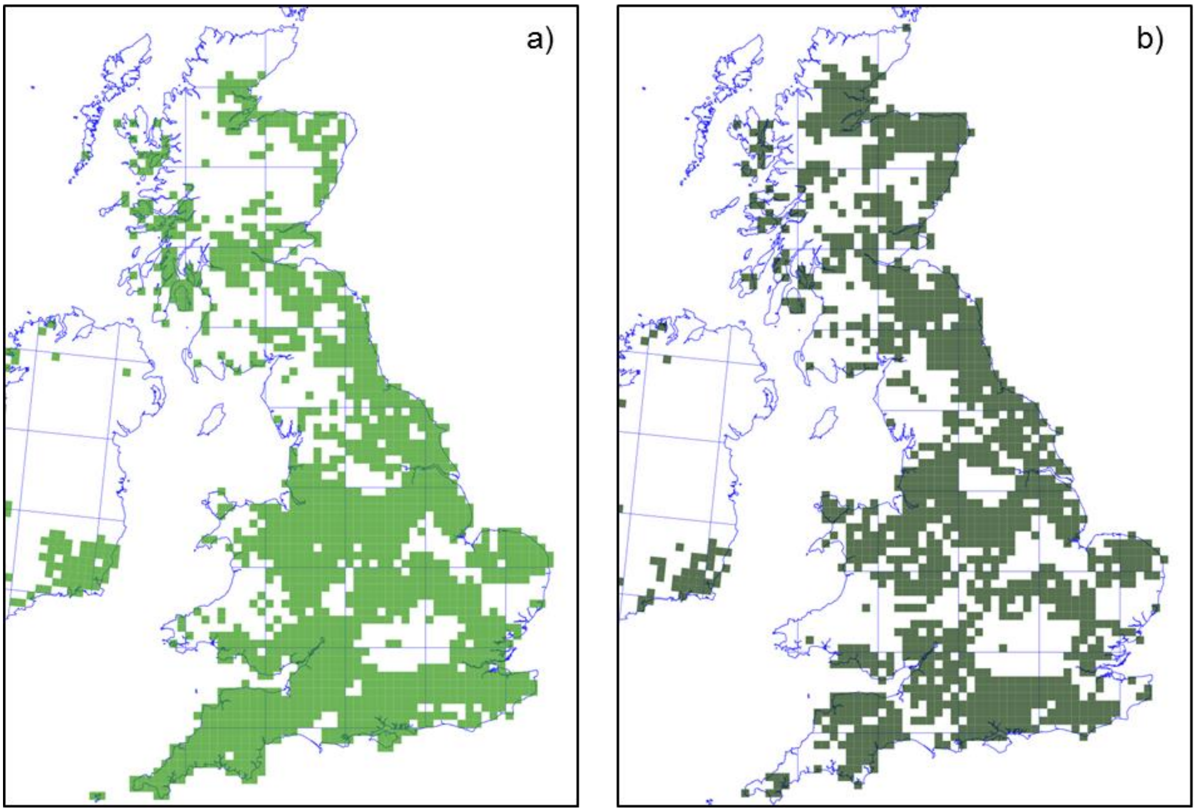

Figure 15: a) The distribution of *Q. robur* across Britain in 2010, b) The distribution of *P. sylvestris* across Britain in 2010 (Botanical Society of Britain and Ireland, 2014).

Overall, according to the Forestry Commission (2003) the area covered in scots pine in the high forest is greater than oak (219,438 ha and 206,154 ha respectively). This would imply that, because scots pine covers a greater area than oak, they would support more invertebrates. What must be considered is the nature of the forest, scots pine was almost removed from Britain until it was reintroduced in commercial plantations (Jordan, 2012). As previously mentioned, commercial scots pine trees are less structurally complex, this could account as to why oak, which is not as commercially grown (Forestry Commission, 2013), supports a greater diversity of invertebrates despite its lower abundance compared to scots pine.

When comparing beech with oak and scots pine no significant relationship was found due to the relatively few number of samples collected in beech in the entire dataset. However, invertebrate communities between oak (*Q. robur*) and beech (*F. sylvatica*) were similar, and this could be attributed to the taxonomic relatedness of the two species (Figure 16). Species of closer taxonomic relatedness are more likely to share the same chemical and physical features and therefore are likely to support similar invertebrate communities (Kennedy & Southwood, 1984).

The NMDS-ordination plot would suggest that tree species does not account for the variation in invertebrate communities between the samples included in this study, as there are no obvious clusters (Figure 15). The canopy is such a dynamic and complex environment, there are numerous factors which could influence its invertebrate community besides tree species, and these could have compounding impacts so that direct influences are indistinguishable.

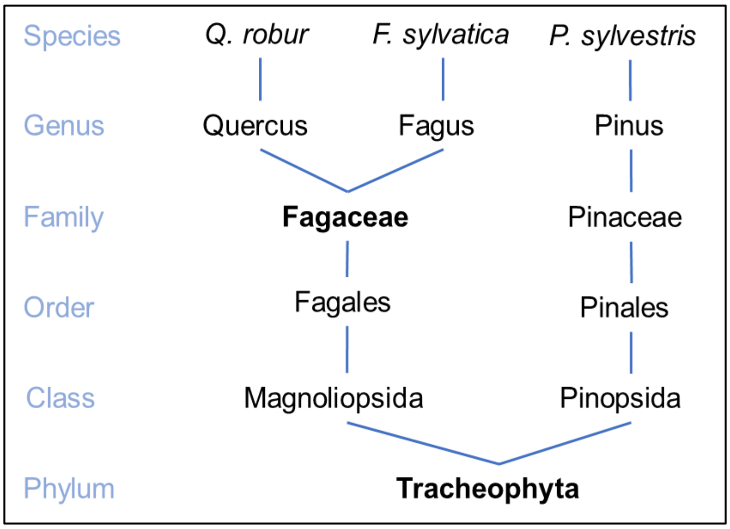

Figure 16: Taxonomic relatedness of Q. robur, *F. sylvatica* and *P. sylvestris*

A widely agreed influential factor is the age or maturity of the tree or stand. Generally, the older the tree, the more invertebrates are associated with it. Unfortunately, the data included in this study did not contain such detail, therefore analysing the influence of tree maturity was beyond the scope of this study. Older trees (150+ years) have more structural diversity as they mature (Allen, 2008). For example, they may develop bore holes, hollows and in-canopy deadwood, and this increases canopy heterogeneity creating more niches for organisms to colonise (Allen, 2008; Fuller, Oliver & Leather, 2008; Alexander, Butler & Green, 2006; Speight, Hunter & Watt, 2008). Isolated mature trees found in the hedgerows and grasslands of the agricultural landscape are particularly high in biodiversity (Deady, 2009; Dunn, 2000). For this reason they are called ‘keystone’ species because of their importance in the landscape of supporting biodiversity (Gibbons *et al*. 2008). In this study, the trees sampled were located in a variety of habitats: grassland, closed canopy, hedgerow, grazed and un-grazed woodlands. This variability was inherent throughout and was a major limitation of this dataset, because each of the individual studies included had their own aims of investigation. Therefore there could be influences from other habitats on the canopy invertebrate sampled in this investigation. For example, in a study by Ozanne *et al.* (1999) the canopy invertebrate community of an isolated tree had an influence from the surrounding heathland invertebrates.

Isolated trees are able to reach their full fruiting and seeding potential as there is relatively little competition with other trees compared to those within a forest stand, which allows such trees to support a greater abundance of invertebrates which depend on fruits and seeds (Alexander, Butler & Green, 2006).

The same concept can be applied at a forest stand scale. Mature woodlands can also have greater diversity and variation of tree species, age class, abundance of deadwood, patches of open and closed canopies. In Oregon, US, Schowalter (1995) investigated the differences in arthropod communities in stands at three stages of maturity and harvesting: intact Douglas-fir and western hemlock old growth (>400 years-old) compared to natural mature partially harvested old growth (150 year-old) and regeneration (10-20 year-old) Douglas-fir only plantations. The old growth canopies had less variation in arthropod diversity compared to the 150 year-old stand, and both the older stands had substantially greater arthropod diversity compared to the young regenerating plantation. One exception to this relationship was found in a study by Hill, Roberts and Stork (1989) in Blean woods in Kent, England. They investigated the variation of the invertebrate groups (Diptera, Hemiptera and Arachnid) total invertebrates and total biomass between various coppiced species (sweet chestnut *Castanea sativa* and birch *Betula pendula*), coppice age and mature coppice understorey species (hazel *Corylus avellana,* hornbeam *Carpinus betulus* and sweet chestnut) under mature oak standards. They concluded that age class of the coppice stand had little impact on the invertebrate community. The species of coppice had a significant impact as did the species of coppice understorey. Birch coppice stands had a greater density and biomass of invertebrates compared to sweet chestnut, and understorey canopies of hornbeam had a higher density and abundance (total biomass) of invertebrates compared to hazel and sweet chestnut.

The understorey of a forest was proven to have a significant influence on the canopy invertebrate community. Commonly in Britain, the climax oak (*Quercus*) woodland has a birch (*B. pendula*) understorey which loses it foliage before oak species and, as a result, some invertebrate species migrate from the birch to oak canopies to make the most of the foliage (Stork *et al.* 2001). Therefore depending on the time of year and the understorey species, different invertebrate communities can be seen in oak canopies.

Influence of management

The management of a woodland can have a significant influence on the invertebrate community and this effect can be lasting. Although, the study mentioned previously by Schowalter (1995) found no significant difference between invertebrate communities in the intact mature Douglas -fir and hemlock stand (>400 years- old) and the 150 year-old Douglas -fir mature and partially harvested stand, it would imply that the invertebrate community may resemble old-growth woodland after 150 years. Enhancement of plantations has also been shown to encourage the colonisation of an invertebrate community consistent with those found in naturally established woodlands (Moffatt, Morton & McNeil, 2008). Enhancement methods can include: soil seed bank transferral, direct sowing and planting or large scale translocation of ground flora. A more diverse ground flora (field layer) is able to support more invertebrates because it creates more niches. Natural clearings are typical in ancient woodlands as the forest goes through a natural cycle of tree fall creating openings in the canopy and regeneration by understorey saplings (Rackham, 2001). This dynamic matrix of openings and closed canopy supports a greater diversity of woodland invertebrates. Clearings support open habitat species whereas the denser canopy provides the conditions required by forest specialists (Maleque, Maetc & Ishhii, 2009). Species which rely on the creation of clearings include many butterflies (Lepidoptera), e.g. the pearl-bordered fritillary (*Boloria euphrosyne*) which are dependent on open sunny woodland glades and woodland edges where violets (*Viola spp*), their sole food source, can grow (Forestry Commission Scotland, 2009). Active thinning of woodlands or coppicing can also help to encourage ground flora diversity (Maleque, Maetc & Ishhii, 2009).

Deer population sizes have increased across Britain for the last 200 years due to: increased habitat area, favourable agricultural practices like growing of winter cereals which provide a source of food, large predator elimination, increased controls on hunting which focus on killing males rather than females with calves, reduction in lowland livestock (competitors) and milder winters reducing over-winter mortality (Fuller & Gill, 2001). Deer have a detrimental impact on the richness of woodland biodiversity including invertebrates due to heavy grazing and browsing (Fuller & Gill, 2001; Lindsay & Cunningham, 2009). Grazing prevents the establishment of saplings and other species in the field layer (Rackham, 2001) which would otherwise increase the diversity of niches able to support a rich invertebrate community.

Trapping effectiveness

Of the three trapping methods used in this study, fan traps were found to be the most effective by capturing the greatest diversity of invertebrate families and the greatest number of individuals in British oak canopies. Also, the greatest number of invertebrate families contributing to the remaining 10%, "Other category", were recorded in fan traps. These families may only be present in low abundance therefore fan traps could be argued to be better at capturing low abundance invertebrates compared to pitfall and bubble wrap traps. It is important to note the high variation in the number of families and individuals caught between the three trapping methods and within each method. One explanation why fan traps collected a greater abundance of invertebrates could be due to fact that fan traps actively suck in organisms whereas pitfall and bubble wrap traps are passive, relying on invertebrates flying or crawling into the trap by chance.

Similar results were obtained in a study by Gray (2011) who compared the effectiveness of vortex fan trap, arboreal pitfall traps and chemical knockdown. He concluded fan traps were the most effective trapping method because the method caught the highest number of families and individuals in comparison to the other two methods. Pitfall was also deemed to be the most inefficient sampling method and was recommended to only be used supplementary to other methods (Gray, 2011). It is suggested that trapping methods have a bias to certain communities of invertebrates (Gray, 2011; Walsh, 2012; Ozanne, 2005). In this study the most common order of invertebrates caught were from Diptera. Between each of the trapping methods the families Cecidomyiidae, and Dolichopodidae accounted for a high percentage of the fan and pitfall traps. The other family which contributed to a larger percentage of pitfall traps was the Cicadellidae family of the order Hemiptera. The majority of the invertebrates in these orders are highly mobile flying species (Gray, 2011; Walsh, 2012). Therefore, pitfall and fan traps could be argued to have a bias towards flying invertebrates, which is not surprising given the traps are suspended in the canopy. Bubble wrap traps were dominated by the family Porcellionidae, which accounted for almost 30% of the total families contributing to the samples collected using these traps. This family consists of predominantly woodlice species, invertebrates of relatively poor mobility which prefer dark, moist habitats, namely bark-dwelling invertebrates. Bubble wrap traps were designed in order to sample such organisms (Walsh, 2012). From this perspective, bubble wrap traps are very effective.

In addition to the effectiveness of trapping methods, it is important to recognise the advantages and disadvantages associated with each method. Pitfall traps are one of the oldest and most frequency used traps for sampling invertebrates (Woodcock, 2005). A large number can be deployed over a large area with minimal effort (Woodcock, 2005). They are simple, inexpensive, and easy to deploy and retrieve with minimal disturbance being relatively quiet without the need to send a climber into the canopy to place the traps (Carrel, 2002; Woodcock, 2005). Fan traps have a similar technique for deployment to pitfall traps, however, they are slightly more complex and expensive as they require power from a 12 volt battery (Gray, 2011). Bubble wrap traps are also very simplistic, requiring minimal materials and they too do not require access to the canopy.

Part of the difficulty when sampling the canopy environment is its physical three-dimensional nature (Lowman & Wittman, 1995, 1996). There is high variation in the micro-climates within the canopy (Stork *et al.* 2001). There was no indication given about the spatial placement of traps in the canopy studies which contributed to this investigation. Factors such as temperature, humidity, radiation intensity, shade, and exposure vary within the canopy (Stork *et al*. 2001). For example, temperature will be higher and more stable in the inner canopy, which increases the activity of invertebrates (Schowalter, Hargrove & Crossley, 1986), therefore more invertebrates may be caught in traps placed closer to the trunk. Micro-habitat conditions will also vary, foliage will be asymmetrically distributed affecting food availability (Stork *et al*. 2001). Conditions can vary on aspect of the tree, in temperate woodlands in the northern hemisphere, south-facing side of the tree receives more sunlight which makes the south-side generally warmer and sunnier compared to the north face (Stork *et al.* 2001). Placement of traps should therefore take aspect into consideration.

Climatic and habitat conditions change relating to seasons, in a temperate woodland, defoliation and the emergence of leaves has a significant influence on the canopy invertebrate community. Season was kept constant in this study, all data included was collected in the summer month (May-late September). Generally, a greater abundance and diversity of invertebrates are present in canopies during the late-spring and summer months (Richardson *et al.* 1997; Allen, 2008). A major reason for the increasing population in spring and summer is in relation to when budding occurs. Stork *&* Hammond (2013) studied the diversity of beetles (Coleoptera) in the oaks of Richmond Park. They found the greatest abundance of beetles in late June, which they attributed to the emergence of leaves. Also, the number of specialist species of *Coleoptera* remained constant throughout the year whereas generalists increased during the summer. Stork *et al.* (2001) who also studied the variation in *Coleoptera* in the oak canopies of Richmond Park found the distribution of beetles varied spatially and temporally in the canopy. In April/May beetle population was higher close to the trunk and the reverse was noticed in September/October months. Furthermore, Maguire *et al.* (2014) investigated the vertical variation of beetles and flies (Diptera) in temperate canopies in summer and found fly abundance and diversity increased in the upper-canopy. These changes in distribution and abundance throughout the year reflect patterns in the micro-climatic or micro-habitat conditions, i.e. preferred surface - trunk or branch; temperature; radiation intensity; density of foliage; presence of epiphytes; predator-prey relationship – enemy-free space. For effective sampling, trapping techniques need to consider and account for the variations with the canopy spatially and temporally.

Regional variation

A significant regional difference was found between canopy invertebrate communities the south-west of England and Scotland. However, the analysis was not able to compare samples collected in the same tree species; samples in Scotland were collected in scots pine and those in the south-west of England were collected in oak trees. Therefore, no definitive difference can be attributed to location because, as shown in previous analyses, tree species has a significant influence on canopy invertebrates. As found when comparing oak and scots pine, trees in the south-west of England had a greater abundance and diversity of invertebrates compared to those in Scotland. This regional difference could be explained by the difference in the climatic envelope between the two regions. Scotland has a higher number of days of sleet/snow fall (40-130 days annually), cooler temperatures (4.5 - 7.5^{o}C annual average) and fewer hours of sunshine (900-1700 hours annually) on average compared to the south-west of England (0-15 days, 10-12^{o}C, 900-1650 hours respectively) (Met Office, n.d.; Table 2). Scotland's climate is harsher than in the south-west of England therefore species would need to be adapted to such conditions. The climate in the south-west of Britain is milder and relatively stable throughout the year compared to Scotland, therefore species would not need to be as specialised and more generalist species could exist which would not survive in the Scottish climate. With climate change a shift could be seen in invertebrate distribution, however, migration for invertebrates with poor mobility, usually canopy specialist could be difficult as woodland across Britain is very fragmented (Travis, 2003).

Limitations of study

The main limitation of this study was the fact that different tree species were compared in the regional analysis, oak in the south-west of England and scots pine in Scotland. As already shown in the analysis, tree species had a significant influence on invertebrate communities, therefore the two regions are not comparable so no definitive difference could be inferred from this study. To compare the canopy invertebrate communities across Britain, a number of factors would need to be kept constant. From this study it is clear that tree species would need to be the same and the trapping method and positioning would need to be consistent. Also, other factors such as time of year, woodland type, habitat, tree age and woodland management would all need to be considered to keep variation to a minimum. These variations mean that the data in this study could only be compared at a broad scale, patterns relating to trap position, location of tree in stand and tree maturity were not detectable. Moreover, invertebrates were only identified to family level, to identify specific changes in distribution between tree species and regions, organisms would need to be identified to species level, although this would be challenging and time consuming due to the diversity of invertebrates.

Experimental limitations of the data was the lack of metadata, details on factors like tree age, location of trap within the canopy, weather, greater description of habitat and management of woodland. A further limitation was that collector and identifier of invertebrates was not consistent, which could have resulted in discrepancies in methodology and identification. Such detail could only be controlled if data had been collected by one person or group.

Many results from studies on canopy invertebrates are based on small scale, individual studies (Murica, 1995; Walsh, 2012). However, this study analysed data from a number of sources, collected over several years and from different locations and the findings from analysis agree with those referenced in literature, which helps to validate conclusion from individual studies.

Conclusion

The main findings from this study suggest that tree species has a significant influence on the abundance and diversity of invertebrates found in the canopy. Oak canopies are able to support a greater diversity and abundance of invertebrates in comparison to scots pine. These results coincide with the widely agreed hypothesis that deciduous trees support the highest diversity of invertebrates (Ozanne, 1999; Hill, Roberts & Stork, 1989; Southwood, 1961). Reasons for this being due the greater architectural complexity of oak canopies relative to scots pine, the foliage of oak being more palatable and its abundance in Britain being greater than scots pine. Of the three trapping methods, fan, pitfall and bubble wrap, fan traps appear to be the most effective because they captured the greatest diversity and number of invertebrates. However, consideration would need to be given to the type of trapping method used to sample invertebrates in relation to the aims of the study. Results suggest that fan traps are most effective, however, if bark-dwelling invertebrate communities were to be investigated then bubble wrap traps would be more suitable. The study was unable to draw reliable conclusions on regional differences in the canopy invertebrate communities found in the south-west of England and Scotland because tree species was not consistent. In addition, this study highlights the dynamic nature of the canopy environment and the high spatial and temporal variation within a single tree or a woodland. Therefore sampling methods and placement of traps would need to recognise and account for this variation in the canopy.

Further investigation would be advised into comparing regional differences in canopy invertebrates. A greater awareness of the patterns in invertebrate abundance across Britain at species level could be used to show the effects of climate change (Kremen *et al.* 1993). Mobile species found in southern Britain could begin to migrate northwards with changing temperatures. Canopy specialists with poor dispersal ability may be lost, as they are unable to adapt to the fast pace in climate change (Travis, 2003). This would change the structure of canopy invertebrate communities; which management and conservation efforts would need to account for, especially in the fragmented forests of Britain.

Acknowledgements

I would like to acknowledge Nathan Gray, Rachael Castle, Nicola Marks, Claire Giles, Reanne Kelf, David Searle, Leona Sutton and Natalia Jovanovic for permitting me to use their data in this study. I would also like to thank Dr Stephen Burchett for suggesting the project and for his continuous help and advice in processing and analysing the large dataset, and especially for his expertise in using the Primer software. Finally, I would like to thank Dr Paul Lunt, my advisor, for his support and advice throughout my various dissertation projects and then for helping me settle and rapidly progress on my final project.

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