Building resilient wooded landscapes: How can we support saproxylic invertebrates into the future?

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Abstract

Decaying wood hosts a diverse network of saproxylic invertebrates. These play important roles in forest functioning, including pest control, pollination, and nutrient cycling. However, declines in ancient and veteran trees in UK landscapes threaten saproxylic communities. The present research sought to address this through investigating multiple aspects of saproxylic habitat use and creation.

Previous studies of saproxylic invertebrate landscape use have identified scales at which habitat density is most important. However, many of these studies were done in dense woodlands and none have been attempted in the UK. This research sought to fill these knowledge gaps by investigating habitat density scales of importance to invertebrate populations in English open-grown oak landscapes. Flight interception trapping data showed that higher veteran tree densities over a 250 m radius positively correlated with saproxylic community diversity, whilst higher densities over smaller scales support rare species.

The second aspect of this research explored beetle boxes as a deadwood habitat creation method. The present research built upon previous studies by investigating a novel ground-level design to replicate basal tree hollows. It also tested the potential of different construction materials and content variations in improving beetle box function. Results showed that plastic beetle boxes contained similar abundances and diversities of deadwood-associated beetles than those made of wood. However, the wood mould in plastic boxes became significantly drier than that in wooden boxes. The addition of poultry faeces to beetle boxes as a source of nitrogen was associated with higher abundances and diversities of some beetle groups. No evidence of the basal hollow specialist, *Limoniscus violaceus*, was found in beetle boxes; however, more long-term monitoring is needed to thoroughly investigate this. This research also noted the potential for beetle boxes to function as a public engagement tool to promote a widespread appreciation of the importance of deadwood ecosystems.

Declaration

I certify that this thesis represents my own work, unless otherwise identified by references, and has not been submitted to any other institution for any other degree other than the Doctor of Philosophy being studied at the University of East London.

Name: Stephanie Katherine Skipp Date: 22/01/2023

Signature: [redacted]

Preface

Ian Humpheryes provided statistical assistance to this research by carrying out the principal components analysis (PCA), Nonmetric multidimensional scaling (NMDS), Redundancy analysis (RDA), analysis of similarities (ANOSIM) tests used in Chapter 2.

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1. Introduction

1.1. Saproxylic invertebrates – their diversity and importance

Global insect declines are a topic of growing concern over recent years (Wagner *et al*., 2021). However, a lack of data on population trends is a key limiting factor in understanding how invertebrate populations respond to the various stressors applied to them (Wagner *et al*., 2021). The invertebrates of decaying wood are a group that have experienced considerable past declines and remain under threat (Hall, 2018). The present study seeks to gather new data surrounding these, to improve understanding that could feed into their conservation.

The saproxylic fauna

Decaying wood provides habitat for diverse communities of invertebrates (Stokland *et al*., 2012). The term 'saproxylic' is used to describe invertebrates that rely on deadwood to complete their lifecycles.

The original definition of 'saproxylic' by Speight (1989) is as follows:

> "Species of invertebrates that are dependent, during some part of their life cycle, upon the dead or dying wood of moribund or dead trees (standing or fallen), or upon wood-inhabiting fungi, or upon the presence of other saproxylics."

Since this publication, the definition of 'saproxylic' has expanded to reflect deadwood niches that fall outside of this description (Alexander, 2008). A large proportion of saproxylic species are not limited to dead or moribund trees, and many utilise microhabitats found on live trees (Alexander, 2008). Further definitions sought to encompass the niches of old, live trees by replacing 'dead or dying' with the word 'senescent' (Anon, 2003; Alexander, 2008). However, this further fails to incorporate the fact that younger trees can develop deadwood characteristics earlier in their lives (termed 'veteran trees')

(Alexander, 2008; Woodland Trust, 2021a). A more widely encompassing definition of ‘saproxylic’ has been suggested by Alexander (2008):

> “Saproxylic organisms are species which are involved in or dependent on the process of fungal decay of wood, or on the products of that decay, and which are associated with living as well as dead trees. Conventionally two further groupings of organisms are included within the definition: i) sap-run associates are included within the term saproxylic, i.e. species dependent on fluxes of sap and its decomposition products, and ii) organisms other than fungi that feed directly on wood.”

One reason for the extensive diversity of the saproxylic fauna is that the broad definition of the group encompasses invertebrate species with a wide variety of life history strategies (Stokland *et al*., 2012). This ranges from those that feed on deadwood and spend their entire lives within it (except for occasional dispersal journeys), to species that may only use deadwood for protection during their vulnerable immature development phases (Stokland *et al*., 2012). Functional groups within this diversity include deadwood feeding (xylophagous) species, species that feed on decaying material (saprophagous) and those that feed upon other saproxylic species, including fungivores and predators of other saproxylic invertebrates (Stokland *et al*., 2012).

In addition to this, deadwood itself provides a large diversity of microhabitat resources, the adaptation to which has facilitated extensive insect diversification (Speight, 1989; Stokland *et al*., 2012). For example, some insect groups including Aradidae flat bugs and Cucujidae beetles have evolved dorsoventrally flattened body forms to allow movement through tight crevices in the cambium layer under tree bark (Smith & Sears, 1982; Speight, 1989; Marchal *et al*., 2012). Other deadwood microhabitats that host subsets of saproxylic diversity include sap runs, tree hollows, fungal fruiting bodies, old insect burrows, old birds nests and dead trunks and branches of trees in a variety of diameters, both standing and fallen (Speight, 1989). The specific traits that best suit life in these situations vary (Speight, 1989). For example, adaptations towards longer-lived habitats may include a lower tendency to disperse, in comparison to those towards more ephemeral resources such as rotting fallen deadwood or a fungal fruiting body (Ranius & Hedin, 2001).

The age of the deadwood also contributes to saproxylic diversity. The more extensively decayed a deadwood resource is, the less residual tree defence chemicals remain (Stokland *et al*., 2012). The need to adapt a tolerance to these chemicals is a factor that causes species to specifically target certain species of tree (Stokland *et al*., 2012). Therefore, there is a tendency towards less tree-host specificity in species that use more extensively decayed niches such as wood mould, in comparison to species that bore directly into recently dead wood (Stokland *et al*., 2012).

Some saproxylic species also exhibit preferences for different decay fungi (Arya, 1993; Yee *et al*., 2006). Wood decayed by red-rotting fungi is nutrient-poor and has a low Ph (Fukasawa, 2021). Adaptations to these conditions have resulted in a distinct saproxylic community associated with red rot (Fukasawa, 2021). In contrast, some saproxylic invertebrates have strong associations to white and soft rotting fungi (Arya, 1993; Yee *et al*., 2006) This is likely because these invertebrates have greater abilities to metabolise the various chemical components present in wood decayed by these respective fungi (Fukasawa, 2021).

Global/ European saproxylic diversity

The global richness of saproxylic species (including all taxonomic groups) has been estimated to be in the range of 0.4-1 million (Stokland *et al*., 2012). However, the absolute total number of global saproxylic invertebrate species remains unknown (Stokland *et al*., 2012). Saproxylic knowledge is constantly expanding, and new species continue to be discovered and described at a high rate (Darby, 2017). With many species being elusive and rarely encountered during general fieldwork, a large amount of targeted study would be required to truly begin to understand global saproxylic invertebrate diversity.

Various country- and region-specific research projects have been undertaken in Europe with the intention of developing understanding of local saproxylic faunas and aiding their conservation. Key publications on several of these initiatives are summarised below in Table 1.1.

Table 1.1. A summary of key European initiatives collating information on local saproxylic species.

Country(ies)	**Reference**	**Taxonomic groups covered**	**Summary**
France	Bouget, Brustel & Zagatti, 2008	Coleoptera	The FRench Information system on Saproxylic BEetle Ecology (FRISBEE) was developed with the intent of organising information on the ecological requirements of all saproxylic beetle species present in France.
Germany	Schmidl & Bußler, 2004	Coleoptera	All saproxylic beetles known from Germany have been gathered in a list. This contains 1,347 species alongside available information on their feeding guilds, association to Urwald/primeval forest and German Red List status. Recommendations are also given as to the species that should be considered as meaningful indicators of saproxylic quality in landscape studies.
	Müller *et al.*, 2005	Coleoptera	A refined list of 115 beetle species designated as Urwald relics was created. These species may be used as saproxylic indicator species for Germany.

Italy	Carpento *et al*., 2015	Coleoptera	A database is compiled of 2,049 saproxylic beetle species recorded from Italy, including information on their extinction risk and trophic interactions. This review identified 421 saproxylic beetle species as threatened (categorised as critically endangered, endangered or vulnerable according to IUCN criteria).
Norway, Sweden, Finland and Denmark	Stokland & Meyke, 2008	Invertebrates, vertebrates, fungi, mosses and lichens	A shared database is being developed for these target Nordic countries, containing ecological and geographical information on all of their multicellular saproxylic species. When finished, it is expected that this database will encompass approximately 7,000 species.
United Kingdom	Alexander, 2002	Invertebrates	A provisional review of saproxylic invertebrate species, containing information on species habitat requirements and rarity. The list contains 1,792 species; however, it is highlighted that this number does not include all saproxylic species, with additional study needed of difficult groups such as Hymenoptera and Collembola.

UK saproxylic diversity evaluation

The review of saproxylic insect species by Alexander (2002) listed in Table 1.1 remains the most complete summary of saproxylic diversity in the UK to date. The invertebrate groups with the highest documented UK saproxylic diversity were Coleoptera and Diptera, with 700 and 730 species respectively (Alexander, 2002). Due to recent discoveries of saproxylic invertebrate species new to Britain (for example, *Dermestoides sanguinicollis* (Asaw & Barclay, 2018)), the true saproxylic diversity in Britain is likely to be higher than the numbers listed by Alexander (2002).

UK site-assessment methods of saproxylic diversity

Historically different approaches to the assessment of saproxylic diversity value have existed between the constituent countries of the UK, causing inconsistencies in conservation priorities (Alexander, 2015). There was also a problem of saproxylic diversity being historically undervalued in site assessments (Fowles et al. 1999). In order to systematise the approach to saproxylic assessment, several attempts have been made to create a consistent method that might be used to thoroughly evaluate saproxylic diversity across sites throughout the whole of the UK (Alexander, 2004; Fowles, 1997; Fowles et al. 1999). Details of these are outlined below:

- **Index of Ecological Continuity**

The saproxylic beetle Index for Ecological Continuity (IEC) was developed by Alexander (1988) based on a species list by Harding & Rose (1986) with the intention of creating a consistent, UK-wide method for saproxylic site assessment (Fowles *et al*., 1999). The focus of this method was not on rarity, but rather the ecological requirements of the saproxylic beetle species present, using the beetle fauna as a proxy for decaying wood habitat continuity and quality (Alexander, 2004). Species were designated as strong habitat indicators in accordance with the likelihood that they are remnant species from the ‘wildwood’ condition of Britain in the prehistoric era (Alexander, 2004). This method was based on the work of Rose (1974) on epiphytic lichens and is a similar approach to that used to designate priority species in Germany (Schmidl & Bußler, 2004). The species chosen are particularly faithful to relic ancient woodland and are sensitive to change due to limited dispersal and colonisation abilities, making them useful indicators of stable, continuous woodland (Alexander, 2004). Using the IEC, sites can be identified as being of international, national or regional importance (Alexander, 2004).

Although the IEC is a useful method for assessing woodland continuity, there are several factors that should be considered during its application. One of these is that the effectiveness of the IEC is dependent on the recording effort that has been applied at a site (Alexander, 2004). Because of this it should ideally be based upon saproxylic beetle survey data covering all seasons over several years (Alexander, 2004). Additionally, the extent to which some saproxylic species are associated with relic woodland is changing with climate change (Alexander, 2004). This is causing some species previously included in the list to become weaker continuity indicators, highlighting the need for regular review of the species list used for assessment (Alexander, 2004). For example, *Agrillus biguttatus* was previously considered an ancient woodland specialist but has extended its range considerably since the 1980s and is now widespread over much of south-east England (Alexander, 2004). Finally, it was noted that the IEC demonstrated a bias against areas of the UK that had a generally lower saproxylic species richness, such as those in the far north and west. This has potential to cause sites in these areas to register as unimportant in terms of their saproxylic fauna, despite some being home to nationally rare species (Alexander, 2004).

- **Saproxylic Quality Index**

The Saproxylic Quality Index (SQI) is a list of saproxylic species weighted by rarity (Fowles, 1997 & Fowles et al. 1999). This list can be used to grade site species lists and assess their relative saproxylic value (Fowles et al. 1999). It is designed to aid in the quantification of such diversity so that resources for saproxylic conservation can be effectively designated (Fowles et al. 1999). The application of the Saproxylic Quality Index is heavily dependent on surveying effort and works best when at least 40 species are included per site (Fowles et al. 1999). Ideally, similar surveying effort should be applied to each site in instances where the SQI is used to make direct site comparisons (Fowles et al.

1999). Due to its requirement for relatively long species lists, there is a concern that the SQI may overlook sites where the resident saproxylic beetle fauna forms only a short list that nonetheless contains species that indicate the presence of ancient, relict woodland (Alexander, 2004). Because of this, the application of the SQI alongside the IEC can prevent important sites from being overlooked.

Ecological roles of saproxylic diversity

Historically, there has been a widespread impression among forestry workers that invertebrates, especially beetles, bring largely negative impacts on woodland health and tree productivity due to the action of a few species as tree-pests (Winter, 1992). This is further compounded by the fact that the economic impacts of these species on forestry is a key driver of saproxylic-based research, drawing particular negative public attention to saproxylic pests (Flint *et al*., 2009; Holmes *et al*., 2009). Although tree pests can be damaging, the aforementioned perceptions overlook the range of useful processes to which deadwood invertebrates make an essential contribution. Furthermore, contrary to these beliefs, woodlands that are managed to promote ecological diversity are likely to be more resilient against pest activity as a result of lower concentrations of host tree species and greater activity levels of natural enemies (Jactel *et al*., 2005; Dalin *et al*., 2019; Stokland *et al*., 2012). A summary of the vital roles that saproxylic invertebrates play towards the provision of ecosystem services is summarised below:

- **Decomposition**

One of the most important ecological roles performed by saproxylic invertebrates is the decomposition of deadwood (Stokland *et al*., 2012). Invertebrates work alongside other organisms including fungi, slime moulds and bacteria to break down deadwood, returning the nutrients to the soil and making them available for other organisms (Stokland *et al*., 2012; Harderson & Zapponi, 2018). The activity of saproxylic insects has a significant impact on decomposition rate of deadwood and directly influences the activities of other decomposing organisms (Ulyshen *et al*., 2016; Mestre *et al*., 2018; Wetherbee *et al*., 2022). Saproxylic beetles that penetrate tree bark provide entry points for other decomposing organisms to access the wood beneath (Hardersen & Zappioni, 2018). In moving through the wood, beetles also open up galleries which further increase the surface area of wood that is accessible to decomposing organisms (Hardersen & Zappioni, 2018). In addition to this, beetles play a role in the transport of free-living microbes including fungi, directly inoculating deadwood with propagules found on their exoskeletons or in specialised spore-carrying organs called mycangia (Batra, 1963; Harrington, 2005; Strid *et al*., 2014, Ulyshen *et al*., 2016). Some beetles carry microbial species in their gut flora, which aid in the decomposition of chemical components in deadwood that are difficult to break down, including lignin (Gieb *et al*., 2008). Examples of beetle families that exhibit this trait include Passalidae, Lucanidae and Cerambycidae (Suh *et* al., 2003; Gieb *et al*., 2008; Tanahashi *et al*., 2010). Both beetle and fungal diversity have been found to correlate positively with deadwood decay rate, highlighting the importance of protecting biodiversity in deadwood ecosystems (Kahl *et al*., 2017).

- **Engineering ecosystems**

Saproxylic insects can alter deadwood habitats in ways that improve their value for a range of other species (Buse *et al*., 2008; Harderson & Zappioni, 2018). For example, as mentioned in the previous section, the activities of some insect species promote the initial colonisation of deadwood by saproxylic fungi and increase wood decomposition rate (Harderson & Zappioni, 2018). This increases the suitability of the deadwood resource for a wider diversity of insect colonisers that feed on partially decayed wood and fungi (Harderson & Zappioni, 2018).

The influence of some saproxylic species is so pronounced that they have been noted as ‘keystone species’ or ‘ecosystem engineers’. One example is the Cerambycid beetle, *Cerambyx cerdo* (Buse *et al*., 2008). The larvae of this species create large galleries in living trees, which have been found to constitute important structures for a variety of other woodland species (Buse *et al*., 2008). In a study of oak beetle fauna, Buse *et al*. (2008) found that the richness of saproxylic beetle species had a significantly positive link to *C. cerdo* colonisation, with greater numbers of red-listed species found on colonised trees. Furthermore, 63 beetle species were found exclusively on trees inhabited by *C. cerdo*, almost half of which were red-listed (Buse *et al*., 2008). The intensity of *C. cerdo* colonisation of a tree was found to be a stronger influencing factor on overall beetle species richness than other physical factors such as trunk diameter or sun exposure, indicating that its presence exerts a direct influence on other beetle species (Buse *et al*., 2008). A possible reason for this is that the galleries of *C. cerdo* may provide increased space for the activities of predatory beetle species that primarily use bark-denuded patches of wood (Buse *et al*., 2008). The value of this structural niche is not restricted to invertebrates, as *C. cerdo* larval galleries have also been shown to be an important habitat for hibernating bats including the species, *Pipistrellus nathusii* (Gottfried *et al*., 2019).

The above evidence shows that the protection of key species such as *C. cerdo* can have prominent benefits for saproxylic biodiversity, including benefits for other threatened species. As *C. cerdo* is itself a threatened species that inhabits sun-exposed mature trees, its persistence is threatened by inappropriate management of wood pasture (Luce, 1997; Buse *et al*., 2008; Alexander, 2016a). This highlights the importance of the research described in Chapter 2 of this thesis, which aims to investigate optimal management approaches to promote the conservation of saproxylic invertebrates in pasture woodland systems.

Cetoniine Scarabaeoid beetles are another invertebrate group containing saproxylic members that are known to positively impact other saproxylic species through their interactions with deadwood habitats (Jönsson *et al*., 2004; Micó *et al*., 2011). The larvae of species including *Cetonia aurataeformis* and *Osmoderma eremita* which develop in tree hollows have been found to produce frass enriched with high levels of nitrogen and phosphorus (Jönsson, *et al*., 2004; Micó *et al*., 2011). This contributes to the nutrient richness of the wood mould in tree hollows, improving the resources offered by these habitats to other species (Jönsson, *et al*., 2004; Micó *et al*., 2011). As a result, the presence of *C. aurataeformis* and *O. eremita* larvae in tree hollows have been found to predict the richness of other saproxylic species (Ranius, 2002; Sánchez-Galván, 2014). A specific example of benefits gained from Cetoniine larval presence can be found in *Myathropa florea* larvae, which have been shown to develop at a higher rate, with improved resulting adult fitness, when reared in substrates enriched with *C. aurataeformis* frass (Sánchez-Galván, 2014). Understanding the influence of these keystone species upon their saproxylic habitats can be useful from a management perspective. Chapter 3 of this thesis utilises this knowledge to investigate optimal conservation techniques focussed on tree hollows.

- **Pollination**

In addition to their interactions with deadwood habitats, many saproxylic species also utilise floral resources (Falk, 2021). As a result, a proportion of saproxylic biodiversity provide the ecosystem service of pollination (Falk, 2021). Falk (2021) highlights over 320 invertebrate species of saproxylic pollinator found in Great Britain, including approximately 130 beetles, 85 flies, 75 wasps and 35 bees. This diversity encompasses species using a wide range of different deadwood resources for a variety of purposes (Falk, 2021). The plants visited most by saproxylic species include the common native species, hawthorn (*Crataegus monogyna*), bramble (*Rubus fruticosus*) and umbellifers such as hogweed (*Heracleum sphondylium*) (Falk, 2021). Saproxylic pollinators can also benefit agricultural systems (Proesmans *et al*., 2019). For example, forest cover within 200 m radii has been shown to have a significant positive influence on the activity of saproxylic hoverflies that provide pollination services in intensively managed agricultural landscapes (Proesmans *et al*., 2019). Not only do these pollination activities further highlight the value of saproxylic habitats to biodiversity and ecosystem functioning, but they elucidate the importance of habitat heterogeneity in woodland ecosystems for the conservation of the deadwood fauna (Falk, 2021).

- **Pest control**

High levels of biodiversity contribute to the functioning and resilience of ecosystems (Stokland *et al*., 2012; Mori *et al*., 2017). Key contributors to the stability of saproxylic invertebrate communities are the predators and parasitoids, which act to control the population sizes of their hosts (Stokland *et al*., 2012; Hilszczański, 2018). These are particularly vital for the control of pest species, reducing population growth through top-down control and limiting the extent of damage they can cause (Hilszczański, 2018). For example, 35 parasitoid species and a range of other predators have been found to play a role in controlling populations of the southern pine beetle, *Dendroctonus* *frontalis*, preventing numbers from reaching infestations that can be difficult and expensive to control (Thatcher *et al*.,1981; Berisford, 2011). Therefore, a diversity of natural enemies of pest species in productive forests can decrease economic losses from reduced tree yields (Thatcher *et al*.,1981). The control of pests also helps to maintain forest health, preventing the loss of canopy cover through pest-induced tree death, thus preserving the air, water, and soil regulatory functions of the forest (Thatcher *et al*.,1981; Brockerhoff *et al*., 2017).

Not only are the invertebrates of ancient trees valuable for control of forestry pests, but they can also provide pest-control benefits in agriculture. Wetherbee *et al.* (2020) found that the diversity of invertebrate predators was higher around veteran trees than around young oak trees. Similarly, greater rates of attack from invertebrate predators were made on artificial caterpillars in the veteran trees (Wetherbee *et al.*, 2020). It is possible that these veteran trees were able to accommodate a greater number of predator species because of their structural complexity. A study by Perez-Alvarez *et al.* (2019) showed that complex landscapes with an abundance of semi-natural areas had fewer antagonistic interactions between predatory invertebrate species, allowing them to co-exist and facilitate improved biocontrol of agricultural pests. As a result of these effects, the conservation of ancient and veteran trees in farmland can be considered an important aspect of integrated pest management (IPM), potentially lowering the need for the application of other pest control methods and reducing the associated costs (Woodland Trust, 2021a).

1.2 – Threats to saproxylic invertebrate populations

Saproxylic decline

The European Red list of saproxylic beetles describes 18% of the 700 assessed European saproxylic beetle species as being at risk of extinction (Hall, 2018; IUCN, 2018). A key reason for this is the depletion of deadwood resources from ancient trees across European landscapes (Stokland *et al*., 2012). Woodland cover has historically declined catastrophically and, although tree cover in Europe is now rising again, many woodlands are increasingly lacking the resources needed for saproxylic invertebrates to thrive (FAO, 2020; Woodland Trust, 2021b). A recent review found that only 7% of native woodland in the UK was in good ecological condition, with the majority of woodland lacking in deadwood supply, veteran tree numbers, and structural diversity (Woodland trust, 2021b).

Woodland cover loss

The state of current woodland in the UK is heavily shaped by historical clearance activities, with an estimated 50% of England's wildwood having been cleared by 500BC to make way for agriculture (Rackham, 1986). A result of reduced woodland cover is that many remaining ancient woodland patches now exist in a highly fragmented state, with little connectivity to allow for species dispersal (Butler *et al.*, 2002; Rackham, 2008; Defra, 2011). Because of this, woodland species are likely to have a lowered resilience to stochastic events and future challenges such as those brought by climate change (Bailey, 2007). Although woodland cover is now increasing in the UK, valuable trees outside woodlands, such as those in hedgerows continue to be lost (Woodland Trust, 2021b) Hedgerow trees can provide high quality deadwood resources and increased landscape connectivity for saproxylic species, meaning that their loss further contributes to the increasing isolation of ancient woodland patches (Dodelin *et al.*, 2017; Parmain *et al.*, 2018).

Suboptimal woodland planning

With increasing motivations for climate, health and other ecosystem services, there has been a strong drive to accumulate new areas of woodland (Woodland Trust, 2021b). As a result, the amount of woodland cover has more than doubled over the past 100 years and, for the past five years, the rate of new woodland recruitment in the UK has averaged close to 10,000ha per year (Woodland Trust, 2021b). Despite the positive image portrayed by these figures, many new areas of woodland suffer from poor planning and often comprise ecologically poor, non-native tree species (Woodland Trust, 2021b).

Where these non-native trees are imported from other countries, they can also carry the risk of spreading pests and diseases (Woodland Trust, 2021b).

Tree planting methods used to create new broadleaved woodlands often follow the approach used when planting wood plantations, with close, homogenous spacing between trees (Fuentes-Montemayor *et al.*, 2022). This does not replicate natural tree recruitment and is unlikely to result in the open, light conditions required to support tree growth into old age (as discussed in section 1.4) (Ferris-Kaan, 1995; Kirby *et al.*, 1995). It is clear that this approach is not conducive to future saproxylic biodiversity maintenance.

Tree planting projects also often lack a long-term perspective and do not document the process of tree maturation over time (Burton *et al.*, 2018; Fuentes-Montemayor *et al.*, 2022). As a result, there is a dearth of knowledge regarding extent to which new woodlands are able to develop a functioning ecosystem that can support saproxylic biodiversity (Burton *et al.*, 2018; Fuentes-Montemayor *et al.*, 2022). This is particularly the case for broadleaved sites, as a majority of research centres around coniferous plantation woodland creation (Burton *et al.*, 2018).

Without appropriate planning and monitoring, there is a risk that future woodlands will be unsuitable to support populations of saproxylic invertebrates. As a result, saproxylic biodiversity may continue to decline through a lack of appropriate resources, despite increasing tree cover. It is essential that future woodland areas are created with ecological consideration to avoid wasting conservation resources. The present research will aim to provide insights into appropriate tree spacing and deadwood resource provision that may inform afforestation practices in the future to increase their biodiversity value.

Deadwood depletion in existing woodland through management

The management techniques employed in any woodland are a key factor in determining the deadwood resources available for saproxylic invertebrates. Forest management practices have historically failed to promote sufficient ecological continuity of deadwood habitats through space and time to support saproxylic species that are vulnerable to isolation (Grove, 2002). Managed forests also generally contain lower volumes of deadwood than unmanaged, old-growth forests (Goodburn & Lorimer, 1998). As a result, intensive management has caused large proportions of European woodland areas to become ecologically depleted, with a lowered ability to sustain suites of saproxylic species (Grove, 2002). Aspects of current woodland management that are antagonistic to the preservation of saproxylic diversity include:

- **Intensive wood extraction**

As forestry practices have become more efficient over time, attempts to reduce waste have led to increasingly intensive extraction from forests (Stokland *et al*., 2012). This results in less wood being left in situ to provide resources for invertebrates. Trees are also being harvested at earlier stages in their lifecycle, meaning that little opportunity is given for deadwood resources to accumulate (Stokland *et al*., 2012). Where deadwood does occur, it is often of low value to many saproxylic species, not representing microhabitats typical of a late decay stage (Goodburn & Lorimer, 1998; Stokland *et al*., 2012). For example, Siitonen *et al*. (2000) found that the available deadwood in managed forests consisted largely of logging residues, cut stumps and short logs, most frequently of low diameter classes, whereas old-growth forests contained more high-diameter logs, snags and standing dead trees. In addition to its implications for deadwood, extensive extraction also involves intensive machine traffic through woodlands which can disturb organisms (Bouget *et al*., 2012).

- **Removal of deadwood for sanitary reasons**

There has long been a belief that allowing deadwood to remain in woodlands constitutes a risk of pest outbreaks and disease (Winter, 1993; Stokland *et al*., 2012). Past devastating effects of beetle species such as *Ips typographus* on tree stocks in productive European forests contributed to these fears (Winter, 1993). Consequently, sanitation felling and burning of trees is a common forestry practice, constituting attempts to prevent the source of apparent sickness in trees from spreading (Winter, 1993). The majority of damaging insect pest problems in forestry occur in plantations of coniferous trees and, in areas where the tree species in plantations are non-native, these woodlands constitute little biodiversity potential (Winter, 1993). However, when sanitation practices are carried over into deciduous woodland, conflicts emerge between wildlife conservation and industry. Aside from few specific examples of insects facilitating deciduous tree damage, such as that of *Scolytus* spp. and the spread of Dutch Elm Disease, the overall threats of insects to deciduous trees and wood harvesting are minimal (Winter, 1993). As a result, strict sanitation of broadleaved woodland is often unnecessary and damaging to overall woodland health.

Tree age gaps

Even within remaining areas of ancient woodland, historical tree felling has led to biases in tree age structures and a paucity of trees in certain important age categories (Woodland Trust, 2021b). This is likely to cause gaps in the continuity of saproxylic habitat through time, where there is an absence of trees entering their decay stage available to replace old trees that are deteriorating beyond usability for certain invertebrate groups (Harding & Rose, 1986). For example, mature trees are predicted to be lost in agricultural landscapes over the next 180 years under current management regimes as a result of tree losses combined with low tree recruitment (Gibbons *et al*., 2008). Periods of poor deadwood availability has the potential to damage saproxylic invertebrate populations, especially for species that are less able to disperse to different areas of habitat to find new resources (Harding & Rose, 1986). As a result, the age-structure problem is thought to be a major contributing factor to declines in saproxylic habitat in European woodlands (Hall, 2018). This has instigated new research threads into innovative methods of mitigating the threats of age gaps, such as the application of beetle boxes as intermediary tree-hollow resources discussed later in this chapter (Jansson, Ranius, *et al*., 2009; Carlsson *et al*., 2016). The present research provides a key contribution to this field.

Tree disease

A further threat to deadwood habitats, and consequently to the saproxylic fauna, is tree disease (Woodland Trust, 2021b). A recent example of this is ash dieback, caused by the fungal pathogen, *Hymenoscyphus fraxineus*, which has caused widespread reductions in population sizes of European ash trees

(*Fraxinus excelsior*) (Baral *et al*.,2014; Hultberg *et al*., 2020). These declines have direct impacts on a number of saproxylic invertebrate species (Littlewood *et al*., 2015). One of these is the violet click beetle (*Limoniscus violaceus**), which relies heavily on ash trees at Bredon Hill in Worcestershire and at a further site in Gloucestershire (Whitehead, 2003; Littlewood *et al*., 2015). As these sites constitute two of three sites in the UK in which *L. violaceus* is found, losses of ash trees through ash dieback in these areas are likely to severely impact its survival potential in the UK (Whitehead, 2003; JNCC, 2019). Chapter 3 of this thesis addresses the conservation of *L. violaceus* at Bredon Hill in respect to dwindling habitat resources in more detail. Overall, the continued decline of ash trees carries high regional extinction risks for species with obligate or strong associations to them, demonstrating the cascading effect that can result from widespread tree disease (Littlewood *et al*., 2015; Hultberg *et al*., 2020)

Invasive Species

In addition to introduced pathogens, the introduction of new invasive species can have implications for forest health and the future availability of saproxylic habitats. An example illustrating this can be found in the Asian longhorn beetle (*Anoplophora glabripennis*), which is native to China and Korea and has been accidentally introduced several times to areas of North America, Europe and Australasia, where it acts as a pest species (Haack *et al*., 2010; Faccoli & Gatto, 2016). Infestations of *A. glabripennis* can result in tree death, with both young and old individuals of over 24 hardwood tree species being at risk (Faccoli & Gatto, 2016). As a result, the establishment of this pest species could result in considerable losses of trees, including those with valuable deadwood habitats (Faccoli & Gatto, 2016). This demonstrates the potential impacts of

*A recent reclassification synonymised *Limoniscus* with the genus *Gambrinus*, causing *L. violaceus* to be renamed as *Gambrinus violaceus* (Etzler, 2019). However, for the purpose of clarity, the previously used name is retained in this research.

invasive pests on deadwood resources and their associated saproxylic invertebrate fauna.

Climate change

Climate change is expected to result in increased incidence of forest disturbance events such as fire, drought and windthrows which can increase tree mortality and alter the structure and composition of woodlands (Seidl *et al*., 2017). These events alongside the general temperature increases will have particularly pronounced impacts on alpine forest systems, which contain some of the highest concentrations of deadwood-rich plots of all of Europe's forests (Brang *et al*., 2013; Puletti *et al*., 2017). In addition, climate change is likely to drive an increase in the frequency and severity of outbreaks of aforementioned pests and diseases that threaten woodland health (Seidl *et al*., 2017; Kurz *et al*., 2020). As mentioned in the previous sections, low connectivity as a result of historically fragmented landscapes and declining numbers of trees outside of woodland leave saproxylic invertebrates poorly prepared to escape the impacts of climate change through dispersal (Bailey, 2007). This is especially the case for species that have adapted to a strategy of infrequent dispersal due to their reliance on typically long-lived, stable habitats (Hedin *et al*., 2008). Chapter 2 of this thesis provides key data that could inform woodland management that promotes dispersal of saproxylic communities, potentially increasing their resilience to climate change.

1.3 - Deadwood connectivity as a limiting factor for saproxylic dispersal

The importance of studying dispersal in saproxylic communities

As identified in section 1.2, dispersal is a critical factor determining the survival of saproxylic species in fragmented wooded landscapes (Harding & Rose, 1986; Ranius, 2006; Bailey, 2007; Svensson *et al*., 2011). For dispersal to effectively take place, the habitat matrix needs to contain a sufficient number of high-quality habitat patches that are spaced closely enough together to accommodate species movement, creating a connected landscape (Hanski, 1998; Ranius & Hedin, 2001). Understanding species dispersal behaviours is critical to predict how species will respond to future habitat changes and to make effective management decisions to support species, for example through the creation of new habitat (Ranius & Hedin, 2001; Ranius & Kindvall, 2006; Svensson *et al*., 2011). Therefore, it is important that research continues into the spatial dynamics of connectivity in saproxylic communities, so that management can be adjusted to benefit as many species as possible and prevent future local extinctions (Watson *et al*., 2018). Chapter 2 of this thesis plays a role in this, contributing new knowledge on saproxylic dispersal in open wooded landscapes.

The dispersal tendencies of saproxylic species that use different decaying wood microhabitats

The dispersal abilities of saproxylic species vary according to the specific deadwood habitat that they use (Ranius & Hedin, 2001). For example, tree hollows take hundreds of years to develop and are very stable, with the ability to persist in living trees for many years (Nilsson & Baranowski, 1997; Ranius *et al*., 2009). Because of this, dispersal is a risky strategy for saproxylic invertebrate species that are highly specialised to tree hollow habitats (Stokland *et al*., 2012). Therefore, saproxylic beetles that inhabit tree rot holes have generally been found to have low dispersal abilities (Nilsson & Baranowski, 1997; Ranius & Hedin, 2001). In contrast, species that utilise more ephemeral resources such as freshly dead wood or dead, fallen trees that decay away quickly tend to have greater abilities to disperse due to the need to constantly find new habitat patches (Nilssen, 1984; Nilsson & Baranowski, 1997; Ranius & Hedin, 2001).

The influence of invertebrate body size on dispersal ability

Relationships have been found between the body size of saproxylic invertebrates and their dispersal ability; however, there are conflicting findings on the directionality of this link (Holland *et al*., 2005; Gibb *et al*., 2006). Holland *et al*. (2005) found that the abundances of longhorn beetles with larger body sizes were influenced by the density of surrounding habitat within larger spatial scales than those of smaller species. This suggests that body size is positively correlated with dispersal ability, with larger species able to make use of more distant habitat patches (Holland *et al*., 2005). Similarly, Gibb *et al*. (2008) found that larger species of parasitic wasps did not respond strongly to habitat abundance at any tested radius, indicating that their abundances may have been influenced by forest cover at scales greater than those covered by the study. A possible reason for these links between body size and dispersal is that larger insects may have greater control of their flight in more exposed areas with stronger wind currents, allowing them to accurately travel to more distant, isolated trees than smaller species (Peng, 1991; Pasek, 1988). Additionally, this tendency may have been driven by the fact that larger organisms have greater energetic needs than smaller individuals, requiring them to travel farther to gather sufficient resources to survive (Pasek, 1988; Holland *et al*., 2005).

In contrast to these findings, Sverdrup-Thygeson *et al*. (2017) found that beetles with specialist habitat requirements had significantly larger body sizes than generalist species, and that the abundance of specialist species was influenced by surrounding habitat density at a smaller scale than generalist species. This demonstrates that multiple factors of species biology may simultaneously influence dispersal behaviours. Therefore, it is important to consider species traits in combination when interpreting the results of dispersal studies.

Differing dispersal tendencies of common and rare species

Another characteristic that has been linked to dispersal tendency is species rarity (Brunet & Isacsson, 2009; Baur, 2014). Brunet & Isacsson (2009) found through window trapping that red-listed and formerly threatened species were less able to disperse over long distances of unsuitable habitat matrices than non-threatened species. It is possible that the lower levels of dispersal observed in rare species is due to smaller existing source populations from which dispersal events originate in these species (Brunet & Isacsson, 2009). Rare species may also rely on more specialist resources, meaning habitat patches that are suitable for them are rarer in the landscape (Gibb *et al*., 2006).

Alternatively, this link may be causal, with the poor dispersal abilities of these species being part of the reason that they are threatened, making them vulnerable to impacts from habitat fragmentation and less able to recolonise areas (Henle *et al*., 2004).

Understanding dispersal impacts in complex saproxylic communities

As shown by the variety of factors influencing dispersal ability addressed above, the extensive diversity of decaying-wood associated insects means the dispersal and resource-related needs at play in saproxylic communities are complex. The presence of species of various guilds and life strategies means that responses to tree density can vary widely across a single beetle community (Bergman *et al*., 2012). As a result, knowledge of the relationship between saproxylic insect diversity and deadwood dynamics at different spatial and temporal scales remains limited (Sverdrup-Thygeson *et al*., 2014)

Several studies have attempted to understand saproxylic dispersal by researching the behaviour of single species (Sverdrup-Thygeson & Mitgaard, 1998; Svensson *et al*., 2011). An example of this was carried out on the fungus-feeding Tenebrionid beetle, *Bolitophagus reticulatus*, which is commonly found in Norway (Sverdrup-Thygeson & Mitgaard, 1998). By quantifying *B. reticulatus* abundances in trees with different levels of connectivity, Sverdrup-Thygeson & Mitgaard (1998) identified that beetles were significantly less likely to inhabit trees with an average distance of greater than 125 m from the nearest three inhabited trees. This shows how patterns of occupancy can provide useful information on species habitat use and dispersal limitations. Chapter 2 of this thesis further explores this concept, using occupancy patterns to identify the distance radii over which habitat was most utilised by range of saproxylic species.

In choosing target species for these studies, it is important not to neglect rarer species as these often have different requirements than more common species (Ranius, 2006). As discussed previously, rare species have a tendency towards lower dispersal capacities, meaning that they require habitat to be more closely connected to colonise new patches (Baur, 2014). As a result, following the ‘umbrella species’ concept, studying the dispersal activities of particularly vulnerable, high priority species, and managing habitats to accommodate these species would theoretically be beneficial for biodiversity as a whole (Baur, 2014; Hedin *et al*., 2008; Svensson *et al*., 2011). For example, the dispersal tendencies of the umbrella species, *Osmoderma eremita* has been extensively researched using a range of different methods including telemetry, mark-release-recapture, and patterns of occurrence across a habitat matrix (Ranius & Hedin, 2001; Hedin *et al*., 2008; Svensson *et al*., 2011; Dodelin *et al*., 2017). The findings of these studies are further explored below, in the ‘Differing Dispersal Tendencies of Common and Rare Species’ section of this chapter.

Another approach used to simplify the study of whole communities is to analyse species dispersal requirements according to their specific functional groups (Pilskog *et al*.,2016; Janssen *et al*., 2017). This approach allows researchers to identify subsets of a population that are most vulnerable to extinction (Pilskog *et al*.,2016). Pilskog *et al*. (2016) found that beetles in the ‘xylomycetophagous’ functional group were present at significantly lower abundances in oak trees that were isolated from other hollow oaks at a 200 m scale. This analysis also ensures that key community processes are considered in dispersal studies, meaning that management decisions based on the results will prioritise the preservation of ecosystem functioning (Pilskog *et al*., 2016; Janssen *et al*., 2017).

Methodologies used to study saproxylic beetle dispersal

Several different approaches have been used to study insect dispersal. A summary of these, partially based on the work of Ranius (2006) is provided in Table 1.2.

Table 1.2. A summary of a range of techniques that have previously been used to study saproxylic invertebrate dispersal, based on a review by Ranius (2006).

Method	Example reference	Pros	Cons
Mark-release-recapture	(Ranius, 2001)	Direct observations can be made of the movement activities of individual specimens.	Dispersal distance observations are limited by the search radius used to recapture individuals. The likelihood of re-finding individuals decreases with distance, as the search area increases exponentially with increasing search radii. May overlook rarer dispersal events. If insects disperse to unexpected locations, they will be difficult to re-find meaning that some dispersal events may not be recorded.
Telemetry using radio-transmitters	(Hedin *et al.*, 2008)	Obtains direct measures of species dispersal in the field.	Requires specialist, potentially expensive equipment.

		Allows observations of dispersal events that end in unexpected habitats.	Radio-transmitters may influence species behaviour. Only possible for larger flying insects that will not be excessively impeded by the attachment of a radio-transmitter. If an individual moves too far it can be difficult to track them.
Observation of insect flight using slow-motion recording equipment	(Farisenkov *et al*., 2020)	Allows detailed analysis of flight behaviours, allowing researchers to better understand species behaviours.	Can be difficult to carry out and requires expensive specialist equipment.
Tracking the colonisation of new habitat patches with knowledge of likely source population locations	(Jonsson & Nordlander, 2006)	Conclusions can be made on species colonisation ability in real world habitat systems. Can be used to understand insect colonisation ability within certain time scales.	It is difficult to understand the influence that the size of the source population has on the results.
Analysing patterns of occurrence	(Bergman *et al*., 2012)	Show the real-world impacts that species dispersal abilities have on their	It may be difficult to draw firm conclusion on species dispersal

throughout a habitat matrix		interaction with habitat matrices. Reflect long-term dispersal trends.	abilities from patterns observed. Results may be complicated by historical changes in habitat patch distributions. It can be difficult to define which habitat patches comprise truly suitable dispersal sources.
Analysis of genetic structuring across a population	(Schmucki *et al.*, 2006)	Show the impact that habitat isolation can have on the species studied.	There may be several possible explanations for trends identified through genetic studies, meaning that they can be difficult to interpret. Due to the need to collect specimens for genetic analysis, it can be difficult and potentially detrimental to conservation to study rare and threatened species.

Chapter 2 of this thesis uses the approach of studying dispersal through existing occurrence patterns throughout a landscape. This method was chosen as it allows observations to be made that are directly relevant to the landscapes studied and the invertebrate communities existing within them. The study carried out in Chapter 2 was designed to develop conclusions to underpin the development of the conservation management plans for these landscapes, and the data gathered using species occurrence patterns were considered likely to best facilitate this. In addition to developing a better understanding of species movement abilities through the woodlands studied, this method can provide information on habitat patches that are ‘hot-spots’ for rare species, which could be prioritised in future conservation efforts (Ranius, 2006).

Spatial scales that are relevant to saproxylic beetle dispersal

Dispersal studies using the above methods have found saproxylic species to be associated with a range of different scales of habitat connectivity (Ranius *et al*., 2011). Several studies into the dispersal of specific beetle species have identified the importance of local habitat presence at a small scale. For example, the majority of dispersal journeys recorded for *Osmoderma eremita* were less than 50 m in length (Hedin *et al*., 2008). Similarly, the distances of less than 100 m between trees can be enough to negatively impact the dispersal of *B. reticulatus* between fungal fruiting bodies (Sverdrup-Thygeson & Mitgaard, 1998).

Populations of other species have been found to be more sensitive to habitat density changes across greater distance ranges, indicating that they can disperse further to access more distant habitat resources (Saint-Germain & Drapeau, 2011). For example, habitat cover at scales between 800 m and 2,000 m were found to be most influential on the abundance of several species of Cerambycidae (Saint-Germain & Drapeau, 2011). Another study found that beetle species that live on hollow oak trees responded to tree density at differing spatial scales, between 52 m^2 and >5,200 m^2 (Bergman *et al*., 2012).

Despite the habitat scale for some species being found to be low, Økland *et al*. (1996) found that 40 x 40 m scale was too small to allow meaningful study of the community-level relationships with habitat density in a flight interception trapping study. This suggests that, although some highly dispersal limited species exist, most saproxylic species are able to disperse further than 40 m and use more widely spaced habitat patches (Økland *et al*., 1996). In fact, Økland *et al*., (1996) found that habitat variations at the largest scale included in the study (4 km^2) were the most meaningful for saproxylic dispersal. Similarly, Bergman *et al*. (2012) found that overall species richness of saproxylic beetle diversity in a tree was most significantly influenced by habitat density at a scale of 2,284 m.

Overall, scales from approximately 50 m^2 to over 5,000 m^2 have been found to be variably important for saproxylic dispersal (Hedin *et al*., 2008; Saint-Germain & Drapeau, 2011; Bergman *et al*., 2012). Chapter 2 of this thesis investigates spatial scales within this range to add to existing knowledge on dispersal strategies. The studies reviewed in this section also highlight that responses to habitat density at a community level, using measures such as species richness may not reflect the nuances of individual species dispersal responses (Bergman *et al*., 2012). As a result, the research in Chapter 2 of this thesis encapsulates both community and species-level dispersal in its findings.

- **A case study of an umbrella species approach to habitat connectivity planning - *Osmoderma eremita***

As community-level responses to habitat density have been found to occur at greater scales than that of some vulnerable species, it is important to ensure that the species with the lowest dispersal capacities are not forgotten in management decisions. To do this, the designation of species with lower dispersal tendencies as ‘umbrella species’ can be a useful conservation practice (Hedin *et al*., 2008). One example of this is the previously mentioned Scarabaeid beetle species *O. eremita* (Ranius, 2002; Hedin *et al*., 2008). In addition to being featured on the red-list, *O. eremita* has a life strategy that involves developing and feeding exclusively within tree hollows, a trait which is associated with low dispersal (Ranius & Hedin, 2001; Ranius, 2002).

Dispersal of *O. eremita*, between trees has been shown to occur infrequently, over generally short distances (Ranius & Hedin; 2001; Hedin *et al*., 2008). Using mark-recapture methods, Ranius & Hedin (2001) estimated the dispersal rate to be 15% of individuals over 5 years. With this low dispersal tendency, *O.eremita* is faced with a challenge of finding new mates in newly inhabited territory. It is thought to overcome this challenge by mating before dispersal to increase the chances of forming a new colony in a new habitat (Svensson *et al*., 2011). However, this may still leave this species under threat of becoming genetically bottlenecked and bring the associated risks of vulnerability to disease or other stochastic events (Bohonak, 1999). As a result of these findings, Ranius and Hedin (2001) suggest that habitat fragmentation at a scale of a few hundred meters could be detrimental to the local population structures of *O. eremita*.

By understanding the needs of this particularly vulnerable species, conservation strategies can be better shaped to ensure that they accommodate species under the highest threat of local extinction. The low dispersal distance of *O. eremita* combined with its preference for high quality rot hole habitats make it an ideal indicator species (Ranius, 2002). Therefore, managing landscapes to protect *O. eremita* would have residual benefits for large proportions of the coexisting saproxylic fauna.

Despite this, using an umbrella-species-led approach can carry a risk of focusing too strongly on the requirements of the chosen species at the expense of other threatened species with differing needs (Ranius *et al*., 2011). For example, the presence of beetle species with greater rarity statuses, including *Elater ferrugineus* and *Tenebrio opacus,* have been shown to be linked to habitat connectivity on larger scales than those required by *O.emerita* (Ranius *et al*., 2011). This means that *E. ferrugineus* and *T. opacus* disperse over longer distances and would benefit from habitat patches at greater distances from their source populations than *O.emerita* (Ranius *et al*., 2011). As a result, these species would require different habitat management considerations than *O.emerita*, with a greater prioritisation of long-distance habitat connectivity (Ranius *et al*., 2011). This shows that, whilst umbrella species can constitute an effective starting point in designating protected areas for habitat connectivity, it is important to maintain a community-wide, site-specific perspective in conservation decisions to ensure that the requirements of other valuable saproxylic species are not overlooked.

Considerations of dispersal in conservation

When making conservation decisions regarding habitat connectivity, it is important to consider the density of habitat patches in combination with habitat quality (Ranius & Kindvall, 2006). The most efficient and appropriate conservation measures for a landscape can vary according to factors such as landscape history, current habitat distributions and the potential for rapid habitat restoration in the area (Ranius & Kindvall, 2006). Therefore, each landscape should be considered for its unique character and invertebrate community when making conservation decisions. To enable this, Chapter 2 of this thesis gathered data on the density and microhabitat characterisation of veteran trees in wooded landscapes, which can feed into conservation decisions at the studied sites.

1.4 - Conservation of saproxylic invertebrates

Protecting existing woodland habitat

As loss of habitat is a key threat to saproxylic invertebrates, the protection of remaining, existing deadwood habitats is a clear priority for their conservation (Davies *et al*., 2008; Woodland Trust, 2013, 2021). Encouraging progress in woodland protection is currently being made, with forest area dedicated for biodiversity conservation in Europe having increased by half a million hectares every year between 2001 and 2011 (Forest Europe, UNECE & FAO, 2011). Despite this, a lack of guidelines ensuring the appropriate spatial design of protected areas, in combination with insufficient collaboration between stakeholders and inadequate funding, mean that current forest protections may not be enough to ensure the long-term persistence of biodiversity (Branquart *et al*., 2008).

Approaches to the protection of deadwood resources

There are various approaches to the preservation of saproxylic resources, including the protection of whole woodlands areas that are rich in deadwood habitats, and the protection of individual trees that confer particular saproxylic value (Pryor & Peterken, 2001). European and UK-specific legislation exists for these approaches to provide guidelines on their application and facilitate their enforcement (Pryor & Peterken, 2001).

Although these coordinated protection regulations provide a useful basis for habitat conservation, they should not overlook the fact that wooded landscapes require individual consideration (Forestry Commission, 2003). There is no one-size-fits all approach to woodland management, and it is important that wooded landscapes are managed according to their unique characteristics and the assemblages of species that they host (Natural England, 2000; Forestry Commission, 2003). For example, wet woodlands benefit from the promotion of natural regeneration through reduced grazing pressures, while many lowland woods benefit from more active management to create open areas (Forestry Commission, 2003). Unfortunately, evidence of the effectiveness of different management techniques for saproxylic invertebrate conservation is currently lacking, as there have been few long-term field studies collecting high-quality data on their effects (Davies *et al*., 2008). Therefore, it is important that management programmes incorporate sufficient monitoring to understand how the activities carried out influence saproxylic populations in practice.

In addition to protecting existing resources, wooded landscapes should also be managed with the future in mind. This may involve the creation of new resources to improve connectivity and ensure habitat representation over time (Natural England, 2000; Jansson, Ranius, *et al*., 2009; Bengtsson *et al*., 2012). The creation of these new resources can take a long time; however, as discussed later in this section, novel research is being conducted into more short-term methods of plugging potential gaps in the continuity of saproxylic habitats (Jansson, Ranius, *et al*., 2009; Bengtsson *et al*., 2012). The research in Chapter 3 of this thesis further builds upon this concept.

Protecting valuable woodlands

There are various regulations under which woodland areas, and the valuable deadwood resources that they contain, receive statutory protection. One of these is the Habitats Directive, which is European legislation that was adopted in 1992 for the protection of rare, threatened, or endemic species (European Commission, n.d.; Council of the European Community, 1992). It forms the basis of the designation of Special Areas of Conservation (SAC) under Natura 2000, a coordinated network of protected areas (European Commission, n.d.; Pryor & Peterken, 2001). European member states are required to implement appropriate conservation measured for SACs and make efforts to prevent their disturbance and deterioration (Council of the European Community, 1992). The Habitats Directive covers various types of natural/semi-natural woodland which are likely to carry valuable stocks of decaying wood (Council of the European Community, 1992).

Since the UK left the EU in 2020, protected sites in the UK are no longer considered a part of the Natura 2000 network (Defra, 2021). Instead, in the UK SACs are considered alongside Special Protection Areas (SPA) in the designation of the National Site Network (Pryor & Peterken, 2001; Defra, 2021; JNCC, 2022a). These SPAs, which began to be implemented in the 1980s, are designated specifically for the protection of birds and are classified under a several sets of regional conservation regulations (JNCC, 2022a). As they are tailored towards birds, SPAs contain a high proportion of wetland areas; however, they do contain some valuable woodland sites including the New Forest and Ashdown Forest (JNCC, 2022b). The condition of SPAs is regularly monitored by Statutory Nature Conservation Bodies (SNCB) and results of this are used to assess the status of protected species within them (JNCC, 2022a).

In the UK, the designation of Sites of Special Scientific Interest (SSSI) is one of the primary mechanisms for statutory protection of areas with ecological and geological interest (Pryor & Peterken, 2001). National countryside government agencies are legally responsible for the protection of their respective SSSIs (Pryor & Peterken, 2001). As of 2001, 23% of ancient semi-natural woodlands were designated as Sites of Special Scientific Interest (SSSI) (Pryor & Peterken, 2001).

A further method of site protection in the UK is the designation of sites as National Nature Reserves (NNR) (Pryor & Peterken, 2001). The status of NNR is designated to sites that are already classified as SSSIs and represent particularly high-quality examples of the habitat/landscape type that they represent (NatureScot, n.d.; Pryor & Peterken, 2001). They are chosen based upon particularly unique and outstanding attributes that are deemed worthy of special consideration in conservation (NatureScot, n.d.). In 2001, England contained 9,185 ha of woodland habitat under NNR designation, comprising a range of Biodiversity Action Plan (BAP) woodland types including mixed deciduous woods, western oakwoods, wet woodland, ancient parkland/wood pasture, beech/yew woods, coniferous plantations, and upland ashwoods (Pryor & Peterken, 2001).

Protecting pasture woodland

Conservation policy has been shaped by a framework based upon set vegetation/woodland categories (Alexander, 2016a). Because of this, closed canopy woodland has historically received the most conservation attention, with pasture woodland, comprising a heterogenous mosaic of habitats and conditions, being misclassified and neglected (Miklín & Čížek, 2014; Alexander, 2016a). The open, sun exposed conditions in pasture woodlands have historically provided trees the opportunity to grow without excessive crown competition, allowing them to reach very old ages and develop a wealth of deadwood habitats (Kirby *et al*., 1995). As a result, pasture woodlands are one of the most important woodland types for saproxylic invertebrates (Alexander, 1999). However, pasture woodlands have experienced considerable depletion (Miklín *et al*., 2018). For example, between 1903 and 1995, 43% of parkland areas in Lincolnshire were lost and a further 23% reduced in size (Kirby *et al*., 1995). This demonstrates that they have historically not been appreciated for their deadwood habitat value in conservation management planning (Alexander, 2016a).

Perception of the value of pasture woodlands is now increasing and recent government guidance states that ancient pasture woodlands should be valued to the same extent as other ancient woodland types in planning decisions

(Natural England & Forestry Commission, 2022). Pasture woodland is now listed as a UK Biodiversity Action Plan priority habitat and is given special consideration in the designation of woodland as SSSIs (BRIG, 2011; Latham *et al*., 2018).

Pasture woodlands are vulnerable to management changes that may cause them to become more shaded and enclosed, such as ‘hands-off/rewilding’ approaches in which succession is allowed to naturally progress (Miklín *et al*., 2018; Ranius & Jansson, 2000). This is because tree mortality increases under enclosed conditions, causing increased losses of valuable veteran trees (Miklín *et al*., 2018). Trees are also more likely to die before reaching a veteran stage under closed woodland conditions (Miklín *et al*., 2018). As a result, techniques that promote disturbance and thinning, such as those used in past traditional management, enhance the health and resilience of pasture woodland (Miklín *et al*., 2018; Clark & Schweitzer, 2016). Therefore, it is important to not only protect pasture woodland areas from loss through development but also to ensure that they are sensitively and appropriately managed to preserve their unique character into the future (Grove, 2002). Chapter 2 of this thesis provides data to fill knowledge gaps on the optimal management strategies for these vulnerable habitats so that protection designations can be most appropriately applied in the future.

Protecting individual trees

Trees outside woodlands such as those found in hedgerows, urban areas, or arable field margins can contribute to important wildlife corridors and provide a refuge that enhance local species richness (Merckx *et al*., 2012; Feber, 2017). However, in a similar way to pasture woodlands, trees outside woodlands can be overlooked in conservation decisions, being vulnerable to loss through development and land use change (Nolan *et al*., 2020). They are afforded some protection through various legislations and guidelines, for example, felling licences are required for the removal of any tree unless it falls within a list of exceptions (such as trees with a low diameter, those that are infected with a quarantined disease/pest or that present a danger to people or property) (Forestry Commission, 2020). Official recommendations also state that trees with arboriculture, landscape, cultural, or conservation value should be retained during construction activities (British Standards Institution, 2005).

Additionally, individual trees may be afforded protection through tree protection orders (TPOs) (Natural England, 2000; Woodland Trust, 2011; Forestry Commission, 2020). These are given at the discretion of local planning authorities, usually to trees with particular landscape interest (Natural England, 2000). Permission from the local authority must be given for work to be carried out on a tree that has been placed under a TPO, with unauthorised work resulting in a fine (Natural England, 2000). Similarly, trees within local conservation areas or other conservation designated zones such as Sites of Special Scientific Interest (SSSI) are afforded protection from unauthorised work (Natural England, 2000).

Trees may also benefit from protections afforded to other species that inhabit them, such as bats (Natural England, 2000; Woodland Trust, 2011). Specific tree-related activities that are controlled for the protection of bats include the removal of branches from mature trees and the removal of woodlands and hedgerows that may be used for bat ‘commuting’ (Natural England & DEFRA, 2014a).

A further safeguarding method that is used to prevent damage of notable trees during construction work is the enforcement of root protection areas (RPA) within which soil disturbance should be avoided in order to maintain root and tree health (Woodland Trust, 2011). This is calculated as 12x the diameter of a tree trunk diameter breast height (DBH), although a greater area of 15x the DBH is recommended for particularly vulnerable ancient trees (Woodland Trust, 2011). This is particularly important as root compaction has been reported as the most common threat to ancient trees (Nolan *et al*., 2020).

Unfortunately, the weak enforcement of these protections and the fact that many valuable trees fall outside of their scope mean that veteran trees remain under threat in the UK landscape (Woodland Trust, 2021b). This further exacerbates the decline in deadwood resources and the resultant impacts on saproxylic communities, which drives the conservation-based research of the present study.

Protecting connectivity features

Hedgerows can act as corridors to aid species movement between woodland patches (Zhang & Usher, 1991; Beier & Noss, 1998; Petit & Usher, 1998). Woodland associated mammals, birds and invertebrates benefit from the structural complexity of hedgerows as protective cover when moving across otherwise more hostile landscape types (Davies & Pullin, 2007). Such connectivity positively influences gene flow and the resilience of species to changing conditions such as those brought by climate change (Coulon *et al*., 2004; Heller & Zavaleta, 2009). In the UK, hedgerows receive government protection when they meet criteria relating to length, age, location and associated species (Natural England & DEFRA, 2014b).

Monitoring woodland resources to understand deadwood distributions

Creating inventories of veteran trees and woodland is essential for the protection of saproxylic resources, as it is important to have a comprehensive understanding of where trees of greatest value lie so that they may be protected. Within the UK, several initiatives have endeavoured to gather records of ancient and veteran tree resources to allow improved conservation planning and habitat protection. One of these is the ancient woodland inventory (AWI), which was initiated by Natural England in 1981 (Spencer & Kirby, 1992; Whittet *et al*, 2015). This aimed to aid the selection of sites for SSSI status and to identify priorities for future survey work (Whittet *et al*., 2015). A problem with the AWI is that it does not represent ancient trees that occur in low-density situations such as pasture woodlands (Natural England & Forestry Commission, 2022). To account for this, Natural England has also formed a Wood Pasture and Parkland inventory (Frith *et al.*, 2009). This was collated using a combination of existing datasets, historic maps, aerial photography and ground-truthing (Frith *et al.*, 2009).

In addition to woodlands, ancient trees with great ecological value also occur in a wide range of other situations such as hedgerows, arable land and urban areas (Feber, 2017; Forest Research, 2017). Such trees are termed Trees Outside Woodlands (TOW) (Brown & Fisher, 2009; Feber, 2017). In order to ensure that TOWs are recorded alongside those in woodlands, a record of ancient, veteran and otherwise notable trees in the UK has been accumulated in the Ancient Tree Inventory (ATI) through the work of citizen scientists (Nolan *et al*., 2020). Approximately 12,300 ancient and veteran trees have been recorded on the Ancient Tree Inventory with many more awaiting inclusion (Woodland Trust, 2021b). In addition to this, the National Tree Inventory (NTI) periodically analyses maps and aerial photographs to estimate forest and tree resources, with verification carried out through fieldwork in a subsample of sites (Forest Research, 2017, 2019).

Umbrella species for the designation of protected woodland

The ‘umbrella species’ concept mentioned in section 1.3 can be used in a practical context in the selection of protected areas to ensure the persistence of high-quality habitats and vulnerable community assemblages (Simberloff, 1998; Gouix *et al*., 2015; Eckelt *et al*., 2018). There are currently 23 species of saproxylic beetle that are protected through the Habitats Directive, specifically selected for their associations with threatened habitats (Council of the European community, 1992; Hardersen & Zappioni, 2018). By recording the presence of these species, the quality of a woodland can be monitored, allowing appropriate protections and conservation measures to be applied. Additionally, as mentioned in section 1.3, managing landscapes for umbrella species can promote beneficial woodland connectivity (Hedin *et al*., 2008).

- ***Limoniscus violaceus* – a saproxylic umbrella species**

The violet click beetle (*Limoniscus violaceus*) is an endangered species that is currently protected under various pieces of legislation including the Wildlife and Countryside Act and the European Commission Habitats Directive (Wildlife and Countryside Act, 1981; Council of the European Community, 1992; Nieto & Alexander, 2010). It is considered an umbrella species as it requires high-quality basal tree hollow habitat to survive (Gouix *et al*., 2012). It is recognised throughout Europe as a relic of old-growth woodlands and it is generally rare and sparsely distributed throughout its range, having gone extinct in some localities (Gouix *et al*., 2012).

Due to its preference for ancient trees, *L. violaceus* is thought to be associated with pasture woodlands where open-grown trees have adequate light conditions to reach particularly old ages (Alexander, 2009). However, *L. violaceus* is also known to breed in enclosed, unmanaged forests (Gouix *et al*., 2012). This discrepancy is likely linked to the fact that *L. violaceus* exhibits little preference for specific tree species, having been recorded from a range of broadleaved trees including beech (*Fagus* spp.), oak (*Quercus* spp.), ash (*Fraxinus* spp.), alder (*Alnus* spp.), elm (*Ulmus* spp.), and others (Gouix *et al*., 2012). These tree species mature differently in more enclosed forest conditions, resulting in some species developing appropriate microhabitats under greater levels of shade, whereas others require the sun exposure that is typical of pasture conditions (Ligot *et al*., 2014). This lack of specialisation of *L. violaceus* regarding tree species highlights the homogenising effect of extensive decay on the nature of deadwood, as unique tree-associated defence chemicals and wood structures are broken down (Stokland *et al*., 2012).

L. violaceus is known to prefer large diameter trees that have extensive hollowing at the base containing wood mould that forms a continuous gradient with the soil below (Gouix *et al.,* 2015). It uses more solid clumps of decaying wood as a pupation site, so a lack of uniformity of wood mould texture is beneficial (Gouix *et al*., 2012). The moisture content of wood mould substrate has also been found to be an important factor in *L. violaceus* habitat selection (Gouix *et al*., 2015; Cuff, Müller, *et al*., 2021). As in many other species of saproxylic insect, *L. violaceus* has been observed visiting flowers (Whitehead, 2003; Falk, 2021). Specifically, it has been recorded on the blossom of hawthorn trees on two separate occasions at different sites in the UK (Whitehead, 2003). This supports the tendency of *L. violaceus* to survive well in pasture woodlands, as hawthorn is a staple of such open, grazed situations and is rarely found in more shaded forest situations (Quelch, 2000; Jørgensen & Quelch, 2014).

Finding and monitoring umbrella species

For umbrella species to be used effectively in site designation and protection, they must be monitored to gain an understanding of their distributions and success levels at different sites. This constitutes a problem for saproxylic umbrella species such as *L. violaceus*, as they are very reclusive and rarely observed outside of their tree-hollow habitats (Whitehead, 2003). It can be difficult to investigate such habitats thoroughly without negatively impacting the target species, because survey methods such as the excavation of wood mould can cause disturbance and damage to their habitats (Gouix & Brustel, 2012). Other methods, such as pitfall trapping, introduce an increased risk of killing specimens of the target species (Woodcock, 2005). They can also require extensive time investment of researchers when emptied frequently to reduce killing risk, which can be costly in funding-limited research projects.

To circumvent these problems, less intrusive and time-intensive species surveying techniques are being investigated, for example the use of species-specific sex hormone pheromone lures to attract males present in an area (Svennson *et al*., 2012; Musa *et al*., 2013). A notable example of this was a pheromone successfully developed for the uncommon saproxylic beetle *Elater ferrugineus* which also inhabits tree hollows (Svennson *et al*., 2012; Musa *et al*., 2013). The pheromone has subsequently been used to elucidate the true extent of *Elater ferrugineus* populations and better understand their habitat requirements (Musa *et al*., 2013). Whilst no pheromone has yet been developed for *L. violaceus*, work is in progress (D. Harvey, 2019, pers. comm.). If successfully formulated, this would be a valuable tool to properly assess the true distribution of the species. However, pheromones should be used with discretion as the repeated attraction of males to lures could have detrimental impacts on actual mating activities (Svennson *et al*., 2012). Although pheromone work has yet to take place, *L. violaceus* has been successfully lured to cat food baits (D. Heaver 2021, pers. comm.). This could indicate that *L. violaceus* benefits from the presence of incidental carrion in tree hollows.

In addition to lure-based surveying methods, a trained dog has successfully been employed to indicate the presence of adult and larval *Osmoderma eremita* (Mosconi *et al*., 2017). The dog was able to identify *O. eremita* presence to a high degree of accuracy and demonstrated the ability to distinguish the smell of *O. eremita* from that of other Scarabaeidae species (Mosconi *et al*., 2017). This survey approach prevents disturbance and damage of beetle populations that may be caused by manual surveying and has the potential for use with other rare umbrella species.

The analysis of environmental DNA (eDNA) has allowed the successful detection of species (including rare and invasive ones) in substrate samples, for example in freshwater systems (Rees *et al*., 2014). If it was possible to extract and analyse eDNA from samples of deadwood substrates such as wood mould, this could be a useful method of monitoring saproxylic umbrella species. However, attempts to use eDNA in deadwood contexts have so far yielded low levels of success in the detection target beetle species (Winiger *et al*., 2022). This was thought to be a result of extensive degradation of DNA fragments in the deadwood substrates, potentially through interaction with extracellular fungal enzymes and low pH levels (Winiger *et al*., 2022). It has therefore been suggested that eDNA is not currently a reliable method for detecting the presence of saproxylic beetles (Winiger *et al*., 2022). However, it is possible that advancements in sampling and DNA extraction protocols may increase the applicability of eDNA to monitoring invertebrates in deadwood contexts in the future (Winiger *et al*., 2022).

The work in Chapter 3 of this thesis constitutes a potential conservation initiative for *L. violaceus*. Therefore, is possible that several of the innovative monitoring techniques outlined in this section may be applied alongside the experimental infrastructure set up for this study to enable forward research programmes in the future.

Managing woodland resources for saproxylic invertebrates

Tree planting and the creation of new woodland

Despite historical deforestation in Europe, the trend has now switched towards woodland expansion, with forest area in Europe having increased by 5.1 million ha between 2005 and 2011 (Forest Europe, UNECE & FAO, 2011). Woodland cover has doubled in the UK and Ireland over the past 100 years and is now estimated to cover approximately 13% of land (Woodland Trust, 2021b) However, many new areas of woodland in the UK suffer from poor planning and often comprise of ecologically poor, non-native tree species (Woodland Trust, 2021b). This could lead to woodlands of the future being unsuitable to support local saproxylic faunas.

The benefits of future woodlands could be maximised if they were planned in a way that enhanced pre-existing resources. The Woodland Trust (2021b) recommends that new woodland patches should be designed to extend existing native woodland and connect patches of semi-natural habitat where possible. This enhanced woodland connectivity would promote the resilience of local invertebrate communities (Schiegg, 2000a). Natural tree colonisation provides a cost- and resource-effective method to achieve this (The Woodland Trust, 2021b), because natural tree regeneration creates resilient woodlands, rich in structural heterogeneity, which promotes biodiversity (Forestry Commission, 2021). Nonetheless, it does involve some sacrifices, such as the ability of planners to control and predict the nature of the resulting woodland. Where tree planting does occur, strategies such as rigorous border checks of imported trees should be enforced, to minimise associated risks of introducing new pests and diseases (Woodland Trust, 2021b).

Managing existing woodlands appropriately

The management approaches employed in woodlands have a great influence on their saproxylic value. As discussed in section 1.2, intensive extraction of trees and ‘forest hygiene’ practices mean that managed forests typically contain lower volumes of deadwood and lower numbers of decaying wood microhabitats than natural forests (Stokland *et al*., 2012). As a result, managed forests have been found to support a lower saproxylic insect diversity, with the use of clear cutting strongly altering the species composition of saproxylic communities (Siitonen, 2001; Heikkala *et al*., 2016). To support and conserve saproxylic invertebrates, it is recommended that forest management practices leave areas of deadwood where appropriate, including a range of different deadwood types to ensure high quality of habitat (Sippola *et al*., 1998). Leaving selected trees in an otherwise heavily managed woodland can provide open-grown deadwood resources that provide suitable habitat for many species of insect, including several that are rare and threatened (Kalia *et al*., 1997).

Despite commonly perpetuated myths, integrating deadwood into forest management practices is not likely to increase the risk of pest outbreak or forest fires (Stokland *et al*., 2012). Moreover, active deadwood promotion in managed woodlands has been found to significantly increase local saproxylic biodiversity over short timescales (Doerfler *et al*., 2018). This shows the potential for productive woodland to aid in the habitat connectivity of woodland nature reserves over wider landscapes (Doerfler *et al*., 2018). The designation of land as deadwood patches does carry a cost of decreased wood product yield (Zumr *et al*., 2021). However, if the areas designated for biodiversity are chosen carefully, these costs can be minimised, with a compensatory benefit associated with the delivery of woodland ecosystem services through biodiversity, as described earlier in section 1.1 (Stokland *et al*., 2012; Doerfler *et al*., 2018; Zumr *et al*., 2021). In addition to woodland health gains, schemes have also been suggested in which landowners receive monetary compensation for the role that their land plays in biodiversity enrichment (Mitani & Lindhjem, 2015; Zumr *et al*., 2021). This is because increased conservation implementation would help governments meet their targets in environmental protection and improvement (Environment Act, 2021).

Islands of diversity among plantation forests

One method to improve the ecological diversity of productive forests is to leave designated areas of woodland untouched, allowing trees to naturally age and deadwood to accumulate (Lachat & Bütler Sauvaun, 2007). These patches have been termed 'islands of senescence' ('îlots de sénescence') (Lachat & Bütler Sauvaun, 2007). A similar concept, 'islands of ageing' ('îlots de vieillissement'), has also been proposed, whereby trees are allowed to age to a certain extent, but are removed before they die and are not left as deadwood (Lachat & Bütler Sauvaun, 2007; Mason *et al*., 2016). However, it has been argued the 'islands of ageing' approach can be counterproductive, as habitat accumulation is minimal and the removal of trees at an early stage can damage pioneering saproxylic insects that are beginning to use the maturing resources (Lachat & Bütler Sauvaun, 2007).

For the ‘islands of senescence’ method to be effective, they should be large enough to ensure the continued presence of a complete range of decay stages (Lachat & Bütler Sauvaun, 2007). A minimum size of 0.5 ha has been suggested, however, larger decay islands would likely offer greater biodiversity benefits (Jakoby *et al*., 2010; Müller *et al*., 2012). The approach has been put into practice in Switzerland and France, where financial compensation is offered for the inclusion of islands of senescence in productive forests (Bütler *et al*., 2006; Mason *et al*., 2016). Inventories of existing islands of decay have shown that they can contain saproxylic microhabitats at an even greater density to natural forests (Bütler *et al*., 2006; Lachat & Bütler Sauvaun, 2007).

Manmade microhabitat Islands

While ‘islands of senescence’ seek to incorporate ancient woodland features as complete habitat patches on a landscape scale, there are other methods being developed to enhance the presence of individual microhabitats in existing woodland situations (Rotheray, 2004; Jansson, Ranius, *et al*., 2009; Bengtsson et al., 2012). These methods are particularly valuable for increasing the representation of microhabitat-types that can take a long time (as long as several hundreds of years) to develop naturally (Jansson, Ranius, *et al*., 2009; Ranius *et al*., 2009). Examples of microhabitat-focused practices include the veteranisation of trees and the introduction of manmade structures designed to mimic natural tree-decay scenarios (Rotheray, 2004; Jansson, Ranius, *et al*., 2009; Bengtsson et al., 2012). These measures can be employed to supplement areas of woodland that have declined in quality over time, for example where ancient trees approach the end of their lives without the appropriate woodland age structure to ensure a consistent presence of saproxylic microhabitats (Bengtsson et al., 2012). They also have potential for use in improving connectivity of fragmented wooded landscapes by providing habitat stepping-stones to saproxylic species (Hilszczański *et al*., 2014).

- **Veteranisation and habitat maintenance**

Veteranisation is a process by which trees are intentionally damaged in a way that exposes heart wood to air, allowing it to dry out enough to create a suitable moisture level for fungi to grow (Bengtsson et al., 2012). This process may be aided by the direct inoculation of heart-rot associated fungi into specially created holes in trees (Wainhouse & Boddy, 2021). These activities mimic the cumulative damage that occurs over a tree's lifetime and speed up age-associated processes (Bengtsson et al., 2012). Therefore, through veteranisation, trees can exhibit decay-habitat features usually found on ancient trees at younger ages (Bengtsson et al., 2012).

Figure 1.1. An example of a dead tree that has fallen and been re-erected at Windsor Forest.

On the opposite end of the spectrum to promoting the early formation of saproxylic habitats through veteranisation, it is also possible to extend the life of pre-existing resources that are deteriorating. Trials have been carried out involving the re-erection of fallen trees by standing them up vertically and securing them to existing standing structures (Figure 1.1) (Whitehead, 2003). Re-erecting trees aims to slow their decay and increase their lifespan as a cavity habitat for invertebrates, however this process is still at an exploratory stage.

- **Hoverfly lagoons**

One example of a saproxylic microhabitat that has been successfully recreated through human intervention are water-filled rot holes or 'phytotelmata' (Rotheray, 2004; Kitching, 1971). These deep tree cavities filled with water are used as development sites for a variety of insect larvae, notably including a range of hoverflies (Syrphidae) (Ulyshen, 2018). Phytotelmata provide these larvae with food in the form of accumulated bacteria, algae and detritus, as well as with stable temperature conditions to facilitate their development (Kitching, 1971).

Of the hoverflies that use phytotelmata, a few species are considered of conservation concern, including *Callicera spinolae* and *Blerra fallax*, both of which are included in the Biodiversity Action Plan list of priority species (JNCC, 2007; Rotheray, 2004; Rotheray, 2012; Rotheray *et al*., 2016). To supplement the conservation of both of these species, successful trials have been carried out involving the experimental creation of artificial rot-holes to act as breeding sites in areas where they were present (Rotheray, 2004; Rotheray, 2012). The methods of creating artificial rot holes for hoverflies have included filling plastic bottles with rotting material and using chainsaws to create new hollows in existing tree stumps (Rotheray, 2004; Rotheray & Rotheray, 2012).

Hoverfly lagoons have also been used as an educational tool to teach members of the public about rot-hole specialist invertebrates (Kilburn Junior School, n.d.). They are particularly suitable for this as they are low-cost and can be set up in positions that are easily accessible to aid observation (Buzz Club, 2018). Their accessibility to members of the public has also fed into the use of hoverfly lagoons in a citizen science project in which participants are encouraged to gather data on hoverfly larval numbers (Buzz Club, 2018).

- **Beetle boxes**

Another example of the artificial replication of a naturally occurring deadwood microhabitat can be found in the form of ‘beetle boxes’. These are containers filled with a decaying wood substrate installed into woodland landscapes (Jansson, Ranius, *et al*., 2009). Several variations have been trialled including wooden boxes attached to tree trunks, hollowed tree stumps and even a small out-building filled with decaying wood (Jansson, Ranius, *et al*., 2009; Sherwood Forest, 2022; Blincow & Newton, 2019). These constructions are designed to provide analogous conditions to those found in tree hollows containing a fine, crumbly wood mould (Jansson, Ranius, *et al*., 2009). Beetle boxes have been shown to provide adequate conditions for the survival and reproduction of the rare beetle species, *Osmoderma barnabita* which requires similar habitat to the previously mentioned umbrella species, *O. eremita* (Hilszczański et al., 2014). Similarly, boxes installed in Sweden were inhabited with 91 species of saproxylic beetle, including 11 of conservation concern and several that were known specialists of rot-hole habitats (Carlsson *et al*., 2016).

Beetle boxes require regular maintenance and content top-ups in order to function as habitat patches over longer periods of time as they are susceptible to damage in the field and the wood mould inside them naturally decays away over several years (Carlsson *et al*., 2016). Because of the cost and time associated with this, beetle boxes may be most appropriately used as temporary solutions to support tree-hollow invertebrates until new cavities develop in real trees, potentially through the application of veteranisation practices. Nevertheless, research into the use of beetle boxes is only in its initial stages and they are likely to present several new opportunities for managing saproxylic invertebrates in the future. For example, there are several conservation applications of beetle boxes that have yet to be explored, such as their use in species translocations and as habitat stepping-stones (Jansson, Ranius, *et al*., 2009). Chapters 3 and 4 of this thesis explore several novel applications of the beetle box concept for saproxylic conservation and educational purposes.

1.5. - Study aims and systems

This study aimed to develop new knowledge relevant to key components of the various conservation strategies for saproxylic invertebrates presented above. These included: habitat use and dispersal, practical applications of novel conservation methods, and public education. The key aims of this research are outlined below.

Study aims

Chapter 2 seeks to address concerns related to saproxylic species dispersal by providing new data on the habitat requirements of saproxylic beetles including threatened species. This aims to inform tree planting regimes, so that future wooded landscapes can provide optimally spaced tree resources. Another aim is to highlight the most beneficial areas of a landscape to carry out veteranisation to ensure that habitat features remain sufficiently available (Bengttson *et al*.,2012). With strong enough evidence, these practices could be incorporated into environmental policy for the health of saproxylic communities in future open wooded habitats.

There has been little published research on the dispersal of saproxylic insects based in the UK. Most previous work has been carried out in countries with different invertebrate faunas and often different climatic conditions (Bergman *et al*., 2012; Percel *et al*., 2019). In addition, many studies that have aimed to find the limits of dispersal of specific beetles have focussed on species that are either absent or rare and restricted in the UK (e.g., *Osmoderma eremita*) (Ranius & Hedin, 2001; Ranius, 2006). To address this knowledge gap, Chapter 2 aims to identify trends in the habitat-density dependence of a wider variety of species including those that are more common and widespread across the UK saproxylic landscape. It is hoped that this will generate new understanding relevant to the biodiversity of UK pasture woodland, providing a relevant basis for future policy.

Furthermore, many previous dispersal studies have focussed on enclosed forest habitats (Schiegg, 2000b; Irmler *et al*, 2010). The research programme in Chapter 2 was designed to address this by encompassing veteran trees in a range of more open situations, including arable hedgerows and pastureland. In doing so, it aims to develop knowledge and appreciation for open-grown veteran trees, contributing towards better informed future conservation guidelines. It was envisaged that this work could increase understanding of the role of trees outside woodlands as habitat steppingstones. The knowledge generated from this could have important future implications as climate change increases the need for species to move across the landscape (Alexander, 2012). These motivations resulted in the following key aims of Chapter 2:

- *Investigate how saproxylic invertebrates interact with habitat resources over different spatial distances across a UK open-grown oak wooded landscape.*

- *Explore how the types of deadwood microhabitats represented influence the saproxylic invertebrate species found in veteran trees.*

In addition to better understanding the needs of saproxylic communities, this research was also designed to investigate novel, practical methods to aid in their conservation. The effectiveness of beetle boxes in supporting umbrella species has previously been demonstrated (Hilszczański *et al*., 2016). Chapter 3 sought to build upon this in applying a novel beetle box design tailored towards an umbrella species that uses a different type of tree hollow habitat. The specific design trialled was intended to replicate the conditions in tree hollows at the base of tree trunks, so that it might support local populations of *L. violaceus* and communities of other species using this habitat type. By monitoring these boxes after a year in the field, this study sought to explore colonisation rate of invertebrate communities into them. As a result, the research in Chapter 3 was developed to address the following aims:

- *Investigate the effectiveness of beetle boxes in attracting and supporting basal tree-hollow specialist saproxylic invertebrates.*

- *Understand more about the timescales of species accumulation in newly formed wood mould resources through sampling beetle boxes after one year in the field.*

This research also seeks to identify optimal procedures for the application of beetle boxes regarding their resilience and ecological function. In order to do this, variations in the external construction materials used in beetle boxes are investigated. The research in Chapter 3 explores this by comparing plastic and wooden beetle box designs. The research in Chapter 4 was designed to explore this further through the preliminary trial of a concrete beetle box. In addition, by incorporating variations in the components used to form the internal wood mould, the research was designed to explore the impact of internal environment variation on invertebrate communities. The knowledge gained from this could support the development of optimal beetle box design and management practices. Observations surrounding the box structure and contents could inform changes to future methodologies, for example, by adjusting the moisture or nutrient levels in the wood mould, allowing boxes to increasingly meet the requirements of their target fauna. These intentions resulted in the following research aims:

- *Explore the effectiveness of various construction materials on the ability of beetle boxes to imitate tree hollow conditions and support populations of saproxylic and deadwood associated beetle species*

- *Study whether the addition of manure to beetle boxes affects the communities of colonising saproxylic and deadwood-associated invertebrates.*

- *Identify implications of using sawdust from different tree species in the wood mould of beetle boxes communities of invertebrates inhabiting them*

In addition to the aforementioned applications, this thesis sought to further research the use of beetle boxes for the novel application of public education. Science communication is a growing priority in conservation, as greater understanding of the value of a resource is likely to result in increased consideration of its protection in policy (Bickford *et al*., 2012). The involvement of the public in conservation management schemes through sustained communication and creative opportunities for involvement can lead to greater levels of project success (Druschke & Hychka, 2015). The innovative and unusual nature of beetle boxes has high potential of captivating public attention and increasing appreciation of the invertebrate faunas that they are designed to protect. This could play a key role in the success of future projects involving beetle boxes and deadwood creation in the future. Chapter 4 of this thesis seeks to further investigate this potential by monitoring a beetle box in a more urban setting. The key aim for this was as follows:

- *Investigate the potential of beetle boxes to be used as educational resources to promote public understanding of the importance of deadwood for biodiversity in urban settings.*

Study systems

Invertebrate groups studied

Saproxylic beetles were selected as a particular focus for this research as there is already a well-established research base surrounding their ecology. This means that it is easier to make meaningful interpretations of the results of the present research and fill poignant gaps in the existing research landscape through the study of beetles. In addition, there are several up-to-date identification keys for UK Coleoptera, making the identification of specimens particularly practical (Duff, 2012; Duff, 2016; Duff, 2020; Käfer Europas, n.d.). These recent resources also mean that there is a lower likelihood of errors in identification resulting from out-of-date taxonomy or the absence of more recently introduced species in the older keys that are relied upon for some other invertebrate groups.

In order to maximise the interpretation of sample data, members of other invertebrate groups have been identified in Chapters 3 and 4 of this thesis where practical. These were used to make additional observations in the applications of beetle boxes for the wider community of saproxylic invertebrates that may utilise basal tree hollow habitats.

Sites used to investigate the habitat use of saproxylic beetle in Chapter 2

Previous tree mapping activities by Natural England were a major factor in the choice of using Stowe and Wimpole National Trust sites in this study. The previous survey work streamlined the process of choosing trees for trapping and allowed for local saproxylic-tree density analysis, making this study possible within the limited timeframe available.

- **Stowe**

Stowe is a National Trust-owned landscape containing an extensive medieval deer park, areas of semi-natural ancient woodland and landscaped gardens (Alexander *et al.* 2016). These landscape features surround Stowe House which was initially built in 1676 (Pevsner & Williamson, 1994). The National Trust funded surveys of Stowe’s saproxylic fauna between 1990 and 2000 which yielded several species of interest, including some records that were new to Buckinghamshire (Alexander, 1991; Fowles & Alexander, 1999). Stowe is currently the 33rd highest ranked site in the UK according to the Saproxylic Quality index, with a score of 550.9 (Fowles & Alexander, 1999; Fowles, 2022).

- **Wimpole**

Wimpole Estate comprises of landscaped gardens and parkland which are owned by the National Trust, surrounded by an extensive arable landscape (Alexander *et al*., 2016). The parkland was once a deer park before landscaping work began in the 18th century (Alexander *et al*., 2016). The majority of trees in the parkland area are horse chestnut (*Aesculus hippocastanum*) and common lime (*Tilia* × *europaea*). However, there is a strong presence of scattered old oak trees and the surrounding farmland has many ancient hedgerow trees with strong saproxylic potential (Alexander *et al*., 2016). Several previous surveys have identified Wimpole as a site of particular deadwood interest (Kirby, 2002; Damant & Kirby, 2005) The Saproxylic Quality Index ranking of Wimpole Estate the 27th highest in the UK, with a score of 573.0 (Fowles & Alexander, 1999; Fowles, 2022).

Sites used to investigate beetle boxes in Chapter 3

Windsor Forest and Bredon Hill are two of only three sites where *L. violaceus* is found in the UK. The presence of *L. violaceus* indicates that both sites possess high quality basal hollow habitat. This factor unites these sites despite their structural and compositional differences.

- **Bredon Hill**

Currently under the management of Natural England. Bredon Hill was designated as a Special Area of Conservation (SAC) due to the presence of *L. violaceus* (JNCC, n.d.). It contains areas of pasture woodland with ancient pollards as well as closed canopy Ash woodland and areas of coppice and scrub (Whitehead, 1996; Natural England, 2022). There are also areas of unimproved grassland containing several uncommon plant species which are characteristic of this habitat (Natural England, 2022). It benefits from a historical proximity with a more extensive woodland belt in the region (Whitehead, 1996). Bredon Hill is the second highest ranked site in the UK according to the saproxylic Quality Index with a current SQI value of 854.7 (Fowles & Alexander, 1999; Fowles, 2022).

- **Windsor Forest**

Windsor Park was formed in the 11th century (Natural England, 2019). Windsor Forest is considered internationally important due to the rare saproxylic invertebrates that have been found in its ancient, wooded landscapes (Natural England, 2019). It has even been suggested that Windsor Great Park and its associated forest could constitute the site with the greatest concentration of old oak trees in the world (Butler *et al*., 2002). According to the Saproxylic Quality Index, Windsor Forest is the third highest ranked site in the UK with SQI value of 850.0, only a few points behind Bredon Hill (Fowles & Alexander, 1999; Fowles, 2022). The range of habitats across the site vary from parkland/pasture oak woodland, more shaded beech dominated woodland, ponds, grassland, and scrub (Natural England, 2019).

The study in Chapter 3 took place in one of the more shaded areas of woodland in High Standing Hill. This is an example of the Special Area of Conservation qualifying habitat, atlantic acidophilous beech forest (Alexander, 2019a). Having previously been managed as an open pasture woodland, it also has a number of legacy ancient trees, some of which are known to be inhabited by *L. violaceus* - the target umbrella species for the beetle boxes (Alexander, 2019a; Natural England, 2019). Other rare beetle species found in the High Standing Hill area include *Ischnodes sanguinicollis* (Nationally Notable A) and *Megapenthes lugens* (RDB1) (Webb *et al.,* 2018; Alexander, 2019a). High Standing Hill is also inhabited by several important species of saproxylic Diptera, including the royal splinter crane fly (*Gnophomyia elsneri*), the tree snipefly (*Chrysopilus laetus)* and the band-winged stilt-legged fly (*Rainieria calceata*) (Alexander, 2019a). In addition to invertebrates, Windsor Forest and Great Park support a great diversity of fungi including several rare species (Alexander, 2019a; Natural England, 2019).

The wildlife garden site used to investigate urban applications of beetle boxes in Chapter 4

- **Hilldrop**

Hilldrop is a wildlife garden in North London, near the border to Essex. The value of deadwood has been considered in the planning of the garden, with features such as log piles, veteran hawthorn trees, and a ring of standing deadwood being incorporated (Little, n.d.). Veteranisation practices have also been implemented in a willow tree on site (Little, n.d.). In addition to deadwood, the garden also contains three ponds and a range of other habitat features, many of which have a particular focus on providing resources for invertebrates (Little, n.d.; Gedge, 2017). As part of this habitat development, Hilldrop has been used as a site for the experimental trials of several novel biodiversity initiatives (Little, n.d.; McWaters, 2022). As a result, it has attracted considerable attention, and several workshop and public open days have been being given there to educate people on innovative wildlife gardening techniques (Gedge, 2017).

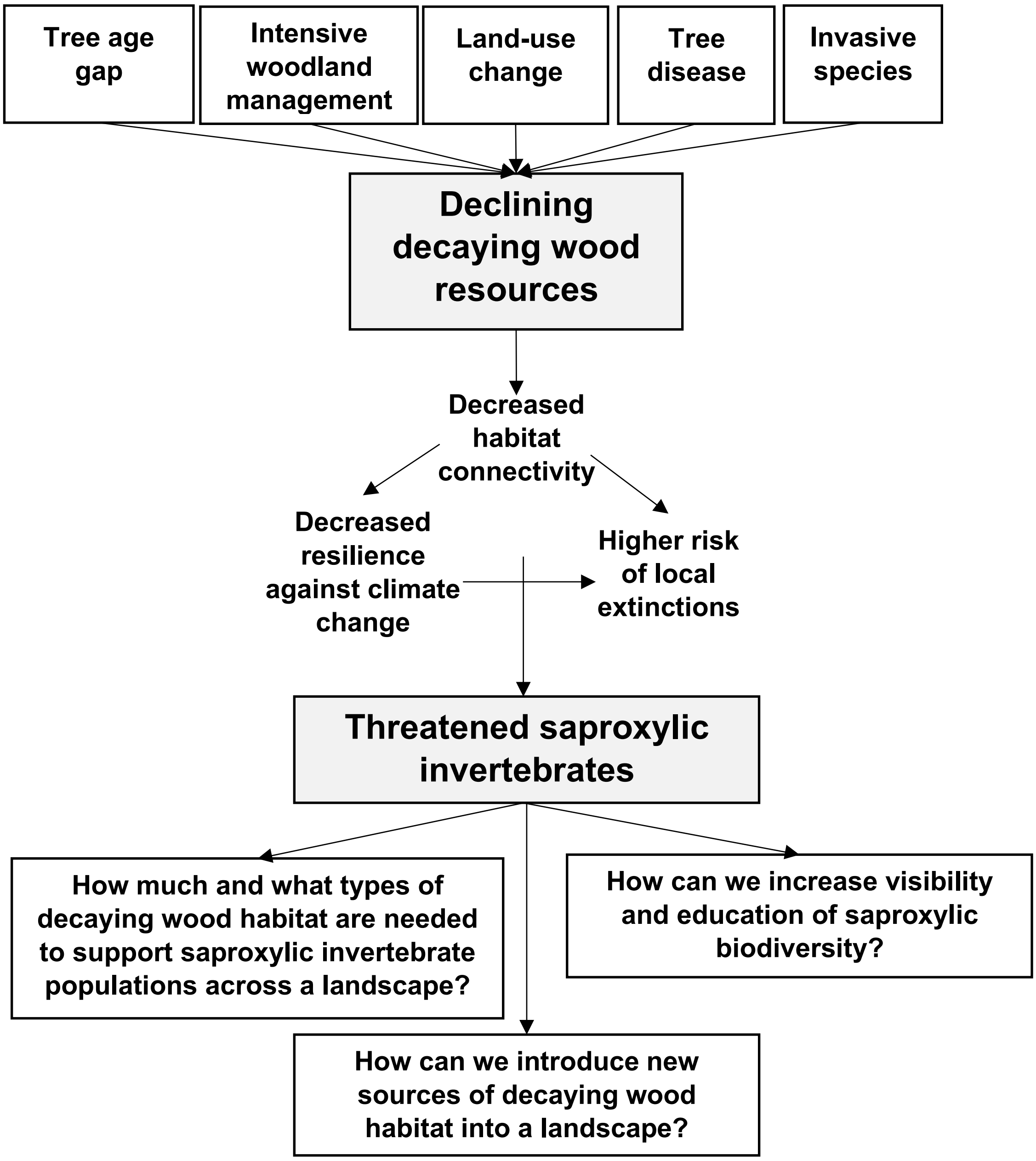


Figure 1.2. A conceptual framework outlining the drivers of this research and the key areas that will be investigated.

Chapter 2 - Investigating the habitat use of saproxylic beetles in open wooded landscapes

2.1. - Introduction

Rationale and basis for study

The value of open grown oak trees

Large mature trees are keystone habitat features for a range of species groups (Fischer *et al*., 2010; Stagoll *et al*., 2012). Old oak trees in particular have been identified as hotspots of value for saproxylic beetle diversity (Sverdrup-Thygeson, 2009). This is because oak supports the greatest diversity of saproxylic invertebrates of all tree species in Europe, including many threatened beetle species (Palm, 1959; Widerberg *et al*., 2012). Oak trees reach their greatest saproxylic potential when they grow in open situations (Widerberg *et al*., 2012; Bouget *et al*., 2014). One of the reasons for this is that the lack of crown competition associated with open conditions best supports tree development into old age, resulting in the accumulation of deadwood microhabitats over time (Alexander *et al*., 2016). Secondly, several oak-dwelling saproxylic species prefer to live in the warmer conditions that result from the consistent trunk sun exposure provided by open conditions (Widerberg *et al*., 2012; Alexander, 2018). As a result, open grown trees have been found to contain significantly different beetle assemblages to those grown within forest conditions (Parmain & Bouget, 2018).

In addition to the value of open-grown oak trees to invertebrate diversity, they also provide other beneficial ecosystem services (Blackshaw & Blacksaw, 1994; Townsend & Barton, 2018). In farmland, open-grown pasture trees can provide areas of shade to prevent grazing animals from experiencing excessive heat stress (Blackshaw & Blacksaw, 1994). There is also evidence that humans gain a sense of safety and wellbeing from large, spreading trees as a result of an evolutionary link with refuge and predator avoidance (Townsend & Barton, 2018). The aforementioned advantages highlight the value that old oak trees confer to landscapes and reinforce the importance of conserving them. This chapter aims to gather further data on the biodiversity value of these trees and to propose conservation measures that will benefit the future perpetuation of old oak trees and their associated deadwood fauna.

Pasture woodland

Old open-grown oak trees can occur in a range of landscape classifications, a prominent example of which is pasture woodland. This is defined as a mosaic habitat in which open-grown trees exist alongside grazing animals in a continuously managed landscape with a strong representation of saproxylic habitats and nectar sources (BRIG, 2011) Pasture woodland once occurred naturally across the British landscape (Alexander, 2012). However, processes that perpetuated this habitat, such as widespread grazing of large herbivores, now rarely occur in nature (Alexander, 2008). Therefore, the persistence of this form of woodland must be managed artificially. In the UK, the National Trust has a leading role in preserving and protecting parkland containing valuable old, open-grown trees. It owns over 100 parkland landscapes across the UK, several of which have nationally significant saproxylic value (Harding & Alexander, 1992). The present study seeks to gather data that is directly relevant to the veteran trees in National Trust landscapes, providing the basis for improved management of these resources to support saproxylic biodiversity.

Trees outside woodlands

In addition to pasture woodlands, ancient trees with high deadwood potential are also found outside of woodland contexts. An estimated 3.2% of the UK's land area is covered by trees outside woodlands, including hedgerow trees, street trees, trees on farms, and trees along stretches of river (Woodland Trust, 2021b). This is greater than the 2.5% of land area in the UK covered by Ancient Woodland (Woodland Trust, 2021b), highlighting that trees outside woodlands have great potential for providing widespread habitat islands and connecting wooded landscapes throughout the country. However, in contrast to the trend of increasing general woodland cover, numbers of trees outside woodlands are declining. In a study of the Eastern Claylands across Essex and Suffolk, only 51% of trees outside woodlands mapped in 1850 still survived today, with 54% of boundary trees and 84% of scattered trees having been lost during this period (Woodland Trust, 2021b). The threat of loss from development is particularly high for trees outside woodlands (Woodland Trust, 2021b).

Agricultural landscapes account for 71% of the UK's land area (DEFRA, 2022). Therefore, trees in agricultural landscapes surrounding old parklands and pasture woodlands are likely to play an important role in the wider connectivity of saproxylic communities (Kirby, 2022). However, agricultural trees have undergone historical declines through intensified agriculture, field reorganisation and tree disease (Rackham, 1986). These declines are predicted to continue under current management regimes, with tree populations suffering from low age diversity through a lack of consistent recruitment through time (Gibbons *et al*., 2008). To prevent this from having negative effects on saproxylic communities, protection of existing trees and more consistent tree recruitment in agricultural landscapes must be prioritised (Gibbons *et al*., 2008). The present study seeks to gather data that will contribute towards the formulation of best practice for the implementation of these conservation methods regarding their value for saproxylic beetle diversity. In addition, novel methods of deadwood habitat recruitment, such as tree veteranisation and the employment of artificial habitats also present opportunities to enhance agricultural deadwood resources and protect their associated saproxylic fauna (Jansson, Ranius, *et al*., 2009; Bengtsson *et al*., 2012). The approach through which artificial habitats such as beetle boxes can supplement depleted deadwood resources is further explored in Chapter 3 of this thesis.

Old tree context ambiguity – pasture woodland/ outside woodland

Trees defined as being part of a pasture woodland and trees outside of woodland situations are known to provide value through their open-grown nature, but ambiguity in the definition of different woodland and non-woodland tree situations has caused problems for researchers (Alexander, 2008; Brown & Fisher, 2009). There are no clear boundaries between definitions of trees in pasture woodland situations and those characterized as being outside of woodlands, with some authors considering pasture-woodland trees to be within the scope of trees outside woodland (Brown & Fisher, 2009; Feber, 2017). These contextual definitions can be useful for conservation and monitoring purposes as they allow valuable habitats to be quantified and protected. However, such definitions are less useful for research at a deadwood microhabitat scale, as they do not necessarily encapsulate the full extent of the deadwood resource that supports saproxylic species (Kirby, 2022). Therefore, it is important to think about wooded landscapes at the tree-scale, rather than according to ambiguous contextual definitions (Alexander, 2008). The present study considers these trees as a matrix of saproxylic value across differing landscape, as this most reflects the way in which deadwood resources are used by their associated saproxylic invertebrate fauna (Kirby, 2022).

Current state of research and knowledge gaps

Microhabitat requirements

The specific habitat requirements of saproxylic beetle assemblages is a key area requiring further study (Harding & Alexander, 1992; Jansson, 2002; Davies *et* al., 2008; Micó *et al*., 2020). Alexander (2002) represents the last comprehensive summary knowledge on the resource associations of UK saproxylic species; however, it is highlighted that the information given is open to change and does not yet constitute a complete review. The present study will combine data on veteran tree microhabitats with data on local saproxylic beetles to formulate objective, empirical inferences on the habitat associations of saproxylic beetle species. This approach has previously been used by Bouget *et al*., (2014). The present study builds upon this work by incorporating data on a greater range of saproxylic microhabitats and by focussing trapping activities specifically on open oak wooded landscapes. Through this, the present research will produce detailed data to fill knowledge gaps on the specific requirements of members of the UK saproxylic beetle fauna in open-grown oak trees.

An important part of understanding saproxylic microhabitat dynamics is investigating how beetle communities interact differently with trees of different ages (Alexander, 2008; Irmler *et al*., 2010). The saproxylic habitats offered by trees changes over time as trees go through a range of distinct life stages, from growth up to their peak height, to retrenchment into old age (Alexander, 2008). At the trees peak height, lower branches often become shaded out by upper canopy, subsequently becoming decayed by fungal communities that prefer these shaded conditions (Alexander, 2008). Following this, the thinning of tree growth rings as the tree enters old age prevents resources from reaching the upper crown, causing death of higher branches and retrenchment into a shorter form (Alexander, 2008). Then, when trees reach their ancient stages, they are often extensively hollow, containing cavities with well-rotted wood mould. (Alexander, 2008). This study will seek to provide further insights into how deadwood features linked to these different tree life stages support saproxylic invertebrates in different ways. This will help to further elucidate the value of younger, veteranized trees in supporting saproxylic beetle populations, providing a basis for future management decisions.

The microhabitat investigation of this study will also investigate fallen deadwood. Due to the aesthetic nature of parkland, especially in historic landscapes such as those owned by the National Trust, there is a tendency for fallen deadwood to be cleared away (PTES, 2022). This has potential to be detrimental for saproxylic diversity, as fallen deadwood has previously been found to benefit rare beetle species (Bouget *et al*., 2014). The present research will examine the levels of fallen deadwood found in managed landscapes such as these and investigate how these may link to local invertebrate faunas.

Density requirements

In addition to understanding which microhabitats are important for saproxylic beetles, it is also important to learn how dense trees with these features need to be in a landscape to support beetle communities most effectively (Alexander, 2008). Different saproxylic species can have a wide range of dispersal tendencies dependent upon their habitat requirements, physical features and life history traits (Holland *et al*., 2005; Bergman *et al*., 2012; Sverdrup-Thygeson *et al*., 2017). Understanding the scales that are relevant for a particular fauna present at a site can help planners make informed conservation decisions that will affect the future connectivity of the landscape for relevant species. The ways in which the present study seeks to contribute to this understanding are outlined in the ‘study aims’ section of this chapter.

Many studies of saproxylic insect dispersal are carried out in areas of enclosed forest (Økland *et al*, 1996; Brunet & Isacsson 2009). Insect dispersal tendencies can be affected by the landscape permeability (Trakhtenbrot *et al*., 2005). Open, wooded landscapes such pasture woodlands and arable tree matrices are likely to present different levels of permeability to insect movement than enclosed woodlands. As a result, dispersal studies in open wooded landscapes are likely to yield useful new insights into how the tree density requirements of saproxylic invertebrates are influenced by specific woodland characteristics.

The spatial scales that are important for saproxylic beetles in hollow oaks have previously been investigated by Bergman *et* al. (2012) in the Swedish county of Östergötland. The landscapes investigated in this study consist of a mixture of coniferous forests and arable fields (Bergman *et* al., 2012). Because of the large spatial scale of this study, it incorporated oak trees from a wide range of different landscape contexts. The present study seeks to replicate this investigation on a smaller scale, to explore whether the findings are applicable for specific pasture landscapes with scattered old oak trees in the UK. The ownership of many of the UK's pasture woodlands by the National Trust, means that conservation decisions will largely be made on the individual site scale. Therefore, it is important to understand how tree density influences saproxylic communities within areas of several km^2. The present study constitutes the first investigation into the impacts of deadwood habitat density on saproxylic invertebrates that is directly relevant to saproxylic faunas and tree distributions in the open-grown woodlands of the UK.

Study aims

Microhabitat requirements

A key aim of the present research is to learn more about the saproxylic value of veteran trees in pasture woodland/ agricultural landscapes. This will be done by gathering data on the representation of different microhabitats across the matrix of ancient and veteran trees present and how this differs across trees of various ages and growth-forms. This information will then be used alongside data on local saproxylic beetle species communities to formulate conclusions on how the incidence of deadwood microhabitats impacts the beetle faunas inhabiting a tree. Through this, the present research also aims to contribute further knowledge on habitat requirements of saproxylic beetle species.

Density requirements

The present research aimed to gather data on the scales at which tree density has the greatest effect on the diversity of saproxylic beetle fauna in open-grown oak woodlands. It did this by quantifying the number of veteran trees present within a range of distance radii that are relevant for UK pasture-woodland situations and identifying how this density impacts saproxylic beetle species diversity. The knowledge gained from this study aims to inform land managers in ensuring that future provisions of deadwood are at the correct scales to meet the needs of the local saproxylic fauna.

Summary

By addressing the above aims, this study will work towards filling key knowledge gaps on the habitat requirements of vulnerable saproxylic beetle communities. The results of this research will allow conservation managers to better understand how the protection of trees with certain deadwood features may influence the saproxylic fauna of open-grown oak woodlands. They will also prove valuable in informing best practice for the potential future implementation of tree planting, veteranisation practices and artificial habitats in open, wooded landscapes.

2.2. - Methods

Study sites

This study was carried out at the National Trust-managed landscapes at Stowe (SP6736) and Wimpole Estate (TL3351). Both sites incorporate ornamental gardens and surrounding areas of grazed pastureland featuring open-grown veteran oak trees. Further details on the history and saproxylic value of these sites can be found in Section 1.5 of this thesis. This study also incorporated areas of farmland surrounding Stowe and Wimpole Estate, in which notable veteran oak trees featured in fields and hedgerows. Areas rich in veteran trees were chosen for this research to ensure that the findings are relevant to the conservation of the saproxylic diversity present in the few ‘high value’ wooded landscapes that remain in fragmented English landscapes. As these sites support the highest numbers of saproxylic species, insights into their effective management are the most impactful for biodiversity conservation on a national level. Investigating diverse sites also generates data on a wider range of species, making it more likely that the findings will be relevant to aspects of the saproxylic fauna in other UK broadleaved woodlands. This means that the conservation insights gathered from the research will be more widely applicable for the enhancement of UK deadwood habitats.

Experimental design

Tree selection

Oak trees were selected for inclusion in a flight interception trapping regime based on visual inspection of trees that had been previously identified as having high trapping potential by the preliminary surveys of Alexander *et al*. (2016). Oak was chosen as it is the dominant tree species at both survey areas, and, within these tree stocks, there are known to be many veteran individuals that support rich saproxylic communities (Alexander *et al*.,2016). Oak trees are particular hot-spots for saproxylic diversity and are therefore a worthwhile study subject for saproxylic diversity (Sverdrup-Thygeson, 2009). Trees were deemed suitable for trapping if they featured at least one visible saproxylic microhabitat feature and had a sturdy branch in the vicinity from which a trap could reasonably be suspended. The main saproxylic features that traps were stationed by included:

- Tree holes
- Tears (recently shed limbs)
- Aerial deadwood
- Areas of denuded bark

Flight interception trapping

A flight interception trapping regime was carried out in 2019. Following the recommendations of Alexander *et al*. (2016), clear cross vane flight interception traps were used for trapping. These are an effective and statistically comparable method of catching saproxylic beetles, while remaining simple to install and collect samples from (Alexander *et al*. 2016; Bouget *et al*., 2008). The traps were deployed from May to September 2019, which is the recommended time-period to survey saproxylic activity (Nageleisen & Bouget, 2009). Due to the extreme winds of Storm Hannah during the first week of trap deployment, several traps were damaged and therefore trapping data from the first week was discounted from statistical analysis. As a result, the trapping data presented covered the period from mid-May to September, which still incorporated the majority of the beetle activity period.

The number of trees sampled were 14 and 16 for Stowe and Wimpole respectively. Initially a greater number to traps were deployed at both sites (17 and 19 for Stowe and Wimpole respectively), however subsequent trap faults meant that the data from six traps (three per site) were deemed to no longer be comparable to that from other traps. As a result, the beetle species data from these traps were not used in statistical analysis. The locations of traps deployed at Stowe and Wimpole are shown in Figures 2.1 and 2.2.

The traps were positioned in the tree as close as possible to at least one of the above microhabitat features. This is because traps placed directly next to visible features such as hollows and beetle exit holes have been shown to capture a higher proportion of tree-specialist species compared to vagrant species (Sverdrup-Thygeson, 2009; Sverdrup-Thygeson & Birkemoe, 2009). Therefore, positioning traps in this way maximises the potential of capturing a higher proportion of the saproxylic diversity of a tree whilst minimising by-catch. The habitat feature closest to the trap on each trapping tree was also noted and included as a variable in analyses to evaluate the influence of trap location on its tendency to capture certain species.

Due to the heterogenous nature of microhabitat locations and suitable branches to hang traps from, the trap height was not standardised between trees. Trap height has been found to negatively correlate with specimen abundance and species richness of the trap catches (Bouget *et al*., 2008). Due to the heterogenous nature of trees, this height variation was unavoidable, and it is considered likely that major differences in results based on microhabitat and tree density will still be evident despite these effects. Nonetheless, this should be considered as a potential limiting factor of the results of the present study.

Figure 2.1. A map of trapping trees in Stowe National Trust landscape and the surrounding arable land. Trees in which trapping occurred are indicated as points on the map. Yellow points indicate traps from which beetle species data were used in the analysis. Pink dots indicate traps that experienced faults, meaning that their species data were excluded from statistical analysis.

Figure 2.2. A map of trapping trees in Wimpole National Trust landscape and the surrounding arable land. Trees in which trapping occurred are indicated as points on the map. Yellow points indicate traps from which beetle species data were used in the analysis. Pink dots indicate traps that experienced faults, meaning that their species data were excluded from statistical analysis.

The impacts of flight interception trapping on local insect population sizes are not well known. As a result, it is important to take precautionary measures to minimise any potential impacts of trapping regimes on vulnerable species. Researchers have recommended using flight interception traps over intermittent time-periods, rather than continuously, to limit potential negative impacts on vulnerable beetle populations (Alexander *et al.*, 2016). Following this guidance, trapping for this study was carried out on a bi-weekly alternating schedule, with the traps actively collecting invertebrates for two weeks, followed by a two-week period with no collecting pot attached. A summary of trapping dates is presented in Table 2.1. Traps were also unbated, avoiding intentional capture of large proportions of nearby populations, instead relying on incidental collisions by any insects flying in the area.

Table 2.1. A summary of the dates during which flight interception traps were actively catching invertebrates at Stowe and Wimpole. * indicates dates during which trap catches were excluded from analysis due to incomplete sampling as result of extreme weather and trap faults.

Sampling session	Flight interception trap deployment dates	
	Stowe	Wimpole
1	*25/04/2019 – 08/05/2019	*19/04/2019 – 03/05/2019
2	22/05/2019 – 05/06/2019	17/05/2019 – 31/05/2019
3	19/06/2019 – 01/07/2019	14/06/2019 – 28/06/2019
4	17/07/2019 – 31/07/2019	12/07/2019 – 26/07/2019
5	14/08/2019 – 28/08/2019	09/08/2019 – 23/08/2019
6	11/09/2019 – 25/09/2019	06/09/2019 – 20/09/2019

The collecting pots attached to the traps contained a mixture of 50% Propylene glycol, 50% water and drop of unscented washing-up liquid to disrupt surface tension and allow invertebrates to sink. This fluid was chosen as it is an effective killing agent that is low-cost, minimally volatile, non-toxic, and environmentally safe (Weeks & McIntyre, 1997; McCravy & Willand, 2007; Weigand *et al.,* 2021). Propylene glycol is also known to retain morphological features of specimens well whilst keeping them flexible, allowing for dissection of genitalia where required for identification (Weigand *et al.,* 2021).

Beetle identification

All beetles extracted from the flight-interception trap samples were visually identified to family level. Beetles belonging to families that contain saproxylic species were then identified to species level using various taxonomic keys (Duff, 2012; Duff, 2016; Duff, 2020; Käfer Europas, n.d.). Beetles of the Staphylinidae were excluded from this study due to the difficulty of their identification, with the exception of those from the subfamilies, Pselaphinae and Scydmaenidae. The exclusion of Staphylinidae is not expected to negatively impact the results of this study, as the diversity and community composition of beetle assemblages that exclude Staphylinidae have been found to correlate highly to that of complete assemblages (Parmain *et* al., 2015). The identified species were categorised as saproxylic according to species lists from the UK and Germany (Alexander, 2002; Schmidl & Bußler, 2003). Only saproxylic species were included in subsequent analyses. Additional data was gathered about the functional guilds and rarity statuses of selected beetle species using a range of sources (listed in table 3.2).

Tree Microhabitat Investigation

In October 2019, each trapping tree was revisited and surveyed to quantify the saproxylic microhabitats that they exhibited. This was undertaken to expand upon the preliminary survey work completed prior to trapping, as limitations on time and volunteer availability prevented the recording of such detailed observations at the time. The survey conducted method was an adapted version of the Specialist Survey Form from the Veteran Trees Initiative (Fay & De Berker, 2003). Changes included the exclusion of certain categories that were considered not relevant to this study, for example whether the tree was single or multi-stemmed (as all trees in the survey were single stemmed) and whether the tree was standing or fallen (only standing trees were included in the study). The features recorded as part of this survey are summarised in Table 2.2.

Table 2.2. A summary of the habitat features recorded for each trapping tree at Stowe and Wimpole.

Habitat feature	Unit of measurement
Tree height (measured using a clinometer)	meters
Diameter at breast height	centimetres
Epicormic growth at the base of the tree	presence/absence
Epicormic growth on the trunk of the tree	presence/absence
Epicormic growth in the crown of the tree	presence/absence
Bark depletion	an estimated percentage of all bark on the tree
Sap runs	number
Split limbs	number

Tears (recently shed limbs)	number
Scars (old tree wounds with evidence of healing)	number
Lightning strikes	presence/absence
Hollowing	rated on a scale from 1-5 as defined by Fay & De Berker (2003)
Holes around the tree base	number
Holes in the tree trunk	number
Holes in tree branches	number
Water-pockets	number
Red rot	presence/absence
White rot	presence/absence
Aerial deadwood (over 15cm in diameter)	meters – estimated
Fallen deadwood (over 15cm in diameter)	meters – estimated
Fungi	presence/absence
Lichen	estimated percentage of tree covered
Moss	estimated percentage of tree covered
Ivy	estimated percentage of tree covered
Signs of invertebrate activity	presence/absence
Signs of bird activity	presence/absence
Signs of mammal activity	presence/absence
Habitat context	chosen from habitat codes listed by Fay & De Berker (2003)
Signs of damage to tree	presence/absence
Shade	estimated percentage of canopy cover over the trapping area
Exposure	Rated on a scale from 0-3 based on the number of aspects of the trapping area exposed to wind

Only habitat features that were visible from the ground were counted as part of this survey. This constituted a limitation in microhabitat recording, meaning that some less-visible features may have been missed or inaccurately quantified. It is noted that this may have influenced capacity of the results of this study to identify the true extent of species links with these habitats. However, as the method of microhabitat evaluation used is based on an established veteran tree monitoring methodology (Fay & De Berker, 2003), it means that the results of this study are maximally applicable to existing survey data. This means that, despite some lack of precision, the data collected in this study are relevant for the management of veteran oak landscapes.

Another limitation of the microhabitat data was that many of the categories recorded are subjective to the surveyor. To ensure a level of consistency to be achieved across all measures, the microhabitat features were recorded by the same researchers for each tree.

Microhabitat data analysis

Microhabitat representation

To analyse the representation of the different deadwood microhabitats across all trees surveyed, the data for each category was converted into presence/absence data. This allowed a percentage of surveyed trees that exhibited each feature to be calculated.

Diameter at breast height links to microhabitat diversity and beetle species richness

Pearsons correlation tests were used to investigate relationship between the diameter at breast height (DBH) of tree trunks and factors associated with saproxylic diversity in trees. One tree was excluded from DBH analysis as it was particularly small, constituting an anomalous data point that was likely to skew the results of correlation testing.

To investigate the hypothesis that older trees carry a greater diversity of deadwood features, Pearson correlation test was carried out to measure the association between the DBH of tree trunks to the diversity of microhabitats (the number of recorded microhabitat types) recorded in a tree. In addition, Pearson correlation tests were run between tree DBH to the richness of all saproxylic species, the richness of rare species (those with a conservation status), and the Shannon diversity index. These tests were intended to investigate the hypothesis that older, larger trees support a greater diversity of saproxylic beetles.

Tree feature variation

Unconstrained principal components analysis (PCA) was used to determine the principal components that best and most simply encapsulate the variation in the tree-feature data. To prepare the tree-feature data for this analysis, all categorical variables were converted into numeric equivalents, using numbers to encode for categories. The tree features that most contributed to the principal component axis were identified. Additional axes of the tree features were overlayed onto the principal component plot to visually represent the extent to which each feature explains the overall variation in tree character along the principal component axes, and also to show which tree features covaried with one another. Points representing individual trees surveyed were also plotted on this graph to display how they varied in their relationships to the various tree-feature gradients.

Differences in saproxylic beetle communities

The differences in saproxylic beetle communities between the two trapping sites (Stowe and Wimpole) were investigated using an analysis of similarities (ANOSIM) test. This used dissimilarity values to identify whether the composition of samples from the same group are significantly different from composition of samples between groups.

Nonmetric multidimensional scaling (NMDS) plots were constructed to elucidate possible groupings within the species data that may represent shared associations to certain habitat factors. This involves constructing an ordination that is based upon a dissimilarity matrix, representing the dissimilarity of samples in a low-dimensional space. Species traits (such as larval feeding guild and rarity status) were indicated in these plots through point symbology to identify any groupings that may occur among species with shared attributes.

Redundancy analysis

Redundancy analysis (RDA) was used to model relationships between the tree-feature variables and the variation in the occurrence of saproxylic species among the trapping trees. This analysis allows the formulation of hypotheses on the habitat associations of saproxylic beetle species based on how the species group together around the constrained axes representing the tree-features. This analysis may be confounded when more than one tree feature is strongly correlated with another. Because of this, it was not always possible to identify specific species-habitat links from the data. To minimise this limitation, existing knowledge of species behaviour and habitat requirements was considered when interpreting the results to identify the most probable factors influencing the abundance of species.

Tree density investigation

Tree surveys

This study used data from tree surveys carried out by Alexander *et al*. (2016). These surveys identified all veteran trees containing saproxylic microhabitats and evidence of hollowing (hereafter termed 'habitat trees') within buffer areas of 2000 m from the central zones of Stowe and Wimpole landscapes (Alexander *et al*.,2016). The tree surveys were carried out by the same group of researchers for both sites, providing consistency in the categorisation of the trees. Due to access permission difficulties, the tree-mapping surveys at Stowe did not include an area around Tile House to the north-east of Stowe landscape. Whilst this introduced a limitation to the data, it was assessed that conducting additional surveys by a different surveyor could introduce inconsistency into the existing data, thereby reducing its overall validity. To compensate for this potential limitation, the radii of tree density used were adjusted, extending only up to 1000 m rather than 2000 m to exclude the un-surveyed area. Whilst this may limit the study from identifying saproxylic relationships with tree density at larger scales, it will still provide data on density requirements at useful scales for local management of the central pasture woodlands and their surrounding arable areas.

The tree-survey data from Stowe and Wimpole parks cannot constitute a complete and definitive catalogue of all habitat trees in the areas with hollowing, as it is not always possible to identify hollowing levels from surveys at ground level. This is because, for lower levels of hollowing, the extent to which decay extends into heartwood is difficult to visually discern (Alexander *et al*., 2016). Nonetheless, the survey data provides an estimate of appropriate saproxylic habitat, and the resultant calculations constitute estimates of local tree density rather than true values. As the tree survey data was collected in 2014 and 2015, there was at least a 4-year period between the tree surveys and the trapping activities of this study. Consequently, it is possible that some changes may have occurred in the trees within this time. Despite this, due to the relatively infrequent rate at which many saproxylic species are thought to disperse, this timing discrepancy is not considered a major constraint to any associations between saproxylic diversity and tree density that may be found (Ranius & Hedin, 2001; Ranius 2006).

Quantification of tree density

To quantify habitat tree density, the habitat trees that were identified by the above survey were plotted onto maps in QGIS. Trees where trapping was undertaken were then added to the map separately. Buffer circles of different distance radii (25 m, 50 m, 100 m, 250 m, 500 m, 750 m, 1000 m) were created around each trapping tree. The number of other habitat trees within the buffer zones of each trapping tree were counted for each of the chosen buffer scales. Figures 2.3. and 2.4 illustrate the distance buffers around each trapping tree used to calculate the density of habitat trees at different scales.

There was a high degree of overlapping in the radii around the trapping trees, especially at the larger scales. Some studies have suggested that this may constitute a lack of spatial independence, leading to pseudoreplication (Holland *et al*., 2014). However, others have suggested that this is not a relevant problem as overlapping landscapes do not induce spatial autocorrelation (Zuckerberg *et al*., 2020). Despite the potential to influence the findings of this research, the present study design was deemed to be the most appropriate as it allowed for higher replication than could be achieved when avoiding any overlapping of spatial radii. With the range of landscape situations encapsulated by this methodology, it is expected that any trends found to be statistically significant will reflect real world influences on tree density upon saproxylic organisms rather than any confounding factors (Oksanen, 2001).

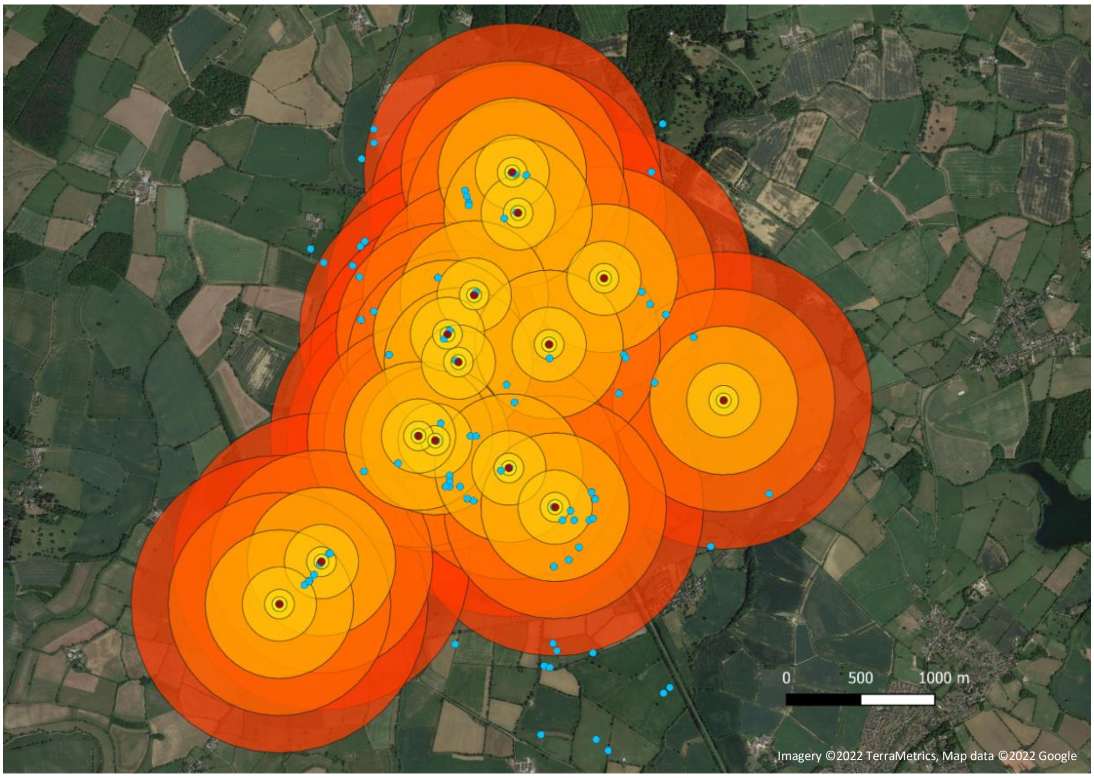


Figure 2.3. A map of buffer radii around trapping trees in Stowe National Trust landscape and surrounding arable land. Trees in which trapping occurred are indicated as dark red dots, whilst other veteran trees in the area (as surveyed by Alexander *et al*. (2016) are shown as light blue dots. Buffers of 25 m, 50 m, 100 m, 250 m, 500 m, 750 m and 1000 m have been created around each trapping tree, shown here on a colour gradient from yellow to red.

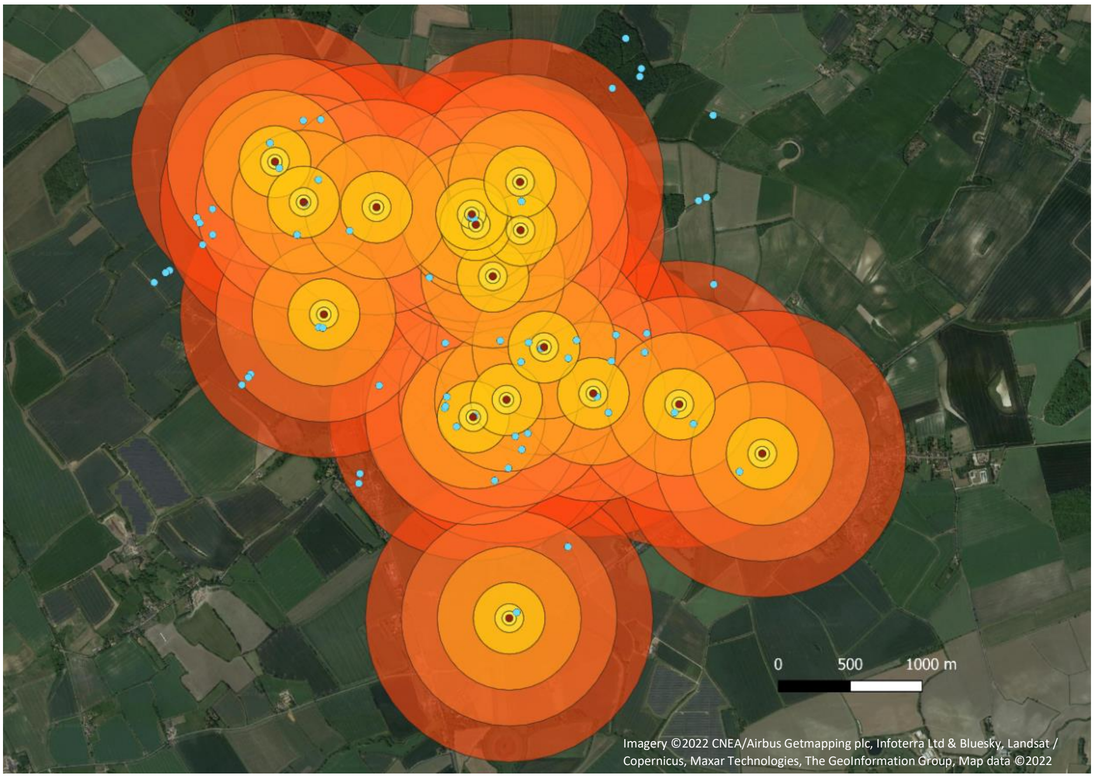


Figure 2.4. A map of buffer radii around trapping trees in Wimpole National Trust landscape and the surrounding arable land. Trees in which trapping occurred are indicated as dark red dots, whilst other veteran trees in the area (as surveyed by Alexander *et al*. (2016)) are shown as light blue dots. Buffers of 25 m, 50 m, 100 m, 25 0m, 500 m, 750 m and 1000 m have been created around each trapping tree, shown here on a colour gradient from yellow to red.

Density data analysis

Analysis of the associations between beetle species richness and habitat tree densities at different scales

To investigate links between the species richness of saproxylic beetles found within a tree and the numbers of surrounding habitat trees within different distance radii of that tree, the richness of saproxylic species found within each trapping tree was first evaluated. Separate Pearson's correlation coefficient tests were then carried out between species richness and the number of veteran trees found within each of the distance radii (25 m, 50 m, 100 m, 250 m, 500 m, 750 m and 1000 m) of the trapping trees.

Separate analyses were carried out to investigate the hypothesis that rarer species are often poorer dispersers that interact with their surrounding landscape differently to common species. Pearson’s correlation coefficient tests were used to measure the relationship between saproxylic species with a conservation status and veteran tree-numbers within the different distance radii of trapping trees.

Analysis of habitat tree density scales relevant for specific saproxylic beetle species

The links between tree density and the occurrence of specific saproxylic beetle species were analysed following the methodology of Bergman *et al*. (2012). Species data was first converted into presence/absence measures for each species at each trapping tree. Generalised linear models were then computed between the presence/absence data of each beetle species with five or more occurrences in the trapping trees with the number of habitat trees within the various radii (25 m, 50 m, 100 m, 250 m, 500 m, 750 m and 1000 m) of the trapping trees. Species were noted when they exhibited significant positive relationships with any of the tree density radius variables. For species with significant density relationships, the Wald statistics were plotted against the tree-density scales tested, indicating the radii in which tree density variation best explained the probability of specimen occurrence within trees.

2.3. – Results

From all trapping activities across both Stowe and Wimpole, 1314 individuals of 122 saproxylic beetle species were found. This included 56 species that were found at both sites, while Stowe and Wimpole both had 33 species that were unique to them and not found at the other site. The beetle communities found at Stowe and Wimpole were found to be significantly different from one another (R= 0.144, p = 0.013). Summaries of the saproxylic beetle species recorded from each trapping tree are provided in Appendices B and C.

At Wimpole Estate, 872 individuals of 89 saproxylic beetle species were found. These included 29 species (32.6%) which had a UK conservation status. The three most common saproxylic species recorded at Wimpole were *Euglenes oculatus* (154 individuals), *Dacne bipustulata* (131 individuals) and *Dorcatoma chrysomelina* (121 individuals).

At Stowe National Trust Landscape, 442 individuals of 89 saproxylic beetle species were found, of which 29 (32.6%) had a UK conservation status. The three most common saproxylic species found at Stowe were *Dacne bipustulata* (61 individuals), *Euglenes oculatus* (39 individuals) and *Hemicoelus fulvicornis* (35 individuals). The present round of trapping at Stowe produced 47 saproxylic species not previously recorded for the site according to the Saproxylic Quality Index site rankings (Fowles, 2022).

Due to the loss of samples through trap faults and weather interference, the data from three traps run at Wimpole Hall and three traps at Stowe were not used in analysis. The removal of the data from these traps meant that the number of saproxylic species used in analysis for Wimpole Hall was 79 (747 individuals), while from Stowe, 81 species (368 individuals) were included. Table 2.3 summarises the species found at both sites and highlights those that were excluded from analysis.

Table 2.3. A list of all saproxylic beetle species identified from flight interception trapping at Stowe and Wimpole.

✓ * indicates species that were only caught in traps that were subsequently discarded from analysis due to faults influencing their function.

Family	Species	Found at Stowe	Found at Wimpole	Larval feeding guild	Adult feeding guild	GB rarity status	Saproxylic habitat	Tree species associations
Aderidae	*Aderus populneus*		✓	Xylophagus[1]	Nectivore[19]	Nationally scarce[2]	Tree hollows[13]	Broadleaved[13]
	Euglenes oculatus	✓	✓	Xylophagus[1]	Nectivore[19]	Nationally scarce[2]	Red rot[13]	Oak[13]
Biphyllidae	*Diplocoelus fagi*		✓	Fungivore[1]	Fungivore[1]	Notable b[10]	Under bark[13]	Beech and oak[13]
Buprestidae	*Agrilus laticornis*	✓	✓	Xylophagus[1]	N/A[1]	None[3]	Live or freshly dead wood[20]	Oak[13]
Cantharidae	*Malthinus balteatus*	✓	✓	Predator[22]	Predator/ nectivore[22]	None[3]	Old deadwood[20]	Broadleaved[1]
	Malthinus frontalis		✓	Predator[22]	Predator/ nectivore[22]	Nationally scarce[3]	Old deadwood[20]	Broadleaved[1]
	Malthinus seriepunctatus		✓	Predator[22]	Predator/ nectivore[22]	None[3]	Old deadwood[20]	Broadleaved[1]
	Malthodes marginatus		✓ *	Predator[22]	Predator/ nectivore[22]	None[3]	Old deadwood[20]	Broadleaved[1]
	Malthodes minimus	✓		Predator[22]	Predator/ nectivore[22]	None[3]	Old deadwood[20]	Broadleaved[1]
Carabidae	*Dromius meridionalis*	✓ *	✓	Predator[1]	Predator[1]	None[5]	Under bark[1]	Broadleaved[13]
	Dromius quadrimaculatus	✓	✓	Predator[1]	Predator[1]	None[5]	Under bark[13]	Generalist[13]
Cerambycidae	*Clytus arietis*		✓	Xylophagus[1]	N/A[1]	None[8]	Live or freshly dead wood[20]	Broadleaved[13]

Table 2.3. continued

Family	Species	Found at Stowe	Found at Wimpole	Larval feeding guild	Adult feeding guild	GB rarity status	Saproxylic habitat	Tree species associations
	Grammoptera ruficornis	✓	✓	Xylophagus[1]	Nectivore[14]	None[8]	Old deadwood[20]	Broadleaved[13]
	Phymatodes testaceus		✓ *	Xylophagus[1]	N/A[1]	None[8]	Live or freshly dead wood[20]	Oak[13]
Cerylonidae	*Cerylon ferrugineum*	✓	✓	Fungivore[1]	Fungivore[1]	None[13]	Under bark[13]	Broadleaved[13]
Ciidae	*Cis bilamellatus*	✓	✓	Fungivore[1]	Fungivore[1]	Not Applicable[13]	Fungi[13]	Broadleaved[1]
	Cis boleti	✓		Fungivore[1]	Fungivore[1]	None[13]	Fungi[20]	Broadleaved[1]
	Cis fagi	✓		Fungivore[1]	Fungivore[1]	None[13]	Fungi[20]	Oak[13]
	Cis micans	✓		Fungivore[1]	Fungivore[1]	None[13]	Fungi[20]	Oak[13]
	Cis pygmaeus	✓	✓	Fungivore[1]	Fungivore[1]	None[13]	Fungi[20]	Oak[13]
	Cis vestitus	✓	✓	Fungivore[1]	Fungivore[1]	None[13]	Fungi[20]	Oak[13]
	Cis villosulus	✓		Fungivore[1]	Fungivore[1]	None[1]	Fungi[20]	Broadleaved[1]
	Ennearthron cornutum	✓	✓	Fungivore[1]	Fungivore[1]	None[13]	Fungi[20]	Broadleaved[1]
Cleridae	*Opilo mollis*		✓	Predator[1]	Predator[1]	Nationally scarce[3]	Old deadwood[20]	Broadleaved[1]
	Tillus elongatus		✓	Predator[1]	Predator[1]	Nationally scarce[3]	Old deadwood[20]	Broadleaved[1]
Corylophidae	*Orthoperus nigrescens*	✓	✓	Fungivore[1]	Fungivore[1]	Notable b[10]	Fungi[20]	Broadleaved[1]
Cryptophagidae	*Cryptophagus dentatus*	✓	✓	Fungivore[22]	Fungivore[22]	Nationally scarce[13]	Fungi[13]	Generalist[22]

Table 2.3. continued

Family	Species	Found at Stowe	Found at Wimpole	Larval feeding guild	Adult feeding guild	GB rarity status	Saproxylic habitat	Tree species associations
	Cryptophagus labilis		✓	Fungivore[1]	Fungivore[1]	Nationally scarce[13]	Under bark[13]	Broadleaved[1]
	Cryptophagus ruficornis		✓	Fungivore[1]	Fungivore[1]	Nationally scarce[13]	Fungi[13]	Broadleaved[1]
	Cryptophagus scanicus	✓	✓	Fungivore[1]	Fungivore[1]	Nationally scarce[13]	Fungi[1]	Generalist[22]
Cucujidae	*Pediacus dermestoides*		✓	Predator[1]	Fungivore[13]	None[13]	Under bark[13]	Broadleaved[13]
Curculionidae	*Acalles misellus*	✓		Xylophagus[1]	N/A[1]	None[13]	Old deadwood[20]	Broadleaved[1]
	Achopera alternata	✓		N/A[25]	N/A[25]	Not applicable[21]	Tree hollows[25]	Broadleaved[25]
	Dryocoetes villosus	✓		Xylophagus[1]	N/A[1]	None[13]	Live or freshly dead wood[13]	Oak, sweet chestnut and beech[13]
	Ernoporicus fagi	✓		Xylophagus[1]	N/A[1]	Notable a[10]	Live or freshly dead wood[13]	Beech, oak and birch[13]
	Euophryum confine	✓	✓	Saprophagus[1]	N/A[1]	Not applicable[13]	Old deadwood[20]	Generalist[13]
	Hylesinus crenatus	✓		Xylophagus[1]	N/A[1]	None[13]	Live or freshly dead wood[20]	Ash, oak and walnut[13]
	Hylesinus varius		✓	Xylophagus[1]	N/A[1]	None[13]	Live or freshly dead wood[13]	Ash[13]

Table 2.3. continued

Family	Species	Found at Stowe	Found at Wimpole	Larval feeding guild	Adult feeding guild	GB rarity status	Saproxylic habitat	Tree species associations
	Kissophagus vicinus	✓ *	✓	Saprophagus[1]	N/A[1]	Notable b[10]	Live or freshly dead wood[13]	Ivy[13]
	Platypus cylindrus	✓		Xylophagus[1]	N/A[1]	Notable b[10]	Live or freshly dead wood[20]	Oak and beech[13]
	Scolytus intricatus	✓	✓	Xylophagus[1]	N/A[1]	None[13]	Live or freshly dead wood[20]	Broadleaved[13]
	Stereocorynes truncorum		✓ *	Xylophagus[1]	N/A[1]	Notable b[13]	Old deadwood[20]	Oak, beech and poplar[13]
	Taphrorychus bicolor	✓	✓	Xylophagus[1]	N/A[1]	Notable a[10]	Live or freshly dead wood[20]	Beech and hornbeam[13]
	Xyleborus dryographus	✓		Fungivore[1]	N/A[1]	Notable b[10]	Live or freshly dead wood[20]	Oak, sweet chestnut, beech and elm[13]
	Xyleborus monographus	✓	✓	Fungivore[17]	N/A[17]	Not applicable[17]	Live or freshly dead wood[20]	Broadleaved[17]
Dermestidae	*Ctesias serra*	✓ *	✓	Detritivore[1]	N/A[1]	None[7]	Under bark and in insect galleries[13]	Broadleaved[13]
Elateridae	*Ampedus cardinalis*	✓		Omnivore[15]	N/A[1]	RDB2[9]	Red rot[13]	Oak[13]
	Ampedus quercicola	✓		Omnivore[15]	Nectivore[13]	Notable b[10]	Tree hollows[13]	Broadleaved[13]
	Elater ferrugineus		✓	Predator[1]	N/A[1]	RDB1[9]	Tree hollows[20]	Broadleaved[1]
	Melanotus castanipes	✓	✓	Predator[1]	N/A[1]	None[18]	Old deadwood[20]	Generalist[13]

Table 2.3. continued

Family	Species	Found at Stowe	Found at Wimpole	Larval feeding guild	Adult feeding guild	GB rarity status	Saproxylic habitat	Tree species associations
	Melanotus villosus	✓	✓	Predator[1]	N/A[1]	None[18]	Old deadwood[20]	Generalist[13]
	Procraerus tibialis		✓	Predator[1]	N/A[1]	RDB3[13]	Tree hollows[20]	Broadleaved[1]
	Stenagostus rhombeus		✓	Predator[1]	N/A[1]	None[13]	Under bark[13]	Broadleaved[1]
Endomychidae	*Symbiotes latus*	✓	✓	Fungivore[1]	Fungivore[1]	Notable b[10]	Fungi[13]	Broadleaved[1]
Erotylidae	*Dacne bipustulata*	✓	✓	Fungivore[1]	Fungivore[1]	None[13]	Fungi[13]	Broadleaved[13]
	Dacne rufifrons	✓	✓	Fungivore[1]	Fungivore[1]	None[13]	Fungi[13]	Broadleaved[13]
	Triplax russica	✓	✓	Fungivore[1]	Fungivore[1]	None[1]	Fungi[13]	Broadleaved[13]
Eucnemidae	*Hylis olexai*	✓		Saprophagus[1]	N/A[1]	RDB 3[13]	Old deadwood[20]	Beech[13]
	Melasis buprestoides	✓	✓	Xylophagus[1]	N/A[1]	Notable b[10]	Live or freshly dead wood[20]	Broadleaved[13]
Histeridae	*Aeletes atomarius*	✓		Predator[1]	Predator[1]	Nationally scarce[6]	In insect galleries[13]	Broadleaved[1]
	Gnathoncus buyssoni	✓		Predator[1]	Predator[1]	Nationally scarce[6]	Birds' nests in tree hollows[13]	generalist[23]
	Gnathoncus rotundatus	✓ *		Predator[1]	Predator[1]	None[6]	Birds' nests in tree hollows[23]	generalist[23]
	Paromalus flavicornis	✓	✓	Predator[1]	Predator[1]	None[6]	Under bark[13]	Broadleaved[13]
	Plegaderus dissectus	✓ *	✓	Predator[1]	Predator[1]	None[6]	Old deadwood[13]	Broadleaved[13]
Laemophloeidae	*Cryptolestes duplicatus*	✓ *		Fungivore[1]	Fungivore[1]	None[13]	Under bark[13]	Broadleaved[13]
Latridiidae	*Dienerella vincenti*	✓		Fungivore[22]	Fungivore[22]	None[18]	Fungi[22]	Generalist[22]

Table 2.3. continued

Family	Species	Found at Stowe	Found at Wimpole	Larval feeding guild	Adult feeding guild	GB rarity status	Saproxylic habitat	Tree species associations
	Enicmus brevicornis	✓	✓	Fungivore[1]	Fungivore[1]	Notable[12]	Fungi[20]	Broadleaved[1]
	Enicmus rugosus	✓	✓	Fungivore[1]	Fungivore[1]	Notable[12]	Slime mould[13]	Generalist[13]
	Enicmus testaceus	✓	✓	Fungivore[1]	Fungivore[1]	None[13]	Slime mould[13]	Generalist[13]
Leiodidae	*Anisotoma humeralis*	✓		Fungivore[1]	Fungivore[1]	None[13]	Fungi and slime mould[13]	Broadleaved[1]
Lucanidae	*Sinodendron cylindricum*	✓	✓	Saprophagus[1]	N/A[1]	None[13]	Old deadwood[20]	Generalist[13]
Lymexylidae	*Lymexylon navale*	✓		Xylophagus[1]	N/A[1]	Nationally scarce[3]	Old deadwood[20]	Oak and sweet chestnut[13]
Malachiidae	*Axinotarsus marginalis*	✓	✓	Predator[1]	Predator[1]	Not applicable[3]	Old deadwood[13]	Oak[13]
Melandryidae	*Abdera biflexuosa*	✓		Fungivore[1]	Fungivore[1]	Nationally scarce[2]	Fungi[20]	Broadleaved[13]
	Abdera quadrifasciata	✓		Fungivore[1]	Fungivore[1]	Nationally scarce[2]	Fungi[20]	Broadleaved[13]
Monotomidae	*Rhizophagus bipustulatus*		✓	Fungivore[22]	Fungivore[22]	None[4]	Under bark[13]	Broadleaved[13]
Mordelidae	*Mordellochroa abdominalis*		✓	N/A[1]	Nectivore[1]	None[2]	Old deadwood[20]	Broadleaved[13]
	Tomoxia bucephala		✓	N/A[13]	Nectivore[13]	Nationally scarce[2]	Old deadwood[20]	Broadleaved[13]
Mycetophagidae	*Litargus connexus*		✓	Fungivore[1]	Fungivore[1]	None[2]	Fungi[20]	Broadleaved[13]
	Mycetophagus multipunctatus	✓ *	✓	Fungivore[1]	Fungivore[1]	None[2]	Fungi[20]	Broadleaved[13]

Table 2.3. continued

Family	Species	Found at Stowe	Found at Wimpole	Larval feeding guild	Adult feeding guild	GB rarity status	Saproxylic habitat	Tree species associations
	Mycetophagus piceus	✓	✓	Fungivore[1]	Fungivore[1]	None[2]	Fungi[20]	Oak[13]
	Mycetophagus populi		✓	Fungivore[1]	Fungivore[1]	Nationally rare[2]	Fungi[20]	Broadleaved[13]
	Mycetophagus quadripustulatus	✓	✓	Fungivore[1]	Fungivore[1]	None[2]	Fungi[20]	Broadleaved[13]
	Stereophilus filicornis	✓		Fungivore[1]	Fungivore[1]	Not applicable[2]	Fungi[13]	Broadleaved[13]
Nitidulidae	*Epuraea aestiva*	✓		N/A[13]	Nectivore[13]	None[13]	Unknown[13]	Generalist[13]
	Soronia grisea		✓ *	Saprophagous[1]	Saprophagous[1]	None[13]	Under bark[13]	Ash[13]
Ptiliidae	*Baeocrara variolosa*		✓	N/A[24]	Dung[24]	None[18]	old deadwood[20]	Generalist[24]
	Oligella intermedia	✓		Fungivore[1]	Fungivore[1]	RDBK[13]	Hummus under old trees[13]	Broadleaved[1]
	Ptinella aptera	✓		Fungivore[1]	Fungivore[1]	None[13]	Under bark[13]	Oak and beech[13]
	Ptinella errabunda	✓		Fungivore[1]	Fungivore[1]	Not applicable[13]	Under bark[13]	Generalist[13]
Ptinidae	*Anobium inexpectatum*	✓	✓	Xylophagus[1]	N/A[1]	None[7]	Old deadwood[20]	Ivy[13]
	Anobium punctatum	✓	✓	Xylophagus[1]	N/A[1]	None[7]	Old deadwood[20]	Broadleaved[1]

Table 2.3. continued

Family	Species	Found at Stowe	Found at Wimpole	Larval feeding guild	Adult feeding guild	GB rarity status	Saproxylic habitat	Tree species associations
	Dorcatoma chrysomelina	✓	✓	Fungivore[1]	N/A[1]	None[7]	Red rot[13]	Oak and ash[13]
	Dorcatoma dresdensis	✓		Fungivore[1]	N/A[1]	Nationally scarce[7]	Fungi[13]	Broadleaved[13]
	Dorcatoma flavicornis	✓	✓	Fungivore[1]	N/A[1]	Nationally scarce[7]	Red rot[13]	Broadleaved[1]
	Dorcatoma substriata	✓	✓ *	Fungivore[1]	N/A[1]	Nationally scarce[7]	Fungi[20]	Broadleaved[22]
	Hedobia imperialis	✓	✓ *	Xylophagus[1]	N/A[1]	None[7]	Old deadwood[13]	Rose and hawthorn[13]
	Hemicoelus canaliculatus		✓	Xylophagus[1]	N/A[1]	Nationally rare[7]	Old deadwood[20]	Poplar and maple[13]
	Hemicoelus fulvicornis	✓	✓	Xylophagus[1]	N/A[1]	None[7]	Old deadwood[20]	Broadleaved[13]
	Ochina ptinoides	✓	✓	Xylophagus[1]	N/A[1]	None[7]	Old deadwood[20]	Ivy[13]
	Ptilinus pectinicornis	✓	✓	Xylophagus[1]	N/A[1]	None[7]	Old deadwood[20]	Broadleaved[13]
	Ptinus sexpunctatus		✓	N/A[22]	Saprophagous[22]	None[7]	Old deadwood[22]	Broadleaved[22]
Salpingidae	*Lissodema denticolle*		✓	Predator[1]	Predator[1]	Nationally scarce[2]	Live or freshly dead wood[20]	Generalist[13]
	Salpingus planirostris	✓	✓	Predator[1]	Predator[1]	None[2]	Under bark[13]	Broadleaved[13]
	Salpingus ruficollis	✓		Predator[1]	Predator[1]	None[2]	Under bark[13]	Broadleaved[13]

Table 2.3. continued

Family	Species	Found at Stowe	Found at Wimpole	Larval feeding guild	Adult feeding guild	GB rarity status	Saproxylic habitat	Tree species associations
Scirtidae	*Prionocyphon serricornis*		✓	Saprophagus[1]	Saprophagous[1]	None[16]	Water-filled rot-holes[13]	Broadleaved[1]
Scraptiidae	*Anaspis fasciata*	✓ *	✓	Predator[1]	Nectivore[1]	None[2]	Old deadwood[13]	Oak[13]
	Anaspis frontalis	✓	✓	Predator[1]	Nectivore[1]	None[2]	Old deadwood[20]	Broadleaved[1]
	Anaspis maculata	✓	✓	Predator[1]	Nectivore[1]	None[2]	Old deadwood[20]	Broadleaved[13]
	Anaspis regimbarti	✓	✓	Predator[1]	Nectivore[1]	None[2]	Old deadwood[20]	Oak[13]
	Scraptia testacea		✓	Predator[1]	N/A[1]	Nationally scarce[2]	Soft rot[13]	Oak, beech and hawthorn[13]
Staphylinidae	*Euplectus karstenii*	✓	✓ *	Predator[1]	Predator[1]	None[1]	Old deadwood[20]	Broadleaved[1]
	Scydmaenus rufus	✓		Predator[1]	Predator[1]	RDB2[13]	Under bark[13]	Broadleaved[1]
	Trichonyx sulcicollis	✓		Predator[1]	Predator[1]	RDB2[13]	Old deadwood[20]	Broadleaved[13]
Tenebrionidae	*Diaperis boleti*		✓	Fungivore[1]	Fungivore[1]	Nationally scarce[2]	Fungi[13]	Birch and poplar[13]
	Eledona agricola	✓	✓ *	Fungivore[1]	Fungivore[1]	None[2]	Fungi[13]	Broadleaved[13]
	Mycetochara humeralis	✓	✓	Omnivore[15]	N/A[1]	Nationally scarce[2]	Tree hollows[13]	Beech, oak and cherry[13]
	Prionychus ater	✓		Omnivore[15]	N/A[1]	None[2]	Tree hollows[13]	Broadleaved[13]
	Pseudocistela ceramboides		✓	Omnivore[15]	Nectivore[1]	Nationally scarce[2]	Tree hollows[13]	Broadleaved[13]

Table 2.3. continued

Family	Species	Found at Stowe	Found at Wimpole	Larval feeding guild	Adult feeding guild	GB rarity status	Saproxylic habitat	Tree species associations
Throscidae	*Aulonothroscus brevicollis*		✓	N/A[1]	N/A[1]	RDB3[13]	Old deadwood[13]	Oak[13]
Trogidae	*Trox scaber*	✓	✓	N/A[1]	N/A[1]	None[1]	Tree hollows[1]	Broadleaved[1]
(1) Webb *et al*., 2018 (2) Alexander *et al*., 2015 (3) Alexander, 2014a (4) Lane, 2021 (5) Telfer, 2016 (6) Lane, 2017 (7) Alexander (2014b) (8) Alexander, 2019b (9) Shirt, 1987 (10) NBN Atlas n.d.-c (11) NBN Atlas n.d.-d (12) NBN Atlas n.d.-e(13) Alexander, 2002 (14) UK Beetles n.d.-k (15) K. N. A. Alexander, 2023, pers. comm. (16) Foster, 2010 (17) Duff, 2016 (18) NBN Atlas, n.d.-a (19) Falk, 2021 (20) Schmidl & Bußler, 2004 (21) UK Beetles n.d.-a (22) Duff, 2020 (23) Lane *et al*., 2020 (24) Duff, 2012 (25) UK Beetles, n.d.-a								

Habitat context of open grown oak trees

The Shannon diversity indices recorded for trees at Stowe ranged from 1.57 to 2.81, whilst for Wimpole they ranged from 1.39 to 2.63. Through visual inspection of maps depicting Shannon diversity indexes of the beetle communities trapped in each tree (Figures 2.5 & 2.6), no patterns could be determined linking trees in particular landscape contexts with higher beetle diversity index values. Trees with particularly high values include those in all habitat contexts including hedgerows, tree-avenues, open fields, and copses of trees.

Figure 2.5. A map of the Shannon diversity indices recorded for trapping trees in Stowe National Trust landscape and the surrounding arable land. Yellow points represent trees that were used for trapping and the point sizes are weighted by the Shannon diversity index of the saproxylic beetle assemblages that were caught in the trap in each respective tree.

Figure 2.6. A map of the Shannon diversity indices recorded for trapping trees in Wimpole National Trust Landscape and the surrounding arable land. Yellow points represent trees that were used for trapping and the point sizes are weighted by the Shannon diversity index of the saproxylic beetle assemblages that were caught in the trap in each respective tree.

The associations of saproxylic beetle diversity with habitat tree density at different scales

Species richness of all saproxylic beetles had significant positive correlations with the number of habitat trees recorded within 50 m, 250 m, and 500 m radii of trapping trees (Figure 2.7). The statistics for the correlation tests carried out are summarised in Table 2.4.

Table 2.4. A summary of the correlation tests carried out between surrounding tree density data and species richness of saproxylic beetles recorded from the trees at Stowe and Wimpole. *, P<0.05; **, P<0.01.

Radius	Test	Statistics
25 m	Spearman's rank correlation	$r_s(28) = 0.228$, $p = 0.122$
50 m	**Spearman's rank correlation**	**$r_s(28) = 0.364$, $p = 0.048$***
100 m	Spearman's rank correlation	$r_s(28) = 0.298$, $p = 0.109$
250 m	**Spearman's rank correlation**	**$r_s(28) = 0.516$, $p = 0.003$****
500 m	**Pearson's correlation**	**$r(28)= 0.378$, $p= 0.040$***
750 m	Pearson's correlation	$r(28) = 0.287$, $p = 0.124$
1000 m	Pearson's correlation	r(28) = 0.186., p = 0.324

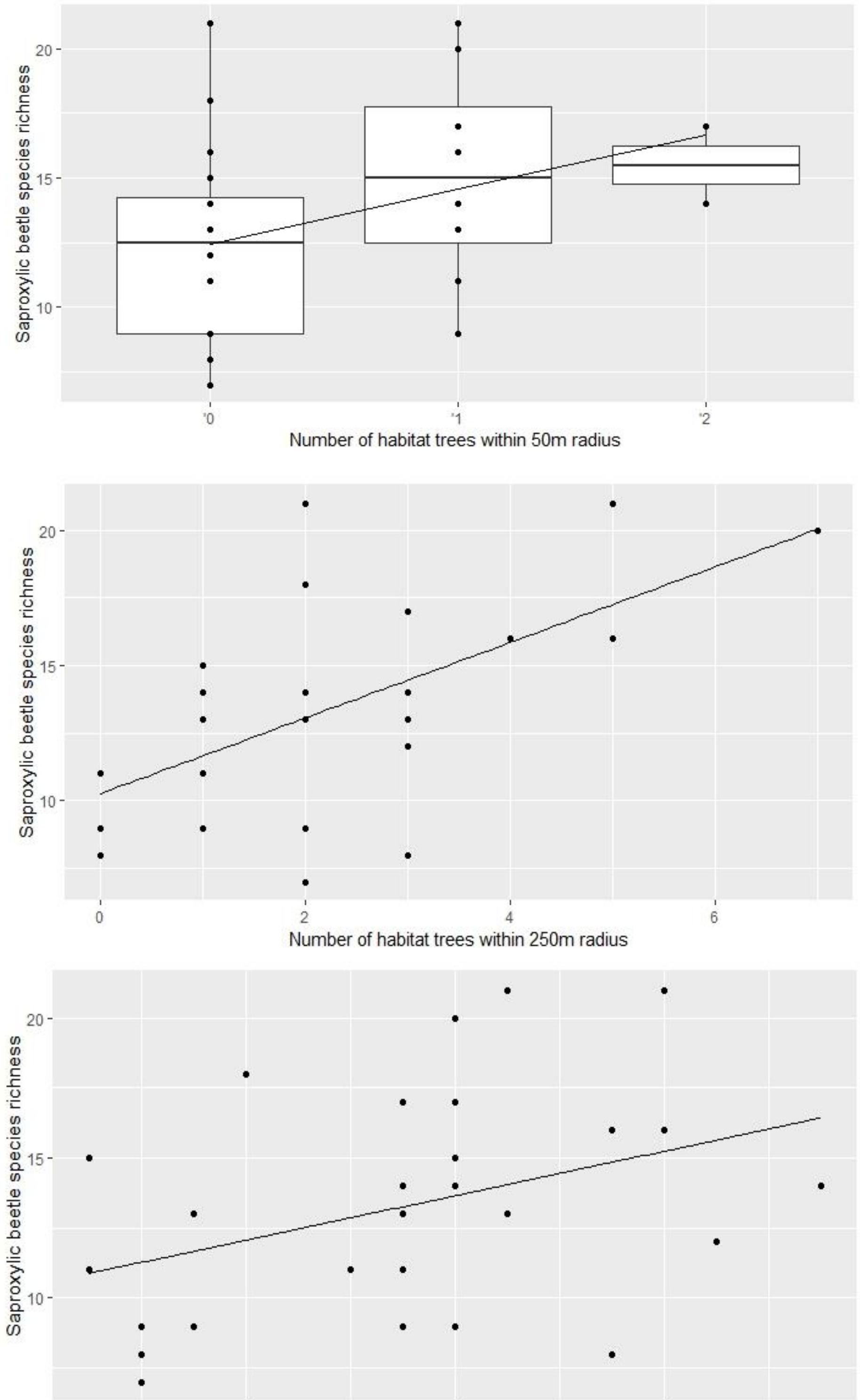


Figure 2.7. The correlation of saproxylic beetle richness against the number of trees containing deadwood habitats recorded within radii of 50m (top) and 250m (middle) and 500m (bottom) of each trapping tree.

The associations of rare saproxylic beetle species diversity with habitat tree density at different scales

The richness of rare saproxylic beetle species (those with a conservation status) was positively correlated with the number of habitat trees recorded within 25 m, 50 m, 100 m, 250 m, 750 m, and 1000 m radii of trapping trees (Figure 2.8). The statistics for the correlation tests carried out between rare saproxylic species richness and tree habitat numbers within different distance radii of the trapping trees are summarised in Table 2.5.

Table 2.5. A summary of the correlation tests carried out between surrounding tree density data and species richness of saproxylic beetles recorded from the trees at Stowe and Wimpole. *, $P<0.05$; **, $P<0.01$.

Radius	Test	Statistics
25 m	**Spearman’s rank correlation**	**r_s(28) = 0.505, p = 0.005******
50 m	**Spearman’s rank correlation**	**r_s(28) = 0.563, p = 0.001******
100 m	**Spearman’s rank correlation**	**r_s(28) = 0.459, p = 0.011***
250 m	**Spearman’s rank correlation**	**r_s(28) = 0.553, p = 0.002******
500 m	Pearson’s correlation (beetle richness log transformed)	r(28) = 0.359, p = 0.051
750 m	**Pearson’s correlation (beetle richness log transformed)**	**r(28) = 0.426, p = 0.019***
1000 m	**Pearson’s correlation (beetle richness log transformed)**	**r(28) = 0.365, p = 0.048***

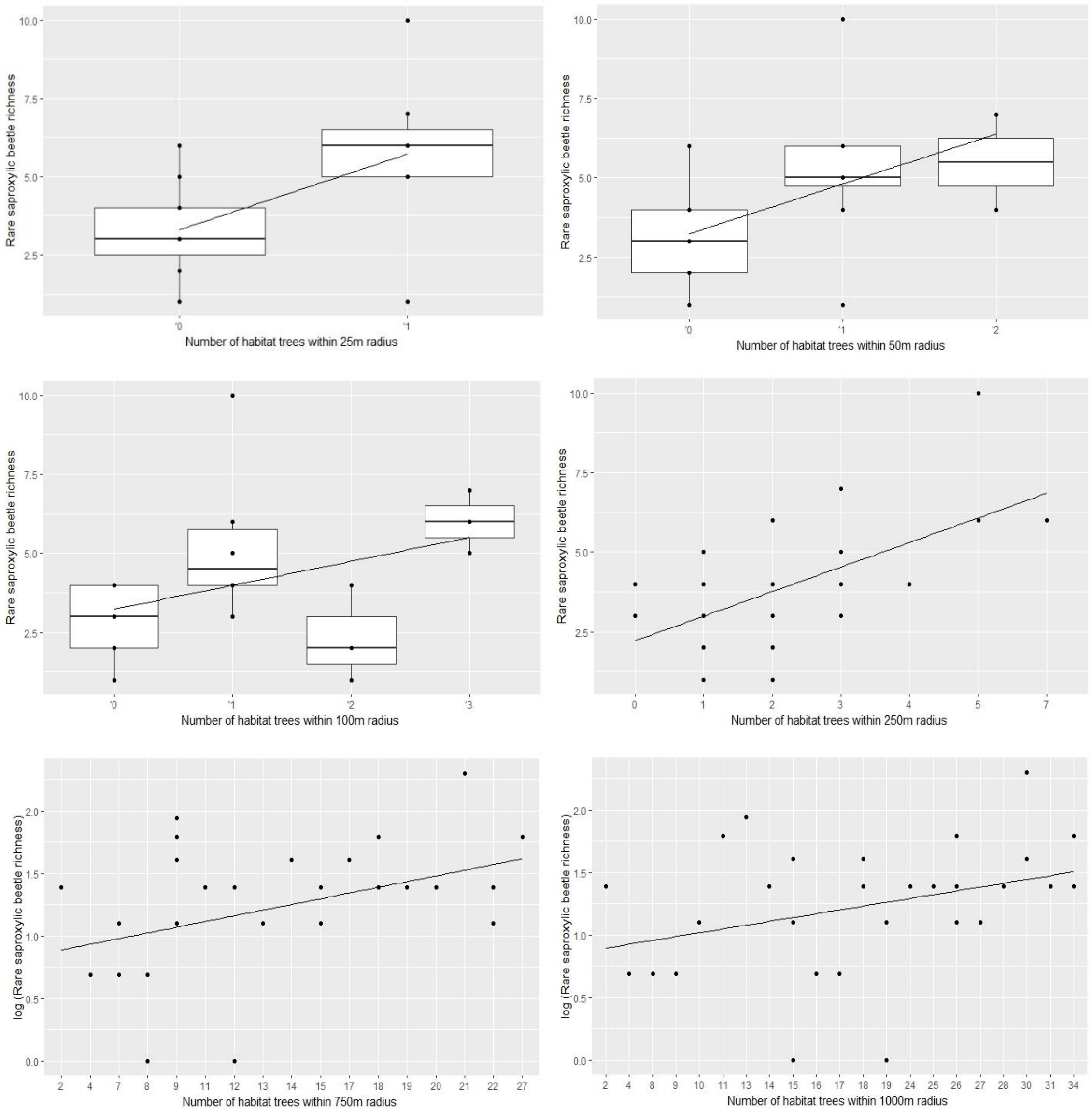


Figure 2.8. The correlation of the richness of saproxylic beetle species with conservation statuses against the number of trees containing deadwood habitats recorded within radii of 25 m (top left), 50 m (top right), 100 m (middle left), 250 m (middle right), 750m (bottom left) and 1000m (bottom right) of each trapping tree.

Links between tree density and the presence of particular saproxylic beetle species

Significant associations of between presence/absence and local tree density at certain scales were found in four of the saproxylic beetle species recorded: *Cis bilamellatus*, *Dorcatoma flavicornis*, *Agrilus laticornis* and *Scolytus intricatus* (Figure 2.9). The radii in which the number of hollow oaks significantly explained the presence of these species are presented in Table 2.6.

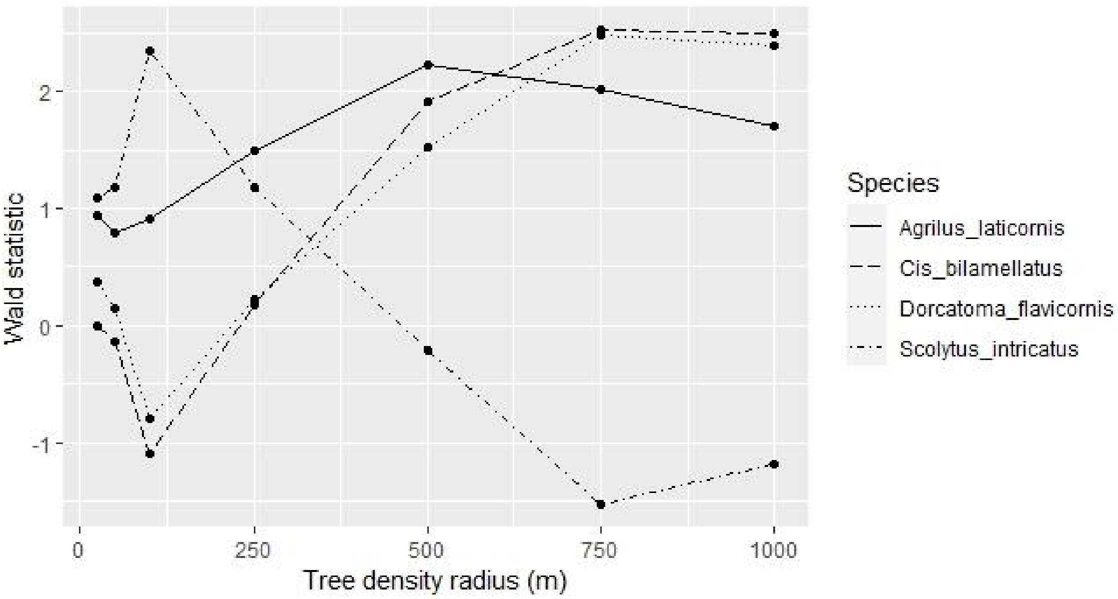


Figure 2.9. A line graph depicting the extent to which the number of habitat trees within different distance radii explained the likelihood of occurrence of four beetle species within a tree. The wald statistic of beetle species that showed significant relationships to one or more tree density radii are plotted against the different distance radii within which habitat trees were counted. Higher wald statistics are interpreted as a higher influence of tree density at a given radius on the likelihood of a species occurring.

Table 2.6. The z- and p-values calculated through generalised linear models, quantifying the relationship between the number of trees within various distance radii of a trapping tree and the occurrence of named beetle species in trap-catches from that tree. *, P<0.05.

Species	Distance radius	z-value	p-value
Agrilus laticornis	25 m	0.94	0.35
	50 m	0.79	0.43
	100 m	0.91	0.36
	250 m	1.49	0.14
	500 m	**2.24**	**0.03***
	750 m	**2.01**	**0.04***
	1000 m	1.71	0.09
Cis bilamellatus	25 m	-0.01	0.99
	50 m	-0.14	0.89
	100 m	-1.10	0.27
	250 m	0.18	0.86
	500 m	1.92	0.06
	750 m	**2.52**	**0.01***
	1000 m	**2.49**	**0.01***
Dorcatoma flavicornis	25 m	0.37	0.71
	50 m	0.14	0.89
	100 m	-0.80	0.42
	250 m	0.23	0.82
	500 m	1.52	0.13
	750 m	**2.48**	**0.013***
	1000 m	**2.39**	**0.017***
Scolytus intricatus	25 m	1.08	0.28
	50 m	1.18	0.24
	100 m	**2.34**	**0.02***
	250 m	1.18	0.24
	500 m	-0.21	0.84
	750 m	-1.53	0.13
	1000 m	-1.19	0.24

The traits recorded in veteran trees used for trapping

The most common microhabitat feature recorded from the trapping trees was attached deadwood, with all trees carrying attached, dead branches to some extent (Table 2.7). Tears and scars were also commonly recorded, indicating that the majority of trees surveyed had dropped branches at varying times in the past (Table 2.7).

The height of trees used for trapping at Stowe and Wimpole formed a normal distribution, with the most-represented height range being 15-20 m (Figure 2.10). The DBH of veteran trees used for trapping at Stowe and Wimpole also followed a largely normal distribution, with the exception of one small tree at Wimpole (Figure 2.10). This was a young tree that had become veteranised through damage. Tree DBH was not found to correlate with the diversity of deadwood-associated microhabitats present on a tree (r(27) = 0.30, p = 0.11). Full summaries of the features recorded from each trapping tree used in analysis are provided in Appendices D and E.

Table 2.7. The percentages of all trees used for trapping in this study featuring particular microhabitats.

Feature	**Percentage of trees (n=30) with feature**
Epicormic growth base	10.0
Epicormic growth trunk	50.0
Epicormic growth crown	80.0
Bark depletion	76.7
Sap runs	43.3
Split limbs	20.0
Tears	96.7
Scars	90.0
Lightning strikes	16.7
Hollowing (beyond category 1)	13.3
Holes base	46.7
Holes trunk	80.0
Holes branches	43.3
Water pockets	20.0
Red rot	66.7
White rot	80.0
Attached deadwood	100.0
Fallen deadwood	56.7
Fungi	46.7
Lichens	96.7
Moss	53.3
Ivy	20.0
Mammal signs	46.7
Bird signs	46.7
Damage	26.7

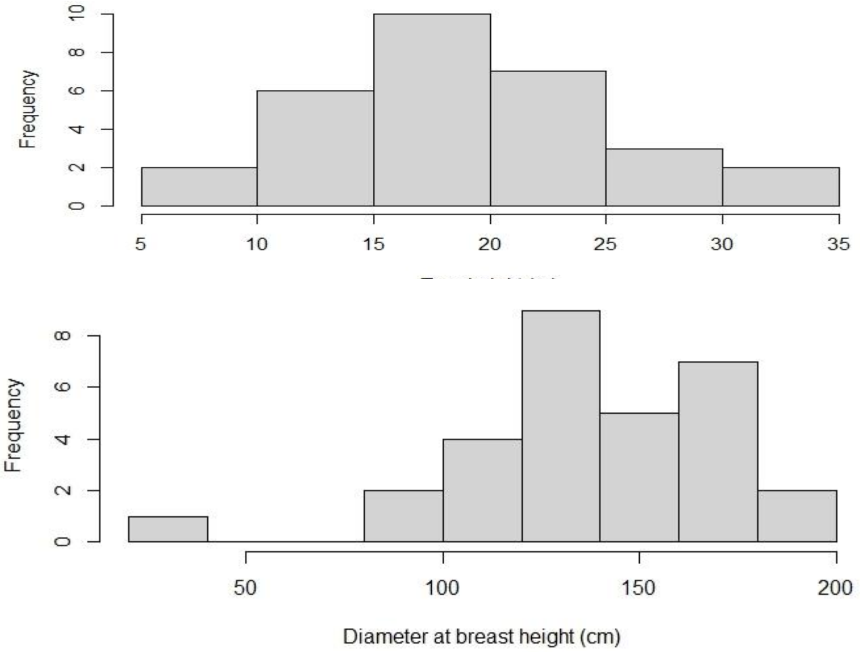


Figure 2.10. Histograms demonstrating the height (top) and diameter at breast height (DBH) (bottom) of trees used for trapping in the present study.

PCA analysis of Tree Traits

The characteristics that proved to be most descriptive of overall tree form based on the variables measured included:

- the presence of lightning strikes
- the percentage of bark depletion
- level of tree hollowing
- the presence of epicormic growth in the crown of a tree
- the presence of evident damage to a tree
- the number of holes observed in tree branches.

Small angles between the vector lines on the PCA biplot demonstrate a positive correlation between the occurrence of lightning strikes, bark depletion, hollowing and holes in the trunk (Figure 2.11). Tree hight has a similarly positive correlation to features including epicormic growth at the base, attached deadwood, tears and holes in tree branches (Figure 2.11).

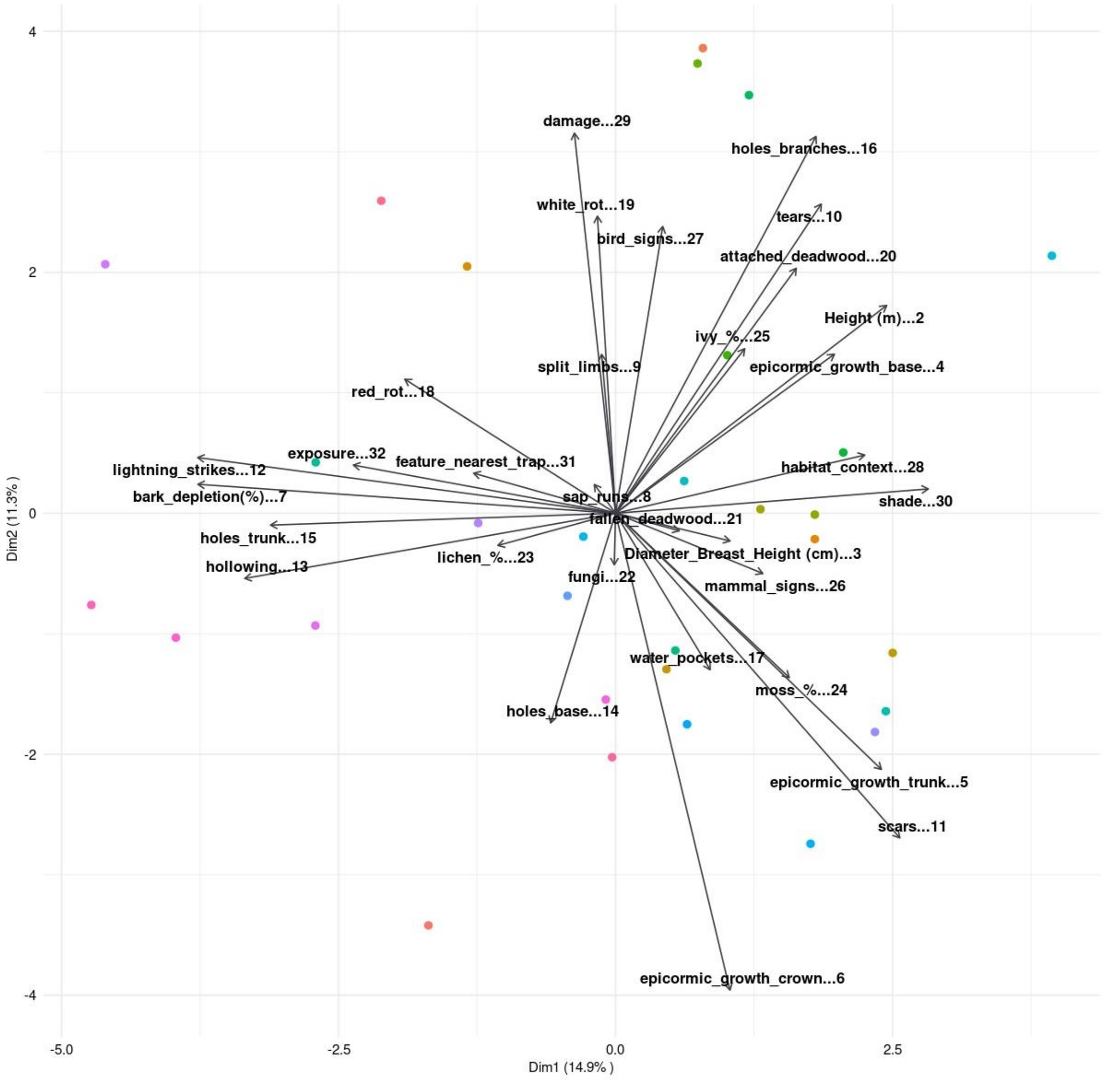


Figure 2.11. A PCA biplot with the tree data/environmental variables depicted as vectors upon which the individual trees are plotted as points.

DBH and Species Diversity

Tree diameter at breast height was not found to have a significant relationship to the richness of all saproxylic species (r(27) = 0.03, p = 0.88), the richness of rare species (r(27) = 0.29, p = 0.12), or the Shannon diversity index (r(27) = 0.06, p = 0.77) of the beetles found in a tree.

Groupings of species by larval feeding guild

The occurrence of beetle species recorded during this study was not found to significantly differ according to their larval feeding guild (R = 0.026, p = 0.10).

The NMDS plot shows a grouping of fungus-feeding species including *Abdera biflexuosa*, *Cis bilamellatus*, *Ennearthron cornutum*, *Dorcatoma flavicornis*, *Dorcatoma chrysomelina*, *Mycetophagus piceus* and *Rhizophagus bipustulatus* (Figure 2.12).

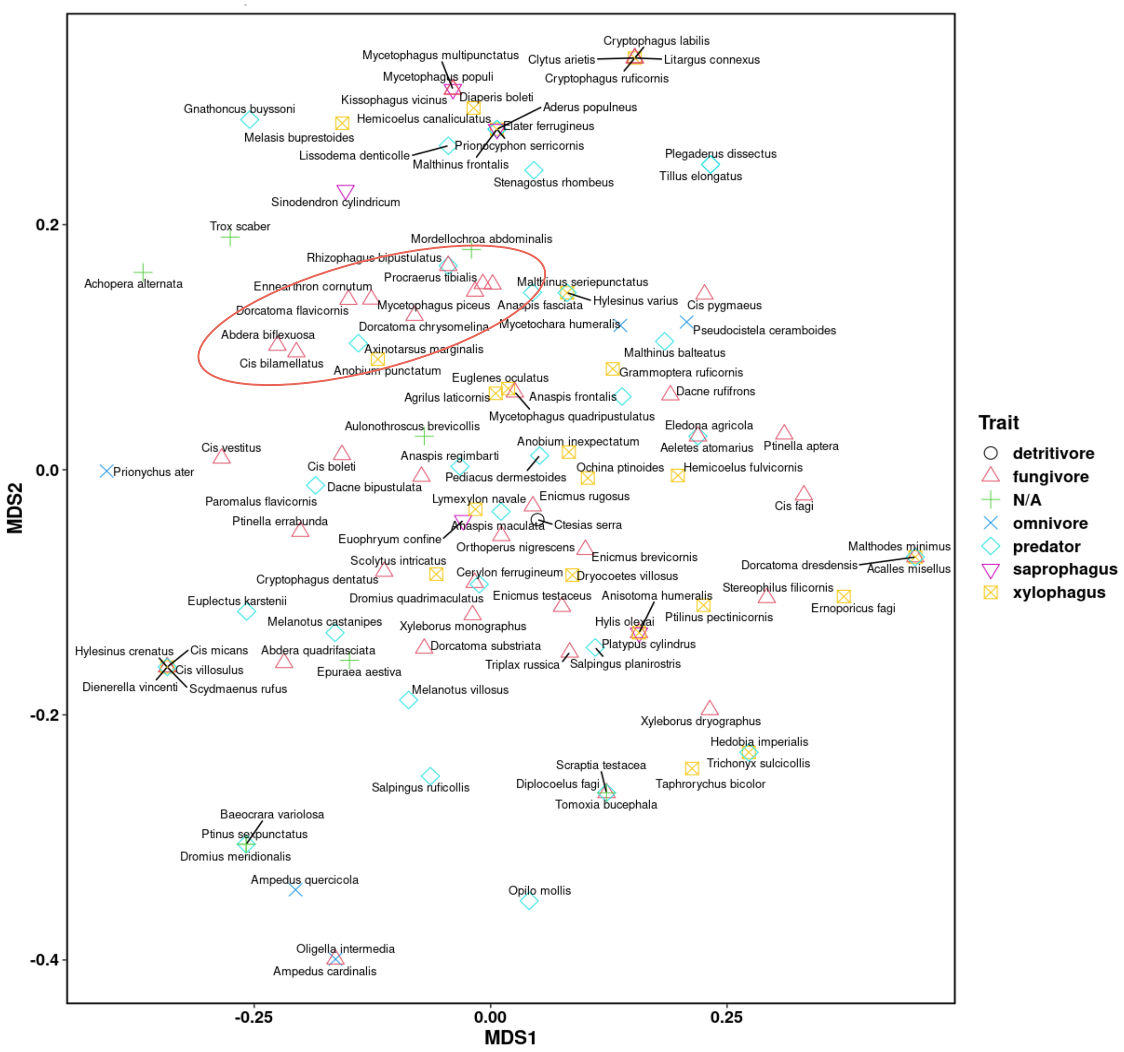


Figure 2.12. An NMDS plot depicting the saproxylic beetle species found at Stowe and Wimpole, positioned in multidimensional space according to the probability for them to occur together across the suite of trees sampled. The point icons depict the larval feeding guilds of the species. A grouping of species with fungivorous larvae is identified using a red circle.

Associations of saproxylic beetle species with specific microhabitats

Species including *Scolytus intricatus*, *Enicmus testaceus* and *Melanotus castanipes* show an association with the presence of observable red rot in habitat trees, with that of *S. intricatus* showing as the strongest of these (Figure. 2.13). The Erotylid species, *Dacne bipustulatus* shows a positive correlation to the extent of bark depletion in trees (Figure. 2.13). Species including *Hemicoelus fulvicornis* and *Eulgenes oculatus* show positive links to the number of tears in trees (Figure. 2.13). The species *Aulonothroscus brevicollis* and *Dorcatoma chrysomelina* are shown to be positively associated with higher levels of shade and the presence of fungi (Figure. 2.13). The extent of tree trunk hollowing is shown to be positively correlated to the occurrence of *Xyleborus monographus*, *Abdera biflexuosa* and *Sinodendron cylindricum* (Figure. 2.13).

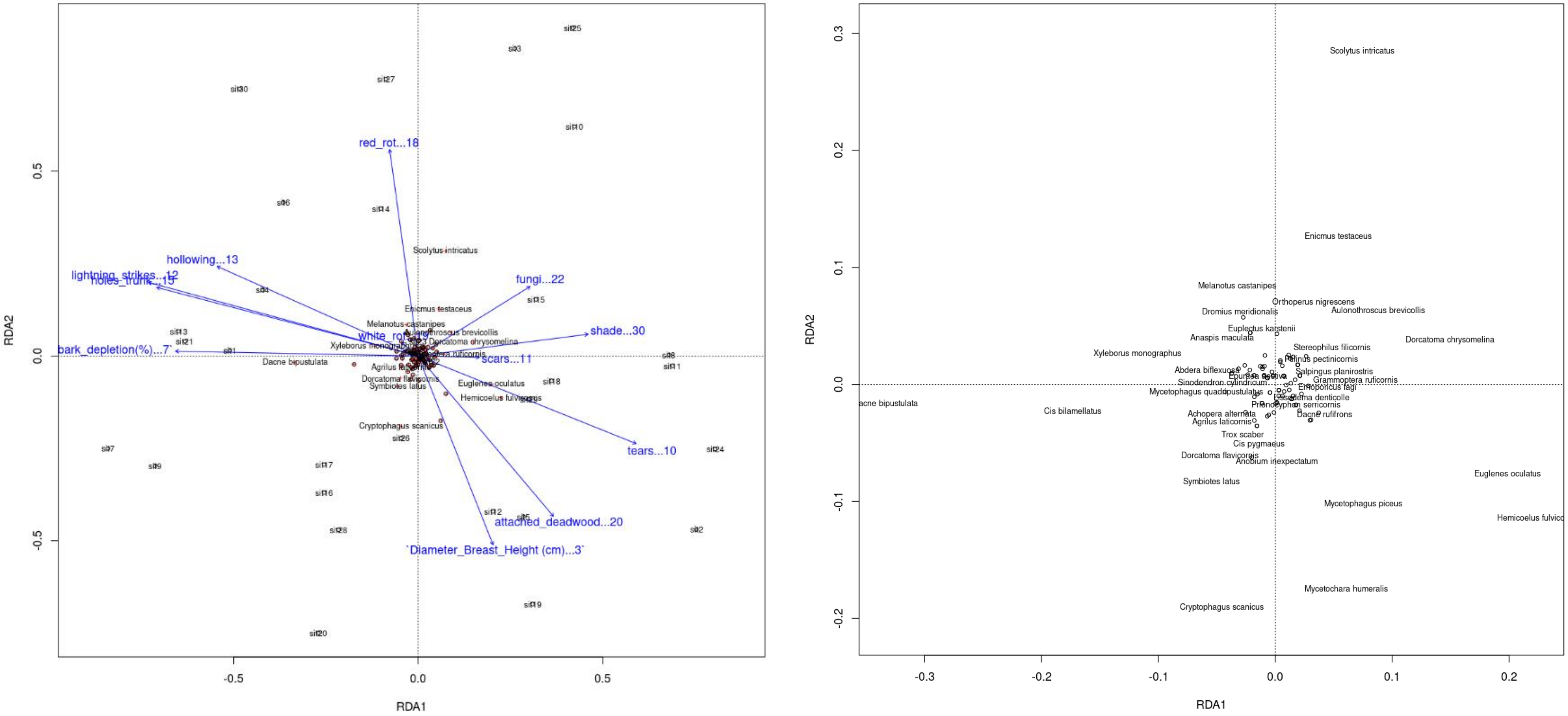


Figure 2.13. An RDA plot showing how the occurrence of beetle species in trees are correlated with the extent of the different microhabitats present. The figure on the left shows the tree numbers and beetle species in relation to the microhabitat axes. The figure on the right presents a closer image of the beetle species on the plot without the other features to allow their locations on the plot to be more easily interpreted.

2.4. - Discussion

More than half of the saproxylic beetle species found at Stowe during the present study had not previously been recorded on the SQI list for the site. In contrast, for Wimpole the number of species not previously listed on the SQI equated to just over one third of the diversity found during the present study. Discrepancies in these proportions reflect differences in the survey efforts that have previously been carried out on the respective sites (Alexander *et al.*, 2016). The saproxylic beetle diversity in the trees at Wimpole has previously been surveyed by Kirby (2002) and Damant & Kirby (2005), whereas Stowe has been investigated to a lesser extent between 1990 and 2000 by the National Trust, including one survey documented by Alexander (1991) (Alexander *et al.*, 2016).

It is important to note that the proportions of species represented on the SQI quoted here are slightly confounded by the fact that the present study based the classification of ‘saproxylic’ on several different lists, meaning that some species considered as saproxylic in this study may not be included by the SQI. However, discrepancies between lists were only found for a small minority of species. This finding demonstrates the importance of regular monitoring of saproxylic invertebrates, as organised trapping regimes can result in considerable new data which can be used to ensure that as large as possible an extent of the saproxylic fauna is considered in the management of wooded landscapes.

Differences between sites

Despite the same number of saproxylic species being found at both sites, the beetle communities at Stowe and Wimpole were found to be significantly different from each other. This is likely to indicate a lack of large-scale habitat connectivity linking these sites over the 67.5 km distance between them. The character of the intermediate landscape is largely arable land and it has been suggested that trees outside woodlands such as those in arable hedgerows may provide habitat corridors to species movement between woodland patches (Feber, 2017). However, research is lacking into the real-world effectiveness of these corridors, especially for saproxylic species (Davies & Pullin, 2007; Parmain & Bouget, 2018). This finding suggests that the network of veteran trees between the Stowe and Wimpole is not consistent enough to enable the extensive movement of all saproxylic species found at these sites. This highlights the detrimental effects of historic fragmentation and isolation of woodland in the UK on the saproxylic fauna (Rackham, 1986).

Despite this, it is important to remember that the sampling of the present study does not constitute an exhaustive list of the saproxylic species at both sites. Overlooked species may prove the sites to be more similar than shown by the present results. Therefore, additional future monitoring would be useful in further understanding the extent of saproxylic differences between these sites and the reasons behind them.

Landscape contexts of trees

No obvious trend is visible in the distribution of beetle diversity across trees in different landscape contexts. This shows that trees have the potential to provide valuable ecological resources for saproxylic beetles, independent of whether they are in a wooded copse, in a hedgerow, in a field margin or in a managed pasture context. Therefore, trees in all these situations should be considered for their individual character and valued equally in conservation decisions.

Saproxylic beetle species of particular interest

Euglenes oculatus

The nationally scarce saproxylic species, *Euglenes oculatus* was the most commonly recorded species at Wimpole (Figure. 2.14). This corresponds to data collected from oak woodlands in Norway, in which *Euglenes oculatus* was also collected abundantly (Sverdrup-Thygeson, 2009). Ancient, hollowing oak trees in pasture-like woodland situations are considered to be a particularly important resource for this species (Alexander, 2002). As *Euglenes oculatus* adults are flower-visiting and perform

Figure 2.14. An image of a specimen of *Euglenes oculatus* trapped during this study.

pollination services, this demonstrates the value of old oak trees for ecosystem services (Alexander, 2002; Falk, 2021).

Mycetophagus piceus

The Mycetophagid beetle species, *Mycetophagus piceus* was found at both of the trapping sites, with higher numbers recorded from trees at Wimpole than Stowe (Figure. 2.15). This species has been previously identified as an indicator species for sites with high conservation priority species index scores (Jansson, Bergman, *et al*., 2009). The presence of *M. piceus* therefore highlights that both Stowe and Wimpole are sites of particular importance for the conservation of rare species. The high diversity of saproxylic species found during the present study supports this finding, with approximately a third of the species found at both sites being of conservation concern.

Figure 2.15. An image of a specimen of *Mycetophagus piceus* trapped during this study.

Elater ferrugineus

The click beetle, *Elater ferrugineus* is a species that specialises on wood mould inside tree cavities (Alexander, 2002; Tolasch *et al*., 2007) (Figure. 2.16). It has been suggested as a potential indicator species for the beetle biodiversity of hollowing trees (Schmidl & Bußler, 2004; Musa *et al*., 2013). Due to its specific habitat requirements, it is threatened by the loss of ancient trees and habitat fragmentation (Tolasch *et al*., 2007). It is considered to be rare throughout its range; however recent developments in the use of pheromone lures for this species is allowing the identification of new sites hosting active populations (Musa *et*

Figure 2.16. An image of a specimen of *Elater ferrugineus* trapped during this study.

al., 2013). The presence of *E. ferrugineus* has previously been noted at Wimpole Estate (Damant & Kirby, 2005; Damant & Warrington, 2006), and the finding of two specimens during the present study confirms its continued presence at the site.

Achopera alternata

A particularly interesting finding of the present study was the discovery of a previously undocumented population of the weevil species, *Achopera alternata* (Figure 2.17). This species is a migrant from south-east Australia and has previously been found at only three other sites in the UK (Duff, 2016). These sites include Erddig Park and Llangollen in Denbighshire and Cassiobury Park in Hertfordshire (Murray *et al*., 2014; Duff, 2016). As a result, this is likely the first discovery of *A. alternata* from the county of Buckinghamshire. This demonstrates the value of regular monitoring of sites with high saproxylic potential in understanding changing species distributions.

The low number of UK observations of *A. alternata* may be partially due to the fact that they are night active and difficult to observe in the field as a result of their tendency to remain very still (UK Beetles, n.d.-a; Murray *et al*., 2014). Most previous observations of *A. alternata* in the UK have been on beech trees; however, one specimen has been found on an oak tree matching the circumstances of the present finding (UK Beetles, n.d.-a; Murray *et al*., 2014). It has been suggested that *A. alternata* may feed on fungi or algae, which, depending on their preferred food species, could explain this lack of tree-specificity (UK Beetles, n.d.-a; Duff, 2016). They are also thought to be associated with birds' nests and it has been suggested that they may disperse phoretically by clinging to birds as they fly to new areas, potentially using the hooks on their tibiae to aid in attachment (UK Beetles, n.d.-a). This is an interesting alternative strategy to consider in the study of saproxylic beetle dispersal, allowing species that may themselves be relatively immobile to cross large distances (Bartlow & Agosta, 2021). With knowledge of this new population of *A. alternata*, it would be beneficial to conduct night surveys at Stowe in the area of this specimen's capture to locate the main population and facilitate future monitoring.

Figure 2.17. Two images of a specimen of *Achopera alternata* collected from Stowe National trust landscape. The images were created using photo-stacking equipment at the Angela Marmont Centre of the London Natural History Museum.

The Impacts of Tree Density on Saproxylic Beetles

Tree density and the diversity of all saproxylic beetle species

This study found the that the number of deadwood-habitat trees within the radii of 50 m, 250 m and 500 m had significantly positive relationships to the species richness of saproxylic beetles found in oak trees. This is a narrower range of significance than that identified by Bergmann *et al*. (2012), who found significant positive relationships between species richness and tree density at all scales between approximately 100 m and 5284 m radii. Additionally, the present study found the correlation coefficient for tree density at a radii of 250 m ($r_s = 0.516$) to be similar to the maximum correlation coefficient value ($r = 0.535$) recorded by Bergmann *et al*. (2012), which occurred at the considerably greater radius of 2284 m. As the present study did not measure tree density in radii of this size it is not possible to establish whether a second peak may have emerged. However, as the correlation coefficients found in the present study decreased between 250 m to 500 m and no significant correlations were found between species richness and tree density in the largest radius measured in this study (1000 m), there is no evidence of an upward trend towards a second peak.

This finding suggests that the saproxylic beetle communities at Stowe and Wimpole were generally moving between deadwood resources within shorter distances than those recorded by Bergmann *et al*. (2012). However, this may reflect the larger area that was surveyed by Bergmann *et al*. (2012) than in the present study. The large study area allowed Bergmann *et al*. (2012) to minimise autocorrelation caused by overlapping distance radii from each trapping area in which tree densities were measured. In contrast, the smaller sites surveyed by the present study necessitated some overlapping of radii, especially over the larger distances. The inclusion of the same habitat trees in the distance radii for multiple trapping trees may have reduced the levels of variation in species diversity that may have otherwise occurred if the trees within the radii of each trapping tree were entirely independent. This potential reduction in beetle diversity variation may have decreased the likelihood of trends over large distance scales becoming evident in statistical analysis.

Alternatively, this difference in the scale at which tree density most impacted species richness may have resulted from differences in the landscapes sampled. The present survey focussed specifically on open-grown wooded landscapes including pastureland, incorporating few trees within denser woodland situations, meaning that the species found in the present study were likely to be typical of pasture fauna. In contrast, the landscape surveyed by Bergmann *et al*. (2012) included areas of coniferous forest in addition to arable fields, likely producing more variability in the growth situations of the oak trees. Hollow oaks trees in open-grown situations such as pasture and parkland have been found to host higher proportions of saproxylic beetle species associated with tree cavities than hollow trees in denser woodland situations (Sverdrup-Thygeson *et al*., 2010). This trend may explain the greater significance of closer habitat patches to the overall saproxylic diversity in the present study, as hollow associated species are thought to have particularly low tendencies for dispersal (Ranius & Hedin, 2001). Moreover, as Bergmann *et al*. (2012) conducted their research in Sweden, differences between the saproxylic faunas of Sweden and the UK may have also played a role in the difference found between peak response radii.

Pilskog *et al*., (2016) found that isolation of hollow oaks from each other at a distance of 200 m negatively influenced the abundances of xylomycophagous and oak semi-specialist beetle species. This is a similar distance to that which were linked to the greatest changes in species richness in the present study

(250 m). Therefore, this supports the finding that habitat connectivity at over distances of approximately 200/250 m is important in promoting the vitality of saproxylic invertebrate populations in oak woodlands. However, as Pilskog *et al*., (2016) did not analyse habitat density at any other distance radii lengths, this cannot be presumed to be the most influential habitat scale in the woodland studied.

Schiegg (2000b) found that species richness of saproxylic insects was positively influenced by deadwood connectivity within 150 m of trunk-window traps. The study conducted by Schiegg (2000b) differed from the present methodology in that they investigated the density of both standing and lying deadwood pieces, rather than that of exclusively living veteran trees. It is therefore surprising that the connectivity was found to influence species richness at a similarly small scale to the present study, as the fauna associated with more ephemeral deadwood resources such as quickly decaying logs are hypothesised to have greater abilities to disperse over longer distances than species associated with stable habitats such as tree hollows (Percel *et al*., 2019). A possible reason for this is that Schiegg (2000b) only measured deadwood distribution within radii from 50-200 m, meaning that they may have missed associations of the saproxylic community with deadwood on larger scales. Additionally, Schiegg (2000b) carried out their research in woodland dominated by *Fagus sylvatica* and *Picea* sp. trees. The growth tendencies of these tree species dictate that this study was done in more enclosed woodland conditions than the present study. It is not clear how this may have influenced the results of this study as little research has been carried out into the differences in dispersal tendencies of beetle communities in different woodland types (Schiegg, 2000b). This is an area that would benefit from additional future research to better understand which woodland features are linked to dispersal tendencies.

The sun-exposed nature of trees is thought be a key factor in supporting high saproxylic diversity in open wooded landscapes, as invertebrate species benefit from the rich accumulations of deadwood habitats and the increased warmth in these trees (Horak *et al*., 2014; Alexander *et al*., 2016). Therefore, it is expected that a point would be reached at which increases in density of trees within small radii would begin to negatively influence saproxylic species richness, as the shading effect of the closely spaced trees would decrease the extent of this sun exposure. Theoretically this would result in a curvilinear relationship, in which the positive relationship of saproxylic diversity with tree density would switch to a negative relationship after a certain number of surrounding veteran trees. This trend is not evident in the tree density graphs for this study, possibly suggesting that the trees measured did not include those experiencing a sufficient level of shade to induce these trends. This lack of datapoints at the particularly high tree density mean that it is not possible to discern the validity of this theory from the present results. This study could be expanded by studying landscapes with stronger gradients of trees under different density and shade levels to investigate this further.

Tree density and the diversity of rare saproxylic beetle species

The richness of saproxylic beetle species with conservation statuses (hereafter termed ‘rare species’) showed significant positive correlations with the number of habitat trees within a greater range of distance radii than overall saproxylic beetle richness. The significant relationships found between the richness of these rare species also had higher correlation coefficients at almost all distance radii than the significant correlations found with overall species richness. This indicates that rarer species could be particularly sensitive to changes in local tree densities in open-grown pasture woodlands over many scales and are likely to be a subset of the community that are most negatively affected by habitat isolation in these landscapes.

One of the radii at which the richness of rare species was most strongly correlated with tree number was 250 m. This is consistent with the finding of Brunet & Isacsson (2009) who found that red-listed beetle species richness was linked with the density of snags in a beech forest at a scale of 200-300 m. This is perhaps an unexpected consistency as beech forests are generally very different to the oak landscape studied, with the beech woodlands constituting denser, shadier environments than the largely open sun exposed oak trees in the present study. It is unclear how these landscape variations may have impacted the results of these studies, as the differences in dispersal tendencies in saproxylic beetles inhabiting different types of woodland have not been extensively investigated. Nevertheless, this finding further supports the observation that 250 m is a scale of particular importance for rare saproxylic beetle species.

In addition to the 250 m scale, particularly high correlation coefficients (r > 0.5) were also found between rare saproxylic beetle richness and the number of habitat trees within the radii of 50 m and 25 m. These strong positive associations with tree density within the lowest distance radii measured support the finding of Brunet & Isacsson (2009), that red-listed species have generally more limited dispersal tendencies than more common species, making local habitat patches particularly important resources for them. These findings contradict Økland *et al*. (1996), who found that 40 m was too small a scale to allow meaningful study of the relationships of species presence.

In contrast to the findings of the present study, Pilskog *et al*. (2016) did not find that isolation of trees from other hollow oaks at the scale of 200 m produced any significant influence on the diversity or abundance of red-listed species. This may be a result of differences in the methodology used between this and the present study, with Pilskog *et al*. (2016) placing trees into 'high isolation' and 'low isolation' categories and using this categorisation as a variable in generalized linear mixed effect models. It is possible that the cut-off chosen to distinguish between 'high isolation' and 'low isolation' in this study was not at the most appropriate level to constitute a meaningful difference in habitat availability for red-listed species.

It may be possible that limitations in data collection played a role in the lower correlation coefficients found between rare species richness and habitat tree numbers at higher distance radii in the present study. As mentioned in the previous section, the autocorrelation caused by overlapping radii of larger distances meant that the same habitat trees were included in the radii for several trapping trees. The repeated inclusion of the same habitat trees may have caused reduced variation in the saproxylic species diversity available to disperse to the trapping trees over these distances in comparison to an entirely independent study. Therefore, it should not be discounted that the true influence of tree density over greater scales may be stronger than the trends presented by these data.

Links between tree density and individual saproxylic beetle species

The present study identified significant positive relationships between species occurrence and habitat tree numbers within various distance radii for four species. Three of these species (*Agrilus laticornis*, *Cis bilamellatus* and *Scolytus intricatus*) had not previously been linked to spatial scales by Bergmann *et al*. (2012). The Wald values for the associations between individual species and tree numbers within associated distance radii in the present study were lower than the 3.90 cut-off value used by Bergmann *et al*. (2012). This suggests that the relationships of species occurrences with tree density found during the present research were not as strong as in the aforementioned work. The higher sampling effort carried out by Bergmann *et al*. (2012) may explain this, as it could have allowed more instances of species presence to be identified than in the present study. Nevertheless, the significant associations identified by the present study provide interesting observations of species habitat use which are discussed below.

Agrilus laticornis

No previous studies have identified a dispersal distance range of importance for *Agrilus laticornis* (Figure. 2.18). Therefore, the links found between the presence of *A. laticornis* and habitat tree numbers over scales of 500 and 700 m during the present study constitute new contributions to saproxylic beetle dispersal knowledge. Buprestidae have a pronounced preference for inhabiting sun exposed wood (Vandekerkhove *et al*., 2015). Therefore, it is possible that the lack of positive associations of *A. laticornis* with habitat density on lower distance scales were a result of this species avoiding trees that were shaded by other nearby veteran trees.

Figure 2.18. An image of a specimen of *Agrilus laticornis* trapped during this study.

In the related species, *Agrilus planipenis*, which is an invasive pest of ash trees in North America, the majority of females were found to have oviposited on trees within 300 m of a host tree, although one larva was found on a tree 750 m away from the source (Mercader *et al*., 2009). The lack of influence of habitat tree number over smaller distance radii found during the present study contrasts to these findings. However, the observation of a single larva at 750 m by Mercader *et al*. (2009) demonstrates the ability of *Agrilus* spp. to move over the distance scales found to be significant in explaining the occurrence of *A. laticornis* in the present study. Despite this, it is important to remember that differences in dispersal tendencies can occur between various species in the same family (Jonesell *et al*., 1999). Therefore, findings on the dispersal of *A. planipenis* cannot necessarily be taken as direct supporting evidence for the observed trends in *A. laticornis* movement.

Dorcatoma flavicornis

Bergmann *et al*. (2012) identified two peak scales (60 m and 1986 m) at which *Dorcatoma flavicornis* presence was best explained by the density of surrounding habitat trees. The second peak (1986 m) occurred as the apex of a wide ark of significant, positive associations of *D. flavicornis* presence with tree density at distance radii between around 200 m and 5000 m, with the significance of the response steadily increasing up to the peak of 1986m and thereafter decreasing (Bergmann *et al*., 2012).The distance radii at which *D. flavicornis* presence was found to be significantly explained by tree density in the present study (750 m and 1000 m) both fall within the scope of this ark, supporting the findings of Bergmann *et al*. (2012). Additionally, the strength of response of *D. flavicornis* presence to tree density remained fairly consistent between the two highest distance radii measured in the present study, potentially supporting the idea that the most important density scale for this species may be greater than 1000m, such as in the second response peak found by Bergmann *et al*. (2012). The ability of *Dorcatoma* spp. to colonise distant habitat patches has previously been noted by Jonesell *et al*. (1999), who observed their readiness to fly over open fields to reach new areas. The present study's finding that *D. flavicornis* is able to make use of habitat patches over considerable distance ranges is consistent with these observed behaviours. It has been suggested that the high dispersal tendencies of *Dorcatoma* spp.

evolved as a mechanism to escape competition and parasitism (Jonesell *et al*., 1999).

In contrast to the link found to habitat density at 60 m by Bergmann *et al*. (2012), the present study did not identify any significant relationship of *D. flavicornis* occurrence with tree numbers within the smaller radii measured. It is possible that the greater sampling effort carried out by Bergmann *et al*. (2012) resulted in the collection of a greater number of *D. flavicornis* specimens, thus allowing a more detailed analysis of the scales relevant for its dispersal. Therefore, it may have been possible to identify weaker associations with habitat density under certain distances using their data than could be identified by the present study.

Scolytus intricatus

The microhabitat used by *S. intricatus* is freshly dead branches (Alexander, 2002) (Figure. 2.19). Attached deadwood was found to be the most ubiquitously present microhabitat on all trapping trees in this study. If this observation is assumed to be consistent across the landscape and such dead branches are also extensively present in the majority of other identified habitat trees, *S. intricatus* is likely to have been relatively uninhibited in the trees that it is able to colonise. With such a high presence of suitable microhabitat, *S. intricatus* is likely to have little need to travel long distances to find new habitat patches. Therefore, this may explain why *S. intricatus* was found to benefit from higher tree numbers at the smallest scale of the four species with significant links to tree density, as all trees within this range are likely to have constituted useable habitat stepping-stones. This may not have been the case for other species with preferred microhabitats that are rarer in the landscape.

Figure 2.19. An image of a specimen of *Scolytus intricatus* trapped during this study.

A study into different *Scolytus* species, *S. laevis* and *S. scolytus* found that beetles were caught more abundantly in traps set within 20-300 m from a woodland edge than in traps set between 1-2km from the habitat, with less than 1% of captured beetles reaching the more distant traps (Anderbrant & Schlyter, 1987). The distance radius of 100 m at which *S. intricatus* was influenced by habitat density identified by the present study falls within this shorter range, supporting the finding that *Scolytus* species tend to disperse over relatively small distances.

Additionally an experiment involving logs placed at various distances from a central dispersal point, Yates (1984) found that the majority of *S. intricatus* specimens were recaptured on the closest logs to the source, at 10 m distance. Beetles were found to disperse to all other distances tested, including 3.5% of the marked beetles to the logs at the furthest distance of 75.8m (Yates, 1984). This supports the finding that *S. inrticatus* readily disperses across smaller distances. A potential reason for the lack of significant associations between *S. intricatus* presence and tree density at the smallest distance radii measures in the present study (25m and 50m) could be because higher numbers of large trees at these small scales carry the tendency for increased shading of the trapping tree. Dry and warm conditions are linked to greater population sizes of *S. intricatus* (Mezei *et al*., 2022). This may be a result of dry conditions causing drought-related stress to trees, making them more vulnerable to *S. intricatus* infestation (Mezei *et al*., 2022). Therefore, increased shading of habitat trees by other surrounding trees within short distances are likely to make them less attractive habitat patches for *S. intricatus*.

Cis bilamellatus

Figure 2.20. An image of a specimen of *Cis bilamellatus* trapped during this study.

The non-native Ciid beetle, *Cis bilamellatus*, was first discovered near London in 1884 (Wood, 1884; Orledge *et al*., 2010) (Figure. 2.20). Originally from the Australasian region, it is thought to have entered the UK through fungal material sent to Kew gardens (Orledge *et al*., 2010). Following its discovery, *C. bilamellatus* went through a slow establishment phase, during which its range grew by less than 1km per year

(Orledge *et al*., 2010). After this, *C. bilamellatus* entered a period of more rapid expansion of approximately 13 km per year, moving around the UK and entering many new vice counties (Orledge *et al*., 2010). This rapid spread is considered to be largely unaided by human activities, demonstrating the high natural dispersal capabilities of *C. bilamellatus* (Orledge *et al*., 2010). These dispersal capabilities are consistent with the finding that *C. bilamellatus* was significantly associated with the abundance of surrounding habitat trees at the greatest distance radii measured by the present study (750m and 1000m).

The present study found that *C. bilamellatus* had dispersal associations to the same distance radii as *D. flavicornis*. In contrast to this, Jonesell *et al*. (1999) found that *Cis* spp. were less effective dispersers than *Dorcatoma* spp.. The study by Jonesell *et al*. (1999) measured dispersal by observing the colonisation of fungal fruiting bodies of *Fomitopsis pinicola* and *Fomes fomantarius*. Therefore, the differences observed may have been influenced by varying preferences of *Cis* spp. and *Dorcatoma* spp.. to these fungal species. In addition, the species of *Cis* and *Dorcatoma* recorded by Jonesell *et al*. (1999) did not include *C. bilamellatus* or *D. flavicornis*. Therefore, it may be that the dispersal tendencies of these species differ from those of other members of their genera.

Tree habitat features

The PCA analysis of the tree environmental and habitat features showed that evidence of lightning strikes, extent of bark depletion, and tree hollowing were the three most explanatory variables in predicting the collection of features present in a tree. These three features were highly positively correlated with each other, with small angles between their vector lines on the PCA biplot. This could suggest that the occurrence lighting strike to a tree influences the formation of hollows and areas of bark denudation. It is not surprising that a catastrophic event such as a lightning strike considerably alters the growth and form of a tree. Tree hollows and peeling bark are both important saproxylic habitat features for saproxylic invertebrates (Alexander, 2002; Bouget *et al*., 2014). Therefore, this indicates that the occurrence of lightning strikes to trees could be an important process in creating decaying wood resources for saproxylic communities.

The value of trees struck by lightning for beetles is supported by the finding that lightning strikes have been previously associated with higher numbers of beetle entrance holes in the trunks of tropical trees (Parlato *et al*., 2020). This may be a result of greater amounts of peeling bark on these trees exposing more of the cambium layer underneath for beetles to access. Due to the value of lightning strikes in creating decaying wood resources, veteranisation procedures have been designed to mimic their activity, with linear fissures being manually carved into trees using chainsaws (Bengtsson *et al*., 2012; Ancient Tree Forum, 2016). The results from the present analysis suggest that this type of veteranisation practice would be particularly beneficial in supporting saproxylic invertebrate species that specialise on tree hollow and peeling bark habitats. Long term studies of the changes in saproxylic invertebrate communities inhabiting a tree in the years after such veteranisation would be useful in further testing this hypothesis.

The links found between tree hight and epicormic growth, attached deadwood, and tears, appears to encapsulate the stage of the tree-aging process in which trees have reached their peak growth and are entering into the retrenchment stage. This occurs when trunk growth slows and new, outer tree rings become too thin to effectively transport water to the tree crown (Alexander *et al*., 2016). At this point, the upper tree branches begin to die (resulting in the increased, attached deadwood observed in this analysis) and some may drop, resulting in the formation of scars (Alexander *et al*., 2016). The tree responds to this stress by producing epicormic growth which may eventually contribute to a new, lower crown (Joye, 2019).

The lack of significant associations between DBH with microhabitat diversity or with any measure of saproxylic beetle richness or diversity was unexpected, as larger trees are thought to contain more heterogenous habitats and support a greater diversity of saproxylic invertebrate specialists (Grove, 2002). This absence of associations may have been a result of the current study specifically selecting trees with generally large DBH and rich microhabitat representation for trapping. As a result, there may not have been sufficient variation in the tree sizes to produce any significant effect on microhabitat representation or saproxylic beetle fauna.

The microhabitat associations of particular beetle species

Red rot

The association found between *Scolytus intricatus* and red rot is unexpected, as this species has been noted to inhabit freshly dead tree branches (Alexander, 2002). As red rot-inducing fungi act slowly and are particularly linked to the heartwood of a tree, it is not a microhabitat that fits with freshly dead branches (Rayner & Boddy, 1988a; Alexander *et al*., 2016). To support this, the microhabitat analysis in the present study did not find that red rot and attached deadwood were correlated with one another. It is surprising that no link was found between *S*. *intricatus* and attached deadwood. This may be explained by trap location, as aerial deadwood often occurs at the top of a tree canopy crown, whereas traps in this study were mostly stationed lower than this level. As a result, the trapping regime may have failed to capture clusters of *S*. *intricatus* occurring in direct association with aerial dead branches.

Bark beetles such as *Scolytus* spp. Are known for their ability to act as vectors for fungi (Anderbrant & Schlyter, 1987). Therefore, it may be through this process that the presence of *S*. *intricatus* in trees is linked to higher fungal diversity, including the presence of red-rotting fungal. Strid *et al*., (2014) found that bark beetle activity impacts fungal species composition in deadwood. However, these interactions were only noted for white rot fungal species in the bark beetles studied (*Pityogenes chalcographus*, *Ips typhographus* and *Crypturgus* sp.) (Strid *et al*., 2014). As a result, further investigation may be required to elucidate the reasons for the link between *S*. *intricatus* and red rot found in the present study.

The positive association found between *Enicmus testaceus* and the presence of red rot and fungal fruiting bodies on trees may be explained by the fact that *E. testaceus* has been documented feeding on ripe slime moulds, particularly the species *Reticularia lycoperdon* (Donisthorpe, 1935; Alexander, 2002) (Figure. 2.21). Slime moulds inhabit moist, shady environments, which are also the preferred conditions for many fungi (Rayner & Boddy, 1988b; Ranius & Jansson, 2000; Smith-Ferguson & Beekman, 2020). Therefore, the links found by the present study with *E. testaceus* may be an indication that inhabited host trees provide particularly suitable moisture and light conditions for the cultivation of fungal and slime mould communities. It is also possible that the link between *E. testaceus* and red rot is more direct, as Jonsell & Nordlander (1995) found that *E. testaceus* was significantly attracted to the odours of the red-rotting fungal species, *Fomitopsis pinicola*. Considering this, the present association with red rot may constitute an undiscovered trophic association of *E. testaceus* with fungi.

Figure 2.21. An image of a specimen of *Enicmus testaceus* trapped during this study.

The association found between *Melanotus castanipes* and the presence of red rot in the trapping trees is supported by current knowledge of this species (Alexander, 2002) (Figure. 2.22). However, Jonsell & Nordlander (1995) did not find that *M. castanipes* showed significant levels of attraction to odour lures for the red-rotting fungal species *Fomitopsis pinicola* or *Fomes fomentarius*. As a result, it remains unknown which fungal species influence the presence of *M. castanipes* and further investigation would be required to elucidate this.

Figure 2.22. An image of a specimen of *Melanotus castanipes* trapped during this study.

It is important to note that this study only takes into account examples of red rot that were visible from external inspection. As red rot is linked to tree heartwood, it is likely that some red rot was not visible, potentially confounding the ability of these results to fully reflect associations with this habitat type.

Tears

One of the saproxylic species shown to be associated with tears through redundancy analysis was *Hemicoelus fulvicornis*. This species is thought to develop in small dead branches (Alexander, 2002). The point for *H. fulvicornis* on the RDA plot was also nearby the axis for attached deadwood, likely reflecting this association. The axis for tears and attached deadwood were shown to be highly correlated with each other through PCA analysis, meaning that these two features commonly co-occur in trees. This may reflect the process of trees beginning to shed their branches through retrenchment (Alexander *et al*., 2016). Therefore, *H. fulvicornis* may have a particular association to trees undergoing this stage of life.

The species, *Euglenes oculatus* was also linked to the number of tares on the trapping tree. This is not an association that has previously been noted (Alexander, 2002). *E. oculatus* are thought to develop in crumbly red-rotten wood in hollowing trees (Alexander, 2002). Tears can represent the beginning stages of hollowing, providing an entry point for fungi to decay away the heartwood of a tree (Ranius *et al*., 2009). However, the axis for tears on the RDA plot points in the opposite direction to that of hollowing and is also not correlated with the red rot axis. This would suggest that the positioning of *E. oculatus* indicates a negative association with hollowing and red rot, which is a surprising finding. Further research would be required to better understand the reasoning for this. A potential reason for the link between *E. oculatus* and tears is that this species is also reported to hide in tree crevices during the day whilst being active on tree trunks at night (UK Beetles, n.d.-b). It could be possible that the crevices formed in the areas where branches tear away provide hiding spaces for adult *E. oculatus*. This is an interesting novel finding that would benefit from additional future investigation through the inspection of tree branch tears in the field.

Shade

Dacne bipustulata was shown to be the species with the most negative association to shade (Figure. 2.23). This is supported by the findings of Lindhe *et al*. (2005) who found *D*. *bipustulata* in significantly higher densities under fully exposed conditions in comparison to semi exposed and shaded conditions. However, this conflicts with the fact that *D*. *bipustulata* inhabits fungi, which generally prefer more moist, shaded conditions (Rayner & Boddy, 1988b; Alexander, 2002). It may be that *D*. *bipustulata* benefits most from a heterogenous landscape, utilising shade-associated resources whilst being most active (and therefore most likely to be trapped) in sun-exposed areas. Further investigation into the resource use and flight activity *D*. *bipustulata* would be necessary to investigate this hypothesis.

Figure 2.23. An image of a specimen of *Dacne bipustulata* trapped during this study.

Fungus

A grouping of beetles that use fungi as their larval food resource was shown on the NMDS plot. Of these, *D. chrysomelina*, *D. flavicornis* and *Mycetophagus piceus* are linked to red-rotten wood through the activity of chicken-of-the-woods, *Laetiporus sulphureus* (Alexander, 2002). This joint association may suggest that the other species in the NMDS plot grouping (*Abdera biflexuosa*, *Cis bilamellatus*, *Ennearthron cornutum*, *Rhizophagus bipustulatus*) also have particular, previously unidentified trophic links to *L. sulphureus*. Alternatively, all of these species may have a shared link to another fungal species, causing them to frequently co-occur in the same trees. In addition, *D. chrysomelina*, *D. flavicornis* and *M. piceus* and *A. biflexuosa* are all noted for their particular association to ancient pasture woodland habitats (Alexander, 2002). Therefore, this grouping may represent a typical community that can be expected to be found associated with fungi in open-grown oak trees.

Tree Case Studies

A large ancient tree limited by isolation

The tree with the largest DBH across all sites (190.35 cm) was found at Stowe and had a relatively low Shannon diversity index, in comparison to other trees surveyed (Figure. 2.24). The numbers of habitat trees surrounding this tree was low at many of the radii measured, with no other habitat trees recorded within in a radius of 250 m. Despite its low diversity index, several rare species were recorded solely from this tree, including the nationally threatened pasture specialist, *Ampedus* cardinalis, as well as Oligella *intermedia* (RDB K) and *Ampedus quercicola* (notable b). The presence of the species *A. cardinalis* is positively associated to oak densities at a scale of 60 m, suggesting that this is a relevant scale for its dispersal (Bergman *et al*., 2012)

Figure 2.24. A large ancient tree in an isolated area at Stowe.

(Figure. 2.25). As the ancient tree discussed here had no other surrounding habitat trees within a radius of 250 m, it is unsurprising that this species was not shown to have inhabited other trapping trees in the area.

Figure 2.25. The specimen of *Ampedus cardinalis* found at Stowe during this study.

This indicates that the saproxylic community in this tree is negatively affected by isolation from other sources of deadwood habitat. It would take many years to increase the surrounding deadwood resource through the growth of new trees (Ranius *et al*., 2009). For this reason, this tree would constitute an ideal situation for the employment of beetle boxes and veteranisation processes in the surrounding area to boost deadwood connectivity. Beetle boxes could be especially useful for the two species of *Ampedus* found in the tree, as they are both associated to decaying heartwood in tree cavities, which is the habitat that beetle boxes are designed to recreate (Alexander, 2002; Jansson, Ranius, *et al*., 2009). Beetle boxes have the potential to act as habitat stepping-stones for saproxylic beetle species to move to and from this tree. As a result, the high-quality habitat in this tree (as demonstrated by the rare specialist species that are able to inhabit it) could be more extensively utilised by a greater range of species. Also, the species that were only recorded in this tree could be released from their habitat isolation and allowed to expand into new trees, making them more resilient to the potential loss of this individual tree in the future.

A small veteran tree demonstrating the potential of veteranisation

It has been suggested that 'bigger is better' in terms of the size of a tree and its value for invertebrates (Grove, 2002). This is logical as larger, older trees have often accumulated microhabitats over their lives that provide a greater range of resources to saproxylic invertebrates with different requirements (Grove, 2002). However, a method that is increasingly being used to artificially increase saproxylic habitats in areas where it is becoming depleted is veteranisation, which increases the representation of deadwood microhabitats in younger trees (Bengtsson *et al*., 2012). This means that smaller trees may play an increasing role in supporting saproxylic invertebrate communities in the future.

The flight interception programme run during this study incorporated one tree of particularly low girth (35.97 cm DBH) from Wimpole (Figure. 2.26). Despite its small size, it showed evident signs of decay, possibly as a result of damage by agricultural machinery due to its location on an arable field margin. The trap positioned in this tree collected a surprisingly high diversity of beetles, with 16 individuals of 9 species and a Shannon diversity index of 2.01. This diversity score is higher than 50% of the other trees at Wimpole Hall Estate. The species found include *Aulonothroscus brevicollis* which has a RDB 3 conservation status (Webb *et al*., 2018). This highlights that veteranised trees can provide valuable habitats to saproxylic species despite younger age and smaller size.

Figure 2.26. A small-diameter veteran tree containing various deadwood microhabitats at Wimpole.

Study limitations

Many of the saproxylic species recorded from oak trees in Stowe and Wimpole have also been found to occur on several other species of broadleaved trees in addition to oak (Alexander, 2002). As a result, it is possible that the presence of veteran trees of other species may have influenced the distribution results. Limited time and resources meant that it was outside the scope of the present study to survey all trees at Stowe and Wimpole to account for this. However, it is presumed that the influence of other tree species was likely small, as oak trees constituted a key species of deadwood value at the surveyed sites (Alexander *et al*., 2016). Additionally, open grown oak trees have been identified as hotspots for red-listed saproxylic species, suggesting that they would have had a strong influence upon the rarer species found during the present study (Sverdrup-Thygeson, 2009).

The conclusions formed from the data collected in this study was based on the species collected from each tree. However, the lack of specimens of a certain species collected from a tree is not definite proof of its absence from that tree (Hirzel *et al*, 2002). Therefore, the results of this study are limited by the effectiveness of the sampling. However, as the trapping effort was equivalent for all trees sampled, the communities of species found were comparable between trees for the analysis carried out. This allowed the results of this study to remain statistically valid despite this potential of having overlooked of some species present.

The species distributions across the landscapes at Stowe and Wimpole are the culmination of historical dispersal events. These may have been impacted by habitat patches that have been lost over time and are therefore not represented in the tree survey data. Without the analysis of old maps, it is difficult to understand how this impacted the study. Time constraints meant that historical map analysis was outside of the scope of the present study. Despite this, the strength of the trends identified suggest that any influence of unaccounted historical trees on the results of this study was minimal.

It is possible that differences in the height of traps in the trees could have caused confounding effects in the findings of this study. Attempts were made to measure the heights of the traps so that this could be accounted for in the statistical analysis; however, unfortunately, these data were lost, meaning that the data could not be included. In addition to height, the natural variation in the forms of the trees used for trapping also meant that traps could not be positioned next to equivalent microhabitat situations each time. The specific positioning is likely to have had some influence on the species captured in each tree. Both of these confounding factors could not be avoided, as the suitable locations for hanging traps in trees are limited by available branches.

As mentioned earlier in this section, the overlapping of radius buffers for the tree density analysis, particularly at greater distances may mean that this study experiences some pseudoreplication. This could have influenced the strength of the correlations identified between species richness measures and the number of trees within larger distance radii. The size of the study sites meant that this could not be avoided whilst also including a suitable number of replicates for meaningful statistical analysis. Despite the overlapping radii, enough variation in tree numbers was achieved over large distance radii to identify significant relationships with the richness of rare saproxylic species and the occurrence of particular beetle species (e.g. *C. bilamellatus* and *D. flavicornis*). This suggests that the data from this study has value in identifying beetle habitat associations. Nevertheless, it is important to consider that pseudoreplication may have had some influence on the conclusions of this research.

Summary of aims

Microhabitat requirements

This study identified a range of links between saproxylic beetle species and particular tree microhabitats. Some of these findings support current knowledge of the biology of respective species, whilst others represent novel observations that may be worthwhile investigating further in future research. The links found in this research may be used to improve the ability to make inferences of the microhabitat-types present in a tree using a species list of saproxylic beetles found within it. Similarly, they may allow estimations to be made of which beetle species a tree may be able to support, based upon the results of a microhabitat survey.

Density requirements

The results of this study suggest that, for open-grown wooded landscapes in the UK, such as those including pasture woodland and trees outside woodland, increased connectivity of deadwood resources within a radius of 250 m is beneficial to local saproxylic beetle diversity. Habitat connectivity at this scale benefits both common and threatened saproxylic species, making it highly suitable for consideration in conservation management schemes. The results also highlight that veteran tree connectivity has particularly high influence on rarer species richness, especially over smaller distance radii. This further emphasises the importance of maintaining and promoting decaying wood resources in the landscape for the conservation of vulnerable portions of the saproxylic community.

This study also shows that saproxylic communities contain species with varied dispersal needs, including species such as *Scolytus intricatus* that was shown to move between habitat trees within 100 m of an inhabited veteran tree, as well as *Cis bilamellatus* and *Dorcatoma flavicornis* which are more likely to occur in trees with greater habitat connectivity over distances of 750 m and 1000 m. This highlights the importance of considering the requirements of individual species in addition to those of the whole community, as over-generalisations may result in suboptimal conservation decisions for certain subsets of the saproxylic community.

Recommendations for future research

The potential problems associated with using overlapping distance radii to measure surrounding tree density may be avoided in future studies by incorporating a greater number of similar sites containing open-grown oaks. Through this, trees could be selected specifically to avoid such overlapping radii. This would give greater confidence in the strength of habitat density associations over greater distances.

The differences in species composition and resource use of saproxylic invertebrates in hollow oaks under different forest conditions have been previously investigated (Sverdrup-Thygeson, 2010; Horak *et al*., 2014). However, little research has been done investigating the influence of forest conditions on saproxylic insect dispersal tendencies. It would therefore be beneficial to conduct a similar trapping methodology as that used in the present study, specifically in oak trees in denser forest situations. This would allow any differences in the ability of saproxylic communities to move through differing landscape structures to be identified. Such information would be useful in informing tailored conservation management plans for saproxylic invertebrate communities in specific landscape types.

Another area that would benefit from additional research would be the long-term effects of the implementation of veteranisation practices or beetle boxes on the connectivity of these sites. Research into these practices remain in their initial stages (Jansson, Ranius, *et al*., 2009; Bengtsson *et al*., 2012). However, their implementation into sites such as these with well-understood saproxylic communities could provide valuable information into their potential applicability for the conservation of species in open-grown oak wooded landscapes.

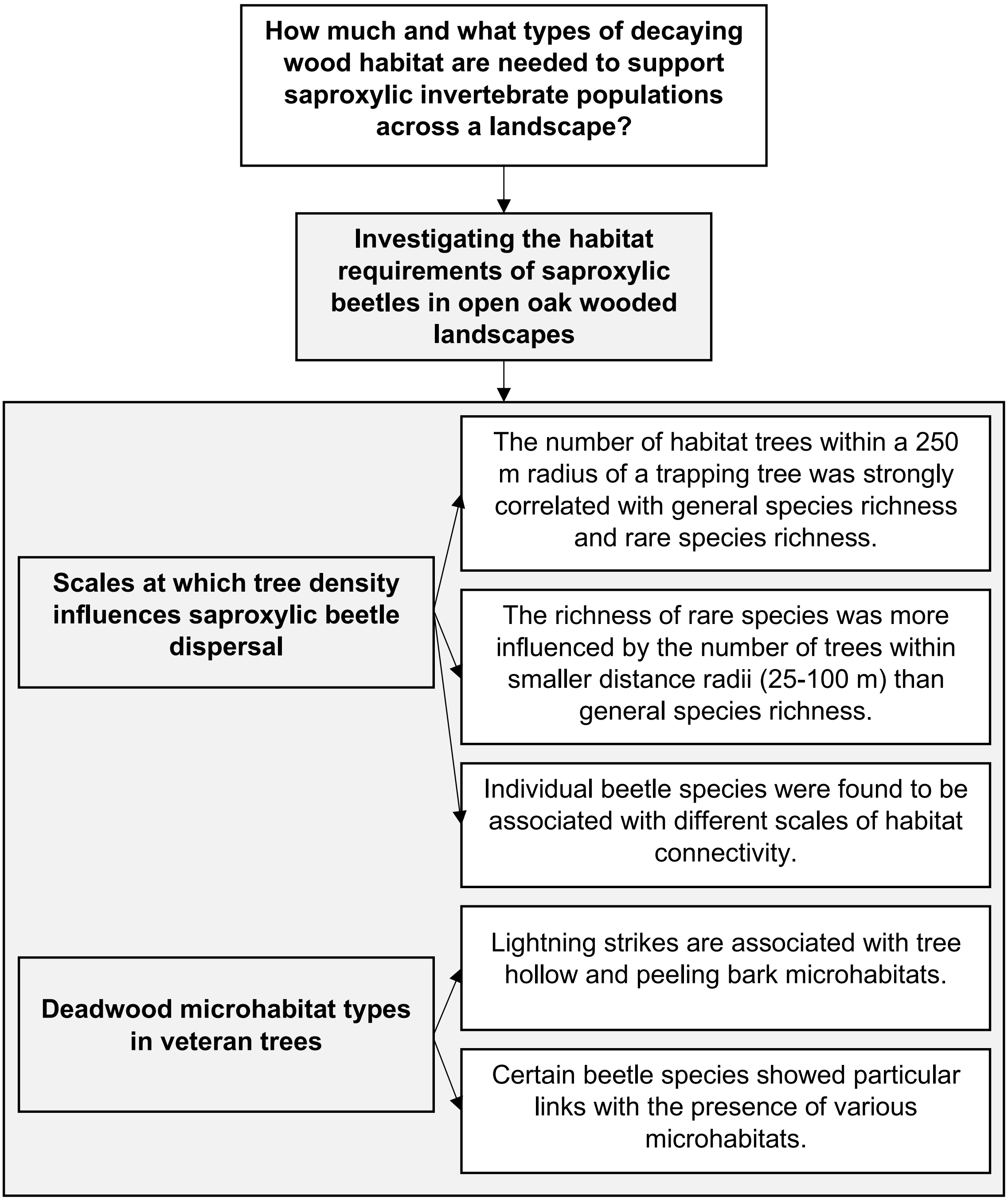


Figure 2.27. A conceptual framework outlining the key findings on the main research areas that this chapter addressed concerning the habitat requirements of saproxylic beetle communities in open oak woodlands.

Chapter 3 – Ground Level Beetle Boxes as a Novel Method of Habitat Creation

3.1. Introduction

Rationale and basis for study

Trees with heartwood decay cavities are some of the most important habitats for saproxylic beetles (Alexander, 2008). However, the stocks of open-grown ancient and veteran trees that carry these hollows are declining on both local and global scales (Lindenmayer *et al*., 2012; Woodland Trust, 2021b). As a result, hollow-dwelling invertebrates are of particular conservation concern. For example, in Germany, 86.1% of beetle species associated with rot holes are identified by the red list as being threatened (Geiser, 1998; Floren & Schmidl, 2008). To mitigate tree-hollow habitat declines, researchers have investigated creating supplementary habitat sources in the form of containers filled with decaying sawdust and other components (Jansson, Ranius, *et al*., 2009; Hilszczański *et* al., 2014; Carlsson *et al*., 2016). These artificial habitat boxes, hereafter referred to as 'beetle boxes', are intended to help sustain local saproxylic invertebrate populations in a landscape while new habitat trees reach their hollowing stage (Jansson, Ranius, *et al*., 2009).

Beetle boxes work in a similar way to bird nesting boxes, introducing extra, manmade habitat into an area to augment existing natural stocks (Jansson, Ranius, *et al*., 2009). They aim to mimic tree cavities, which are the preferred habitat of many threatened beetle species (Alexander, 2002; Jansson, Ranius, *et al*., 2009). Beetle boxes consist of enclosed containers, emulating natural tree hollows by providing sheltered conditions that buffer against external temperature and moisture fluctuations (Coombs *et al*., 2010). The containers are filled with woody substrates that are left to decay over time (Jansson, Ranius, *et al*., 2009; Hilszczański *et al*., 2014; Carlsson *et al*., 2016). This material eventually develops into a fine, crumbly wood mould, similar to that which develops in the base of natural tree cavities (Jönsson *et al*., 2004). This process encourages a suite of fungi, slime moulds, bacteria, and soil invertebrates to accumulate within the boxes, all of which are known to benefit tree-hollow beetle communities (Ulyshen, 2015).

Cavities of greater volume have been shown to better support some target beetle species (Ranius & Nilsson, 1997; Gioux *et al*., 2009). This may be because larger tree hollows tend to have existed for longer periods of time, allowing more opportunities for colonisation by beetles (Ranius & Nilsson, 1997). Alternatively, it has been suggested that tree hollows containing greater volumes of wood-mould provide increased temperature stability than those with shallower mould layers (Ranius & Nilsson, 1997). Due to the links between cavity size and beetle occupancy, most previously trialled beetle boxes have been relatively large, with capacities of around 60-90 litres (Jansson, Ranius, *et al*., 2009; Hilszczański *et al*., 2014; Carlsson *et al*., 2016; Mestre *et al*., 2018).

Previous studies of beetle boxes have proven their ability to support rare and vulnerable saproxylic species (Jansson, Ranius, *et al*., 2009; Hilszczański *et al*., 2014; Carlsson *et al*., 2016). A range of tree-hollow associated species have been recorded from beetle boxes, including *Atomaria morio*, *Prionychus ater*, *Pseudocistella ceramboides* and *Mycetochara humeralis* (Alexander, 2002; Alexander, 2016b; Jansson, Ranius, *et al*., 2009; Carlsson *et al*., 2016). These findings demonstrate the potential of the beetle box concept to achieve its intended purpose of emulating tree-hollow habitats. This indicates that beetle boxes have a high conservation potential for the saproxylic fauna, and that further research into the concept as an interim habitat to plug spatial or temporal gaps in tree hollow habitat is worthwhile.

Conservation applications of beetle boxes

Beetle boxes have the potential to be used in various practical contexts to benefit the conservation of tree hollow invertebrates, in addition to the supplementation of local deadwood habitat. For instance, researchers have suggested beetle boxes could be used as a tool in species translocation schemes such as reintroductions (Carlsson *et al*., 2012). The installation of beetle boxes may ensure that sufficient wood-mould habitat exists at a target site for translocations. They could then be monitored to check for establishment of the target species to assess the effectiveness of the translocation. The potential of this approach has been demonstrated by Rotheray & Rotheray (2012) who successfully translocated the rare hoverfly, *Blera fallax*, to new areas, supplementing local water-filles rot hole habitat at target locations by creating manmade hollows in pine stumps.

Beetle boxes could also be used more directly in species translocations. For example, if a key beetle species was known to inhabit a beetle box, the whole structure could be moved to a target location. This would provide the species with a known suitable habitat reservoir in the new landscape, thereby supporting the species during the spatial transition. Nonetheless, this method should be thoroughly assessed to avoid risks such an unintentional introduction of accompanying non-target species into a new area.

Some concerns surrounding translocation as a conservation tool include uncertainties around its effectiveness and the fear of unintended ecological consequences when introducing a species to a new area (Butt *et al*., 2021). Despite these, it is predicted that translocation or ‘assisted migration’ will become an increasingly important strategy to help isolated species survive the consequences of climate change (Butt *et al*., 2021). This is especially true for species with low tendencies for natural dispersal such as those associated with tree hollows, as their limited ability to escape suboptimal conditions give them a higher risk of extinction (Butt *et al*., 2021). It has been acknowledged that there is an urgent need for novel innovations within this developing field (Butt *et al*., 2021). Beetle boxes have the potential to fill this gap in a saproxylic context, making their study particularly worthwhile.

In addition to these practical applications, artificial habitats could help to minimise damage to valuable old trees during monitoring activities. Some survey methods used to investigate saproxylic faunas carry inevitable consequences of disturbing or destroying existing deadwood habitats. For example, several previous studies of tree cavities have involved the excavation of a considerable proportion or all internal wood-mould (Ranius *et al*., 2010; Cuff, Müller, *et al*., 2021). While this can be necessary for effective surveying, it also carries the potential to disturb gradients of moisture and decay-extent that have accumulated within tree hollows over hundreds of years. Surveying activities may also disturb protected bat species that inhabit tree hollows (Burgar *et al*., 2015). In addition, regular visits to vulnerable ancient trees may result in damage to root systems through trampling (Nolan *et al*., 2020). If beetle boxes are shown to support communities of species that are representative of those found in real tree cavities, they could be used as remote sampling points to investigate local tree hollow invertebrate communities without disturbing ancient trees. Through this method, surveyors could gather data on invertebrate assemblages whilst minimising damage to priority habitats of conservation concern.

Beetle boxes also offer unique opportunities for studying tree-hollow systems to learn more about the processes and community dynamics that occur within them (Jansson, Ranius, *et al*., 2009; Mestre *et al*., 2018; Weatherbee *et al*., 2022). Study into tree hollow habitats may suffer from low replication if there are limited examples of the hollows in an area. Also, natural variation in tree hollow habitats may not be extensive or evenly spread enough to be conducive to a controlled, replicated scientific study. To investigate key influences of tree-hollow dynamics in a more controlled manner, artificial habitats can be used as experimental units and manipulated in a way that provides required levels of variation (Jansson, Ranius, *et al*., 2009; Weatherbee *et al*., 2022). For example, Jansson, Ranius, *et al*., (2009) positioned beetle boxes at controlled distances from source populations to investigate the effects of habitat isolation on the colonisation of wood mould by saproxylic species. Similarly, beetle boxes have been used to investigate the factors influencing wood-mould decomposition and nutrient accumulation within tree hollows (Mestre *et al*., 2018; Weatherbee *et al*., 2022).

Current state of beetle box research and knowledge gaps

Fungal presence and rot type in tree hollows and beetle boxes

The potential for beetle boxes to be employed for the aforementioned purposes is dependent on how effectively they can mimic the conditions in real tree hollows and provide suitable habitat for the target species. Beetle box research is still in its early stages and the results from previous studies indicate that, whilst they show promise, there is a need to further refine the design and contents of beetle boxes so they can support a wider suite of saproxylic beetle species. For instance, after four years of maturation time, Jansson, Ranius, *et al.* (2009) found fewer red listed species in habitat boxes than in wood mould from real veteran tree hollows. This suggests that the wood mould in the boxes had not achieved entirely comparable conditions to a true tree cavity. It is possible that this was due to differing decay processes occurring in the respective habitats.

The fungal diversity in real tree hollows and the rot-process that occur have a strong influence on the saproxylic invertebrate communities that inhabit them (Fukasawa, 2021). The most prominent groups of wood decay fungi include those causing white, red, and soft rot types (Fukasawa, 2021).

White rotting fungi include many basidiomycetes and some ascomycetes (Fukasawa, 2021). White rot is characterised by the decay of lignin, causing wood to develop a spongy, fibrous texture (Fukasawa, 2021). Breaking down lignin allows a range of invertebrates to access the cellulose and hemicellulose inside wood cells (Fukasawa, 2021).

Red rot (also known as ‘brown rot’) is the result of a range of basidiomycete fungal species that decay away the cellulose and hemicellulose of wood cells, leaving the lignin intact (Fukasawa, 2021). This produces a distinctive dry, cubical decay pattern in wood (Fukasawa, 2021) (Figure 3.1). Several tree hollow dwelling beetle species have been noted to have particular associations to red-rotten wood (Alexander, 2002).

Figure 3.1. An image showing the cubical structure of red rotten wood.

Soft rot is caused by Ascomycete fungi, which decay cellulose (Blanchette *et al*., 2004; Fukasawa, 2021). This process produces a muddy, soil like texture in the wood (Fukasawa, 2021). Soft rot fungal species can tolerate situations with a higher moisture content than both red and white rot fungi (Fukasawa, 2021). Soft rot fungi have also been observed to outcompete white rot fungi in nitrogen-rich sawdust (Tokimoto, 1985).

In addition to these key fungal decay types, mycorrhizal fungi are also present in extensively decayed wood that is in contact with the soil at the base of a tree (Rajala *et al*., 2015). The activity of these fungi on wood structures has been less extensively studied than the other rot types discussed here (Baldrian, 2009; Fukasawa, 2021). As a result, the interactions of mycorrhizal fungi with wood are not as well understood.

Deadwood decay occurs through a succession of fungal species which cause these different rot types (Rajala *et al*., 2015; Fukasawa, 2021). Red and white rotting fungi are early colonisers, often entering wood whilst it is alive and peaking in abundance during the intermediate stages of decay (Alexander *et al*., 2016; Rajala *et al*., 2015; Song *et al*., 2017; Fukasawa, 2021). While white rotting fungi adopt a generalist strategy regarding their habitat requirements, red rotting fungi have more specific niches (Rajala *et al*., 2015). This is because fungi responsible for producing red rot are poor competitors but are resistant to stressful situations such as dryness (Song *et al*., 2017; Fukasawa, 2021) As a result, red-rotting fungi are able to dominate in the heartwood walls of tree hollows where the dry conditions mean that there are lower levels of competition from other fungal species (Fukasawa, 2021). Their specialism for heartwood explains why red rot occurs mainly in wood of a greater diameter, in which an internal heartwood zone has become clearly delimited (Yee *et al*., 2006) (Figure 3.2).

Figure 3.2. An image showing differential decay patterns in heartwood and sapwood.

When heartwood in the walls of tree hollows is degraded to the point where it detaches or crumbles from the inside of the trunk, it falls into the base of a tree hollow (Figure 3.3). At this stage, the damp, soil-like condition of wood mould in basal tree hollows inhibits the action of red rotting fungi (Stockland, *et al.,* 2016). As a result, the red rot fungi are no longer able to compete with the highly combative soft rot and mycorrhizal fungi found in the wet wood mould and soil (Boddy, 1993; Rajala *et al*., 2015; Song *et al*., 2017; Fukasawa, 2021). A considerable drop in the prevalence of red-rotting fungi is therefore observed during later decay stages (Rajala *et al*., 2015). Because of this, red rot is not expected to be a significant component of the decay occurring in the wood mould of basal rot holes.

The beetle boxes are expected to mimic the late-stage decay of wood mould (Alexander, 2016). However, as the external structure of the boxes does not feature the delimited areas of heartwood of real trees, it is unlikely that red rot will be strongly represented within them. This is supported by previous studies, which have observed the notable absence of red rot associated beetle species among the community of species found in beetle boxes (Jansson, Ranius, *et al*., 2009; Alexander, 2016b). Despite this, as the boxes are aimed towards the specialist fauna of late-stage wood mould in these basal tree hollows, it is expected that the absence of red rot in the boxes will not significantly impede the boxes' intended conservation function.

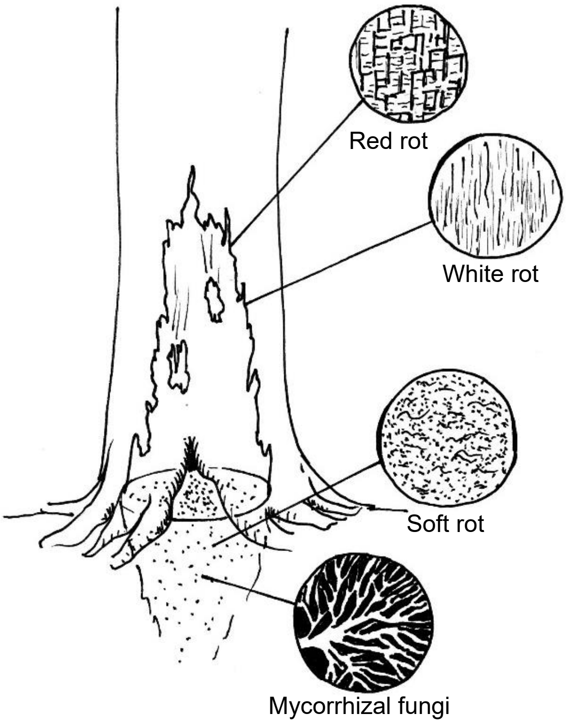


Figure 3.3. A diagram of the predominant rot types in different areas of a tree hollow. Red and white rot types are most prevalent in the intermediate decay stage that occurs in tree hollow walls. In the damp wood mould of the tree hollow base, soft rot and mycorrhizal fungi are dominant. Wood transitions between these stages when pieces become detached from the hollow wall and fall down into the base.

Nitrogen Content of wood mould

In addition to fungi, the nutrient content of wood-mould inside beetle boxes could be another important factor in creating comparable conditions to those in natural tree hollows. Wood mould in basal tree cavities has been found to contain higher levels of nitrogen than surrounding soil and other types of decaying wood (Kelner–Pillault, 1974; Jönsson *et al.*, 2004). This is thought to be linked to the tendency for birds and other vertebrates to nest in hollow trees, resulting in depositions of nitrogen-rich faeces and carrion into the wood mould (Jansson, Ranius, *et al.*, 2009; Micó *et al.*, 2015). Invertebrates also contribute to the high nitrogen content of wood mould (Ulyshen, 2015). Some beetle species fix nitrogen in their gut and produce nitrogen-rich frass (Jönsson *et al*., 2004; Ulyshen, 2015; Wetherbee *et al*., 2022). In addition, fungus feeding invertebrates release nitrogen from fungal fruiting bodies into the mould (Ulyshen, 2015). Finally, the frass of hollow-dwelling insects benefits free-living nitrogen-fixing bacteria that exist independently in the mould (Ulyshen, 2015).

Several studies have addressed the effects of nutrient variation in beetle boxes through adding different ingredients to beetle box contents (Elbourn, 1970; Jansson, Ranius, *et al*., 2009; Carlsson *et al*., 2016). For example, Jansson, Ranius, *et al.* (2009) found that the addition of nitrogen-rich poultry manure to beetle boxes did not influence the diversity or abundance of saproxylic beetles inhabiting the resultant wood mould; however, it is possible that this was a result of the specific volume and type of manure used. As beetle box research remains in its early stages, the influence of nutrient additives in beetle boxes on inhabiting beetle communities is an area that would benefit from additional investigation. The ways in which the present study will further contribute to knowledge on this is explored in the ‘study aims’ section.

Longevity of beetle boxes

Beetle boxes used in previous studies have almost exclusively been constructed from wood to most closely mimic the qualities of a tree hollow (Elbourn, 1970; Jansson, *et al*., 2009; Hilszczański *et* al., 2014; Carlsson *et al*., 2016). However, the lack of resilience of untreated wood to changing weather conditions and constant internal moisture mean that these beetle boxes have a tendency to deteriorate over time (Hilszczański *et* al., 2014; Carlsson *et al*., 2016). Over a ten-year period, 10.4% of boxes investigated by Carlsson *et al*. (2016) became broken beyond usability, yet they found that wood-mould inside the beetle boxes became increasingly suitable habitat for rot-hole specialist invertebrates over this timescale. This improvement in wood mould quality over time is unsurprising, as real cavities in living, veteran trees take a long time to develop and can persist for hundreds of years (Ranius *et al*., 2009). Therefore, the durability of beetle box designs is critical for them to reach their optimum performance and function as a long-term conservation tool.

One of the first trials of the beetle box concept was carried out by Ted Green in 1988, who set out a metal bin and plastic bin liner filled with wood mould in Windsor Forest to provide analogous rot hole habitat (Whitehead, 2003). Although the work of Ted Green played an important role in initiating the ongoing research structure into beetle boxes, the results of these trials were never formally published. Similarly, in 2009, plastic bins filled with wood mould at Bredon Hill were investigated by Paul Whitehead for their beetle content, with these results also remaining unpublished (Alexander, 2016b). The resilience of alternative construction materials such as plastic means that their use in beetle box designs has potential to provide a more long-term habitat option for tree-hollow species, suggesting that further research into its use would be valuable. Due to the lack of published results, the functioning of plastic as a material for beetle boxes remains a gap in the research landscape. In addition, no previous research has conducted a direct comparison of the invertebrate diversity able to inhabit plastic boxes to that in wooden boxes. This lack of comparison data is addressed by the current research, as discussed in the 'study aims' section.

Beetle box design and location

The majority of previous studies into cavity-mimicking box structures have investigated boxes that are mounted on tree trunks, with the intention of mimicking the conditions found in tree cavities occurring above-ground (Elbourn, 1970; Jansson, Ranius, *et al*., 2009; Hilszczański *et* al., 2014; Carlsson *et al*., 2016; Weatherbee *et al*., 2022). As a result of this, there is little available data on the effectiveness of beetle boxes in mimicking cavities that occur at the base of the tree. These basal cavities differ from the aerial cavities in having an increased exposure to soil and the associated invertebrate fauna (Johnston & Crossley, 1996). There are also specific fungal species that infiltrate a tree through the roots, contributing to basal cavity formation which differ from those that enter through tree wounds to form aerial cavities (Boddy, 2001).

Basal tree cavities are particularly important from a conservation perspective as they are the specific habitat of the endangered violet click beetle (*Limoniscus violaceus*) (Whitehead, 2003; Gouix *et al*., 2015). This species has only been recorded from three locations in the UK and is protected under the Wildlife and

Countryside Act (1981). Due to its very restricted range, *L. violaceus* is under threat of extinction in the UK, especially as tree age gaps mean that basal hollow habitats are declining in areas where it is present (JNCC, 2019). Beetle boxes could present a unique opportunity to support *L. violaceus* through these periods of decline in their natural basal hollow habitat. Beetle boxes have previously been used as successful breeding sites for another highly specialised tree-hollow species, *Osmoderma barnabita*, demonstrating their potential to provide suitable resources for umbrella species of conservation concern (Hilszczański *et* al., 2014). There have also been observations of *L. violaceus* using wood-mould sources outside of natural tree hollows, with their larvae having been found inside a bin filled with decaying wood substrate (Whitehead, 2003). This provides evidence that beetle boxes have potential to provide suitable habitat to contribute towards the conservation of *L. violaceus*. The ways in which the present study aims to build on these findings are highlighted in the subsequent 'study aims' section.

Sampling time

Most previous studies into beetle boxes have left the boxes in the field for several years before beginning investigations into their saproxylic beetle communities (Jansson, *et al*., 2009; Carlsson *et al*., 2016). Only one study has investigated beetle box fauna after a shorter exposure time of six months (Elbourne, 1970). This means that there is a gap in knowledge on how the succession of beetle communities inhabiting wood mould in beetle boxes changes over time, especially between the periods of six months and four years (Elbourne, 1970; Jansson, *et al*., 2009). This knowledge gap will be addressed by the present research, as discussed in the 'study aims' section.

Study aims

Nitrogen content

The present study aimed to further investigate the role of increased nitrogen in wood mould and identify how the addition of nitrogen-rich components impacts the ability of beetle boxes to mimic tree hollow conditions. This was done by adding poultry manure to a subset of wooden habitat boxes and observing the effects of this on invertebrate communities inhabiting the wood mould within these. This concept has already been explored by Jansson, Ranius, *et al*. (2009) who did not find the addition of fertiliser to affect saproxylic beetle populations in beetle boxes. However, the present study will introduce novel experimental factors that will help to elucidate whether the lack of trends observed by Jansson, Ranius, *et al*. (2009) were a true reflection of the impacts of enhanced nitrogen on beetle communities, or whether they were a result of the specific methodology used. One of these novel factors was that the poultry manure used in the present study was in the form of pellets, which release nitrogen into the surrounding more slowly than the raw faeces used by Jansson, Ranius, *et al*. (2009) (Hara, 2001). In addition, the present study added greater volumes of manure to the wood mould than Jansson, Ranius, *et al*. (2009) to explore whether this induces a greater effect on invertebrate communities.

Longevity of beetle boxes

To address the problem of beetle box longevity, the present study aimed to investigate beetle boxes made from plastic as a more resilient alternative to wooden boxes. This will be the first time that the ability of plastic beetle boxes to mimic conditions in tree-hollows is compared to that of wooden boxes. To do this, data will be collected on the similarities and differences in communities of beetles and other invertebrates that occur in beetle boxes made of plastic and wood. The current study also aimed to identify differences in how plastic and wood construction materials influence the internal wood-mould conditions of beetle boxes. It is hoped that this might help to explain any differences in the invertebrate communities that are found.

Beetle box design and location

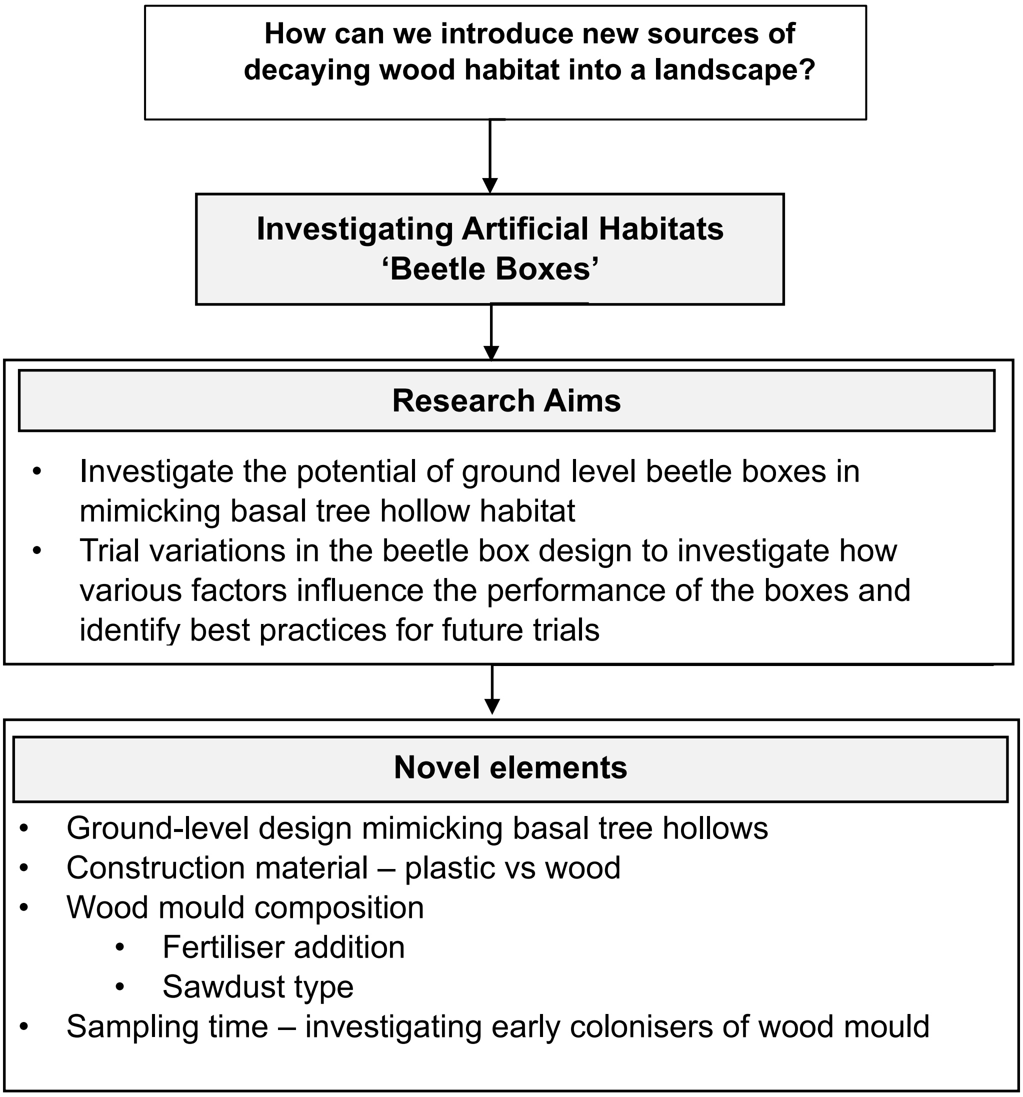
The current research aimed to investigate the novel concept of beetle boxes established at ground level to mimic basal tree hollows. Beetle boxes were specially designed for this purpose, incorporating novel elements intended to closely mimic the features of basal hollows. The extent to which the boxes could mimic this target habitat was quantified by investigating levels of similarity in the communities of beetles and other invertebrates inhabiting them and those found in real tree hollows. This study also sought to identify any signs of the basal hollow specialist, *L. violaceus*, inhabiting the boxes. Wood mould in beetle boxes is known to become increasingly inhabited by hollow specialist beetle species with longer maturation times (Carlsson *et al*., 2016). Therefore, the potential of finding *L. violaceus* in boxes is expected to be low at the planned time of sampling. Despite this, any observations made by the present study will contribute to knowledge on the timescales required for colonisation of wood mould by *L. violaceus*, which will inform future conservation strategies for this species involving beetle boxes. The infrastructure set up for this research could also facilitate longer term research into the inhabitation of beetle boxes by *L. violaceus* over the coming years.

Sampling time

The present study aimed to gather data on the early successional invertebrate colonisers of developing wood mould. This was achieved by gathering data on the beetle and other invertebrate inhabitants of beetle boxes after a single year in the field. The resultant data will work to bridge the gap in knowledge of beetle community changes that occur between six months and four years of beetle box deployment (Elbourne, 1970; Jansson, *et al*., 2009). It will also provide the basis for potential future study into change in saproxylic communities in wood mould over time, should inhabitants of the boxes be further sampled after additional time has elapsed.

Summary

The above research aims were developed to advance understanding of the potential of beetle boxes to contribute to saproxylic beetle conservation approaches. The conceptual framework below summarises the objectives, aims, and innovation in these approaches (Figure 3.4).



How can we introduce new sources of decaying wood habitat into a landscape?

Investigating Artificial Habitats 'Beetle Boxes'

Research Aims

- Investigate the potential of ground level beetle boxes in mimicking basal tree hollow habitat
- Trial variations in the beetle box design to investigate how various factors influence the performance of the boxes and identify best practices for future trials

Novel elements

- Ground-level design mimicking basal tree hollows
- Construction material – plastic vs wood
- Wood mould composition
    - Fertiliser addition
    - Sawdust type
- Sampling time – investigating early colonisers of wood mould

Figure 3.4. A conceptual framework depicting how the research in Chapter 3 fits into the research landscape. It details how the present investigation into ground level beetle boxes is informed by key conservation research motivations and describes the key aims and novel elements of this work.

3.2. Methods

Study sites

Beetle boxes were installed in areas of Windsor Forest (SU9374) and Bredon Hill (SO9439), with permission from Natural England, the Crown Estate, and reserve managers. Both sites are known to have active populations of *L. violaceus* (Henshall *et al*., 2015; Alexander, 2019a; A. Fallon, 2019, personal communication). At Windsor Forest, boxes were installed in the High Standing Hill area, which is dominated by beech (*Fagus sylvatica*) trees (Alexander, 2019a). Despite being a former open, pasture woodland fostering the growth of ancient beech trees, this area has become extensively shaded over time through tree recruitment aided by the removal of grazing pressure (Alexander, 2019a). As a result, High Standing Hill is now characterised by a dense tree canopy that is more typical for enclosed, unmanaged beech woodland (Alexander, 2019a). In contrast, the installation area at Bredon Hill was characterised as an open, grassy clearing surrounded by prominent ancient veteran Ash (*Fraxinus excelsior*) trees, grown in largely open conditions.

The ground at High Standing Hill, Windsor Forest was not notably sloped, whereas the area of Bredon Hill in which boxes were installed was a steep north-west-facing slope, meaning that it was necessary for the majority of boxes at Bredon Hill to be installed in strongly sloped ground. More information on both sites can be found in Section 1.6.

Experimental design

Beetle box design

Two beetle box constructions were trialled for this study: one made from wood, and one from plastic. The specifics of these are detailed below.

Wooden boxes

The wooden beetle box design used in this study was conceptualised with the help of Nicklas Jansson and Sarah Henshall. It was based on trunk-mounted beetle boxes used by Jansson, Ranius, *et al*. (2009) and incorporated several of the same features, including entrance holes in the side, drainage holes and channels in the top, and an insulated basin at the bottom. Novel adaptations were also made to the beetle boxes used in this study to allow them to better replicate the conditions found in basal hollows. These included the addition of an internal shelf and a hole in the base of the box, as well as the box entrance being positioned in the centre of the box rather than near the top. The details and functionality of these features are further discussed below.

The wooden beetle boxes were made from untreated oak wood to the dimensions, 100 cm tall x 35 cm wide (Figure 3.5). The base of the boxes consisted of a tarpaulin-lined basin covering half of the area, with the other half left open to the surrounding soil (Figure 3.5). This structure was designed to retain areas of moisture within the box whilst allowing the passage of soil invertebrates into the internal cavity. This entrance for invertebrates was intended to increase the decomposition-rate of the contents through resultant soil invertebrate activity within the boxes (Griffiths, 2021). Invertebrate groups such as earthworms are key ecosystem engineers for intermediate habitats between plant matter and soil (Desie *et al*., 2020).

The front of the boxes featured two openings – a large square hole in the centre of the box (150x150 mm) and a smaller, circular opening in the upper half of the box (25 mm diameter) (Figure 3.5). The purpose of these design features was to allow crawling and flying invertebrates to easily enter all areas of the box. A sloped shelf was installed above the large square entrance hole to maintain an open cavity in the box-contents material, whilst slowly allowing new material to slide down from the top compartment of the box into the bottom compartment as decomposition progresses (Figure 3.5). This design element was introduced to mimic the slow introduction of new woody substrate into a tree hollow as heartwood continuously decays and drops down. Each box had a lid constructed of the same oak wood, which helped to mimic the enclosed conditions of many basal rot holes. The lid design included four 8 mm diameter drilled holes with shallow channels bored between them to promote the flow of rainwater into the boxes (Figure 3.5). The drainage holes and channels were incorporated into the design to maintain the moist conditions preferred by *L. violaceus* (Cuff, Müller, *et al*., 2021).

Wooden beetle boxes were constructed using funding from the 'Back from the Brink' project in partnership with Buglife – the Invertebrate Conservation Trust.

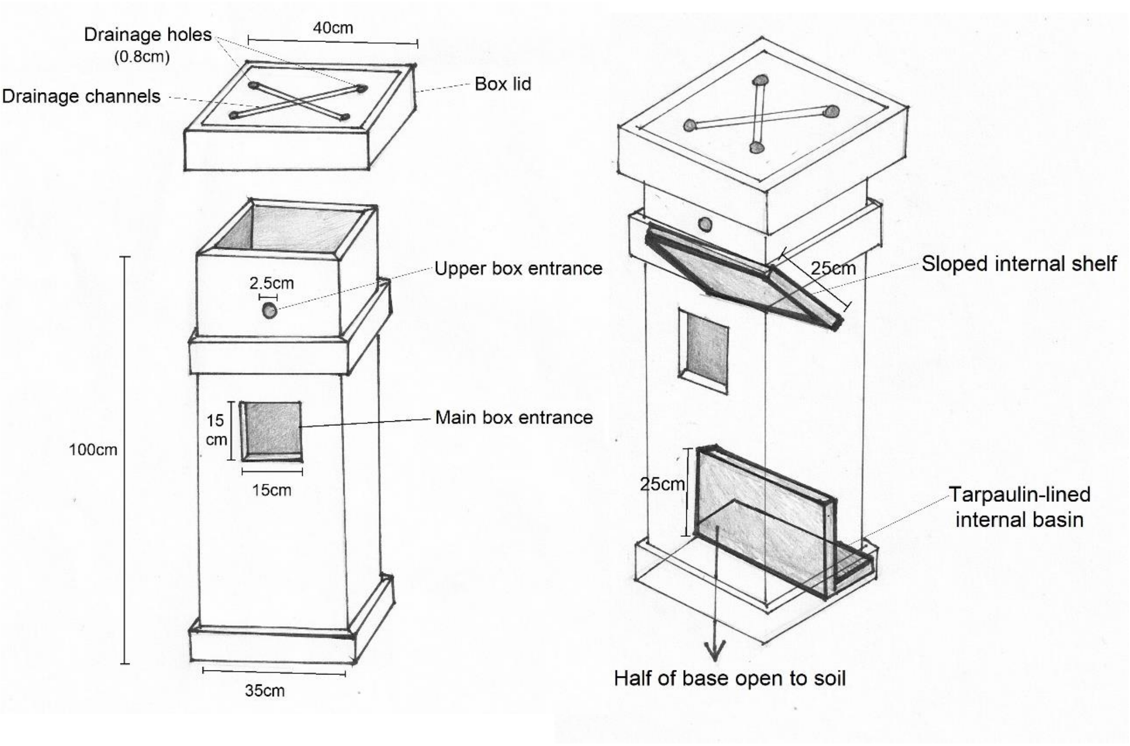


Figure 3.5. Diagrams of the wooden beetle boxes used in this study, with key features and dimensions labelled.

Plastic boxes

Plastic boxes were created for this study to trial a longer-lasting alternative to the more widely used wooden design. These were adapted from 90 litre wheelie bins (92.5 cm tall x 44.5 cm wide) made from polyethylene, which is soil-safe and recyclable (Figure 3.6). The plastic box design included the same key features used for the wooden boxes, but with minor adaptations that were made in response to constraints associated with working with plastic. Adaptations included a smaller sloped internal shelf, a lack of a side panel in the basal basin and a lack of channels bored between the drainage holes in the lid (Figure 3.6). The internal shelf was made smaller as this was an easier design to construct and made economical use of the plastic cut from the entrance hole. The side panel was not included in the base as it was difficult to access the inside of the boxes for the installation of internal components due to the fact that the external structure of the bins was already pre-formed. The drainage channels in the lid were not included as the plastic was too thin to allow these to be carved.

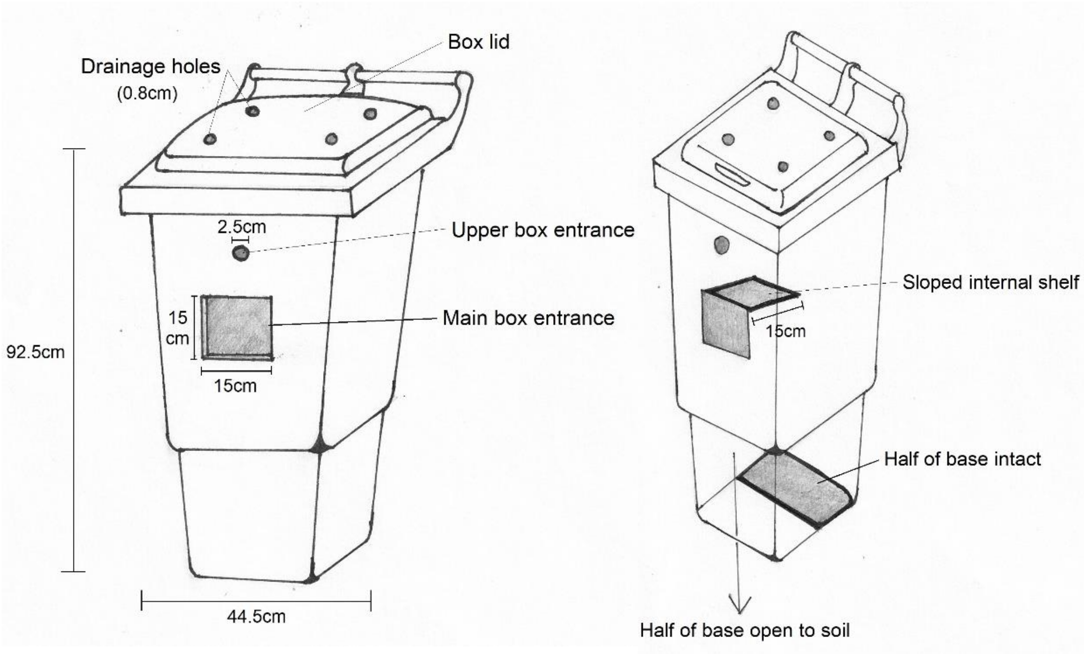


Figure 3.6. Diagrams of the plastic beetle boxes used in this study, with key features and dimensions labelled.

Box content treatments

A total of 32 beetle boxes were installed for this study, 20 boxes at Windsor Forest and 12 boxes at Bredon Hill. Fewer boxes were trialled at Bredon Hill as the sloped conditions on site made box installation considerably more challenging. As a result, time and workforce limitations dictated that a limited experimental design was the most achievable option at Bredon Hill (this is further discussed further below). Table 3.1 provides a summary of the design of the study. In total, 30 boxes were included in grouped experimental set ups. The groups included box treatments that were made from either oak wood or plastic and several treatments included an addition of nitrogenous fertiliser to their wood mould contents (Table 3.1).

Table 3.1. A summary of the beetle box treatments at Windsor Forest and Bredon Hill.

Location	Exterior box material	Type of sawdust in wood mould	Wood mould enriched with fertiliser?	Number of boxes	Experimental design	Installation completion date
Windsor Forest	Wood	Oak	Yes	6	Main grouped design	27/04/2019
	Wood	Oak	No	6		27/04/2019
	Plastic	Oak	Yes	6		27/04/2019
	Wood	Beech	Yes	2	Not included in main grouped design	12/08/2019
Bredon Hill	Wood	Oak	Yes	6	Main Grouped design	21/06/2019
	Wood	Oak	No	6		21/06/2019

All boxes were filled with a mixture of dried, untreated sawdust, leaf-litter, and soil. The leaf litter and soil were sourced onsite. The bottom compartment of each box first filled up to the lower edge of the central opening with a mixture containing 12 litres of leaves, 12 litres of sawdust, 24 litres of soil. Then the top compartment of each box above the internal shelf was then filled with a mixture containing 16 litres of leaves, 16 litres of sawdust, 8 litres of soil. The content composition of the upper and lower halves of each box differed from each other to reflect the gradated change in the composition of wood mould that naturally occurs in tree hollows (Gioux *et al.*, 2015).

Sawdust of *Quercus* sp. was used in all boxes at Bredon Hill and all except two wooden boxes at Windsor Forest, in which locally sourced *Fagus sylvatica* sawdust was used (Table 3.1). It would have been preferable to use sawdust from the tree species that represent the most dominant basal tree-hollow presence at each respective site in all boxes installed there (*Fraxinus excelsior* at Bredon Hill and *Fagus sylvatica* at Windsor Forest). However, sawdust of these species proved difficult to source in large quantities. It was decided that

Quercus sp. sawdust would constitute a suitable alternative to these local species, as many saproxylic invertebrate species that inhabit extensively decayed wood mould habitats are not specific to a particular tree species and can inhabit a range of broadleaved trees (Stokland *et al*., 2012). Nevertheless, the boxes containing beech sawdust were included at Windsor Forest to gather preliminary data on the effects of using the sawdust of the locally dominant basal hollow habitat tree species in comparison to other species.

An additional component of fertiliser (pelletised poultry faeces, sourced from Elixir Garden Supplies) was included in all beetle boxes except a control group of six wooden boxes with wood mould composed of oak sawdust (Table 1). The addition fertiliser was intended to increase the nitrogen content of the wood mould in the boxes, as wood mould in natural tree hollows contains particularly high nitrogen levels (Kelner–Pillault, 1974; Ulyshen, 2015). To investigate the effects of the fertiliser addition on the beetle communities colonising the boxes, fertiliser was not added to the contents of half of the wooden boxes containing oak sawdust so that they could act as a control group.

Cuff, Müller, *et al*. (2021) found that a high, stable water content of wood mould was positively associated with the suitability for *L. violaceus*. For this reason, ten litres of water were added to each of the beetle boxes in the present study after they had been filled with the above dry substrates. This additional moisture was also intended to create moist conditions that promote the growth of bacteria and fungi, aiding the wood mould decomposition process (Rousk & Bååth, 2011).

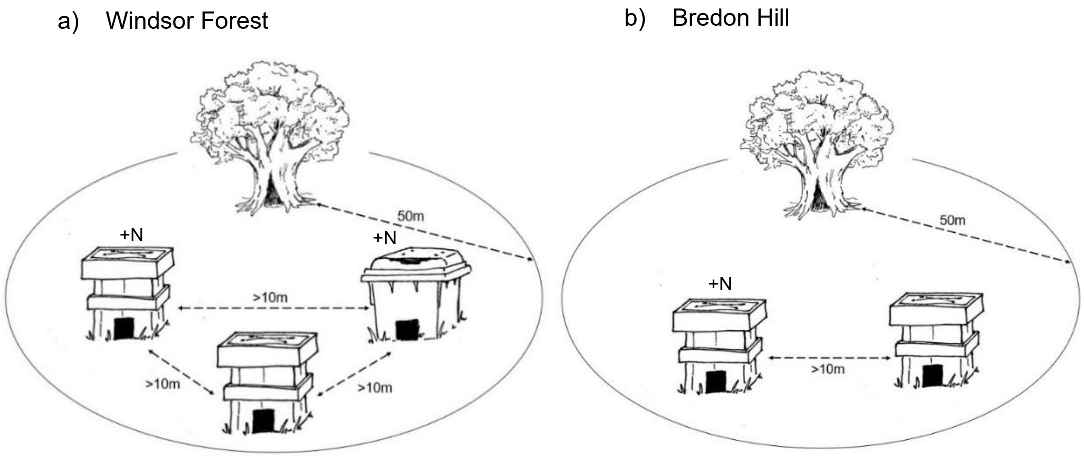
At Windsor Forest, the beetle boxes of the grouped experimental design were arranged in clusters of three, comprising two wooden boxes, one with and one without added fertiliser, and one plastic box with added fertiliser. Plastic boxes were not included in the trial at Bredon Hill, as sloped ground conditions made installation more difficult. Therefore, beetle boxes at Bredon Hill were arranged in groups of two, comprising wooden boxes with and without fertiliser. The mixed groups of boxes at both sites were arranged with at least 10 m space between each box (Figure 3.8). A minimum spacing of 10 m was also used by previous beetle box studies to minimise the extent to which the boxes influenced each other (Jansson, Ranius, *et al*., 2009; Carlsson *et al*., 2016).

Boxes were half buried into the forest floor, so that the lower edge of their main entrances were flush with the ground (Figure 3.7). All boxes were positioned within 5 0m of a habitat tree featuring a basal rot-hole (Figure 3.8). Care was taken to bury boxes outside of root protection zones of surrounding trees to minimise negative impacts on tree health. The habitat trees were selected based on the following criteria: their basal rot holes had been previously found to contain populations of *L. violaceus*; or they were assessed to provide suitable habitat for *L. violaceus* according to known criteria (large DBH and basal hollows with extensively decayed, moist wood mould) (Gioux *et al*., 2015; Henshall *et al*., 2015; Cuff, Müller, *et al*., 2021). Various studies have found saproxylic beetle dispersal abilities to exceed 100 m, although spacing beetle boxes more than 100 m from habitat trees has been linked to a decreased likelihood of colonisation by some saproxylic species (Shiegg, 2000; Ranius & Hedin, 2001; Jansson, Ranius, *et al*., 2009). Therefore, for this study, boxes were installed at a maximum distance of 50 m from habitat trees as this was deemed to be an optimal distance to allow beetle colonisation of beetle boxes from habitat trees to occur (Figure 3.8). The beetle boxes were installed with their main entrances facing away from any uphill slope to prevent excessive flooding of box contents during rainfall. This resulted in their entrances being oriented in varying directions.

The trees that the boxes were positioned around at Bredon Hill were all ash (*Fraxinus excelsior*), whilst at Windsor Forest they were all beech (*Fagus sylvatica*). As stated earlier, it is expected that saproxylic invertebrates will be able to colonise the *Quercus* sp.- based wood mould in the beetle boxes from these trees as the fauna of such extensively decayed habitats are often generalists regarding tree species (Stokland *et al*., 2012).

Beetle box installation was completed in the spring and summer of 2019. The boxes were then left for a year to mature, with occasional checks for damage or other potential problems. Sampling took place in 2020, after one year of maturation. No previous studies of tree hollow mimicking beetle boxes have sampled the diversity of colonising beetles after one year (Elbourn, 1970; Jansson, Ranius, *et al*., 2009; Carlsson *et al*., 2016). Therefore, this approach will provide novel insights into the preliminary phases of saproxylic colonisation of a newly formed habitat resource.

Figure 3.7. Photographs of two beetle boxes, one of wooden construction and one of plastic, that were installed at Windsor Forest.


a) Windsor Forest

b) Bredon Hill

Figure 3.8. Diagrams of the grouped experimental beetle box set ups at Windsor Forest (left) and Bredon Hill (right). The groups of beetle boxes at Windsor Forest contained three box treatments, whilst at Bredon Hill the groups consisted of two box treatments. +N indicates box treatments that had nitrogen-rich manure added to their contents. All box treatments were at least 10 m distant from other beetle boxes and were stationed within 50 m of a habitat tree.

Invertebrate sampling from beetle boxes

On-site invertebrate sampling procedure

Invertebrate sampling from the beetle boxes took place in 2020, with sampling sessions carried out during mid and late summer. Bredon Hill was visited for invertebrate sampling on 29/06/2020 and 10/08/2020, while Windsor Forest was visited for sampling on 06/07/2020 and 17/08/2020. Initially an additional sampling session was planned for earlier in the spring; however, due to Covid-19 restrictions preventing access to sites at this time, this was not possible. Flightless saproxylic and litter dwelling invertebrate faunas are stable throughout the year, with most sampled species occurring in all seasons (Cateau *et al*., 2016). Therefore, the chosen sampling period was deemed appropriate to encapsulate a meaningful representation of beetles inhabiting the wood mould in the beetle boxes.

The sampling procedure involved removing one litre in volume of wood mould from both the top and the bottom sections of the beetle boxes using a soil corer (a total of two litres volume removed from each box per sampling session). The removed soil was thoroughly sieved, and preliminary sorting was undertaken on site in white trays. The sorting was carried out for 10 minutes per sample, which was deemed to be an appropriate duration to extract all visible invertebrate life. This process was done to extract macroinvertebrates and to check for any specimens of sensitive species such as *L. violaceus*. This was necessary as *L. violaceus* is protected by the Wildlife and Countryside Act (1981) in the UK, meaning that the killing or taking of *L. violaceus* specimens is prohibited. No adult *L. violaceus* were found in the samples and any potential *L. violaceus* larvae were photographed and returned to the location on site in which they were found. Other macroinvertebrates were collected using forceps and a pooter and were placed into tubes containing 70% ethanol for later identification. This was chosen as it best preserves the morphology of a wide range of invertebrate groups and is particularly suitable for worms, myriapods and isopods (Krogmann & Holstein, 2010).

Ancient trees with basal hollows were sampled in addition to the beetle boxes to provide a source of comparison of the invertebrate communities in the target habitat. This was done using the same methodology as for the boxes, but with both of the one-litre soil samples extracted from the same hollow. The trees selected for sampling were the same ones that were positioned within 50 m of box groups. They all had features matching the habitat-requirements of *L. violaceus*, including a large diameter and a basal rot-hole containing moist, extensively decayed wood mould (Gioux *et al*., 2015; Cuff, Müller, *et al*., 2021). Samples were taken from three trees at Bredon Hill and six trees at Windsor Forest. Fewer trees were sampled at Bredon Hill as some trees had basal hollows with too narrow an entrance to allow wood-mould samples to be taken. Ancient trees were only sampled during the first invertebrate sampling session (29/06/2020 at Bredon Hill and 06/07/2020 at Windsor Forest) to prevent excessive disturbance of natural basal tree hollow habitats on site.

Following preliminary invertebrate extraction, the remaining soil from the two-litre samples was placed into plastic pots using a plastic funnel. The pots were labelled both internally and externally with the site name, box/tree number and date of sample collection. Internal labels consisted of printer paper marked with pencil and external labelling was done with permanent markers on the base and lid of each collection pot.

Macro-invertebrate extraction using Winkler traps

After being sealed into plastic containers, the wood mould samples were transported off site. They were then left in a cool, dark location overnight to ensure that the invertebrates within the wood mould remained alive until the samples could be processed. The samples were subsequently transferred into mesh bags with 2 mm holes which were then placed into Winkler extraction traps. Winkler extraction traps were chosen as they have been found them to be the most effective method of extracting macro-invertebrates from leaf litter and soil, in comparison to pitfall trapping and Tullgren funnel trapping (Fisher, 1999; Kalif & Moutinho, 2000; Krell, Chung, *et al*., 2005). The traps were therefore used to extract macro-invertebrates that were too small to be effectively detected and extracted manually. Winkler traps were also the most practical option for use during the Covid-19 pandemic, when access to laboratories with large-scale Tullgren funnel trap setups was not possible.

Both of the two samples taken per box/ basal tree hollow during each sampling session were placed into the same Winkler trap. It would have been interesting to extract invertebrates from the wood mould samples taken from the top and bottom compartments of the beetle boxes separately to investigate differences in the invertebrate communities inhabiting the different areas of the boxes. However, the sheltered area available for hanging the Winkler traps during to the Covid-19 pandemic had limited space. By extracting invertebrates from both samples in the same trap, the space available was used most efficiently, allowing all samples to undergo extraction at the same time. Each trap had a collection pot connected to its base containing a 50% propylene glycol, 50% water mixture with an added drop of unscented washing-up liquid. This fluid is a widely recommended entomological killing agent which is low-cost, safe to use and preserves the condition of specimens well (Weeks & McIntyre, 1997; McCravy & Willand, 2007; Weigand *et al.,* 2021).

The Winkler traps were left for six days in a wooden out-building for shelter from the wind and rain. The door of the building was left open on fair days to promote airflow through the traps and encourage optimal drying of the samples within the traps. After this, the collection pots were removed from the traps and the soil samples were then transferred into white trays for further manual extraction of sampled invertebrates. As a final measure to maximise collection of specimens, a standardised three-minute-timed search of soil samples was undertaken, and any remaining invertebrates were collected using a pooter. After this, the soil samples were placed into air-tight buckets and transported back to the sites from which they were collected.

Winkler traps function through the slow drying-out of soil and leaf-litter substrates over time causing invertebrates to burrow downwards and drop into the attached collection pot (Krell, Chung, *et al*., 2005). Because of this, Winkler traps extract the highest proportion of the invertebrates when they are left for long periods of time (Krell, Chung, *et al*., 2005). Due to time and space limitations of the present study caused by the need to sample the boxes at both sites at a similar time of year, it was only possible to leave the samples in the Winkler traps for a maximum of six days. This was nevertheless deemed sufficient to extract a meaningful proportion of the coleoptera fauna in the samples, as Krell, Chung *et al*. (2005) found that approximately 70% of the total beetle specimens extracted from Winkler traps had been collected after 6 days. The final hand-sort of material carried out after Winkler trapping was to address the timing constraint of this element of the study and further ensure maximum invertebrate extraction from samples.

Specimen identification

All invertebrate specimens were extracted from the samples and identified to as low a classification rank as possible. Identification of specimens was aided by a range of taxonomic keys and photograph resources (Hansen & Solodovnikov, n.d.; Käfer Europas, n.d; Blower, 1985; Hopkins, 1991; Barber, 2008; Duff, 2012; Duff, 2016; Legg & Farr-Cox, 2016; Duff, 2020).

Moisture measurement of wood mould

Moisture content of the boxes was measured using a moisture meter (SM150 Soil Moisture Kit). This features a needle probe which is inserted into soil substrates to acquire a reading. All readings were taken on the setting “Peat mix”, as this was best able to capture the range of moisture levels found in the wood-mould. Readings were in the unit of percentage volume of water to soil.

In the late summer of 2020 (10/08/2020 at Bredon Hill and 17/08/2020 at Windsor Forest), moisture measurements were taken in the top layer of wood mould (into the layer of mould on top of the internal shelf, accessed through the box lid), and in the bottom compartments (in the ‘hollow’ area of the box immediately under the internal shelf, accessible through the central box opening) of each box. To gain a representative measure and avoid bias caused by anomalous pockets of moisture or dry areas, three measurements were taken per layer. The locations at which the moisture measurements were taken in the wood mould layers are illustrated in Figure 3.9.

During a second visit in late spring of 2021 (02/06/2021 at Bredon Hill and 24/05/2021 at Windsor Forest), moisture levels were taken from only the bottom level of each box, following the same methodology as in the first moisture measuring session. Only the bottom wood mould layer was sampled because, by this time, the wood mould in the boxes had extensively decomposed, causing the majority of the substrate in the top box compartment to slide down into the bottom compartment. This left little wood-mould in the top box compartments to take measurements from.

Moisture readings were also taken from real tree hollows to provide a point of comparison to the box moisture conditions. These readings were taken on 02/06/21 at Bredon Hill and on 17/08/20 at Windsor Forest. The same methodology was used as for the boxes, with three measurements taken with the moisture probe inserted into the back left hand area, the centre and the front right-hand area of tree hollow wood mould.

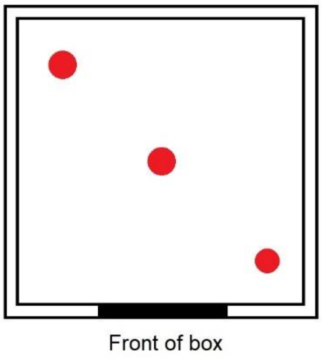


Figure 3.9. A diagram illustrating sampling protocol used to measure moisture levels in the wood mould of beetle boxes. Red dots illustrate the positions at which the moisture probe was inserted into wood mould to obtain moisture readings.

Canopy estimation using image analysis

The level of canopy cover over each beetle box was quantified to allow any influences of levels of openness and exposure to weather conditions experienced by each box on the inhabiting invertebrate communities to be quantified.

On 10/08/2020 (Bredon Hill) and 17/08/2020 (Windsor Forest) each box was visited and an iPhone was placed on top of each box lid, with the front-facing camera positioned over the lid centre. With the phone camera pointing directly upwards, a photograph was taken of the tree canopy above each box.

The resulting images were imported into Adobe Photoshop CC 2019 and converted to black and white using a threshold value of 80. This value was chosen as it was low enough to remove any interference in the black and white image from inconsistencies in sky colour caused by clouds and patches of blue sky. This level did cause some areas of over-exposed foliage to be cut from the image, however the resultant levels of visible canopy still present were deemed to be adequately representative to the initial images to provide a suitable comparative measure. A percentage of canopy cover over each box was obtained from these images using the total pixel count for each image in comparison with the number of black pixels that represented the visible canopy areas.

Data analysis

All statistical analyses were done in R-Studio.

The influence of box treatment on inhabiting beetle communities

Separate analyses were carried out for the boxes at Bredon Hill and Windsor Forest. The sites were analysed separately to account for potential influences of the different grouped experimental setups used at the sites (boxes in paired groups at Bredon Hill and boxes in groups of three at Windsor Forest). In addition, separate analysis allowed an investigation into how the different environmental conditions at Windsor Forest and Bredon Hill may have influenced how beetle communities interacted with the beetle boxes at these sites. Species data from real tree hollows were not included in this analysis as these were sampled to a lesser extent than the beetle boxes (tree hollows were sampled once, whilst beetle boxes were sampled twice). Instead, these data were used to make qualitative comparisons of species presence in tree hollows and beetle boxes.

For the purposes of these analyses, beetle specimens found within the boxes were categorised as either saproxylic, woodland associate, or non-deadwood associated. These terms were defined as:

Saproxylic – Species that require deadwood to complete their lifecycle and cannot survive and reproduce without it.

Woodland Associate – Species with known links to deadwood that are frequently found in a woodland setting, but which have less strict ties to saproxylic habitats and are also found in other habitats such as non-wood based decaying material.

Non-deadwood associated – Species with no known link to deadwood, possessing either generalist life-strategies or those specialised on a non-deadwood habitat resource.

Beetles were assigned to the above categories using information from various sources (Nature Spot, n.d.; UK Beetles, n.d.-c; UK Beetles, n.d.-d; UK Beetles, n.d.-e; UK Beetles, n.d.-f; UK Beetles, n.d.-g; UK Beetles, n.d.-h; UK Beetles, n.d.-i; Palm, 1970; Arnet & Thomas, 2000; Alexander, 2002; Whitehead, 2002; Lott, 2003; Krell, Johnson*, et al*., 2005; Käfer Europas, 2009; Lott & Anderson, 2011; Duff, 2012; Lackner, 2015; Duff, 2016; Hackston, 2017; Duff, 2020; Lane *et al*., 2020; Eakring Birds, 2022; Webb *et al*., 2022) .

Beetle communities from each of these trait categories were analysed individually. In addition, combined measures of saproxylic and woodland associate beetles were analysed to investigate the effects of box treatment on all species with some behavioural connection to deadwood. The species richness and the average abundance of specimens per species from each of these categories were used in analyses.

Versions of statistical tests that consider variables as paired/ repeated measures were chosen to analyse the differences in richness and average abundance of beetles in the different box treatments. This was done as the grouped experimental set-up of the boxes meant that all experimental variants in a group experienced similar environmental conditions. Also, as each group of beetle boxes was centred around a particular tree, this meant that there was an increased likelihood of similarity in colonising beetle faunas between boxes within a group, rather than between boxes in separate groups.

Species data from the boxes in the grouped experimental designs were first assessed for normality using Shapiro-Wilk tests and visual inspection of histograms. Boxplots were then used to identify the presence of outliers. All species data from boxes at Windsor Forest violated the assumptions of parametric tests, so non-parametric tests were used for all Windsor Forest analyses. For Bredon Hill, where data was deemed to be normal and without outliers, it was analysed with a parametric test (two-sample paired T-test). When data was not normally distributed, it was square root transformed in an attempt to achieve a normal distribution. Where this was possible, the transformed data was used in a two-sample paired T-test. Where normality could not be achieved, nonparametric tests were used to analyse the data. For groups of two boxes at Bredon Hill, non-parametric paired Wilcoxon U tests were used to compare beetle communities in the box treatments. As the boxes at Windsor Forest were in groups of three, the beetle communities within these were compared using non-parametric Friedman tests followed up with pairwise Wilcoxon signed rank tests to further identify the specific pairs of boxes between which any significant differences occurred.

Analysis of moisture conditions within beetle boxes

Moisture conditions within different box treatments

The moisture levels in the bottom compartments were tested for differences between the different grouped beetle box treatments using a combined average of all measurements taken across both sampling sessions. These moisture average data were tested for normal distributions and outliers using histograms, Shapiro-Wilk tests and boxplots. The average moisture data from the grouped box treatments at Windsor Forest did not meet the requirements for a parametric test. Because of this, moisture levels were tested for differences between box treatments using a Friedman test. The differences between individual box treatments at Windsor Forest were then further investigated using paired Wilcoxon signed-rank tests.

Average moisture data for the two box treatments at Bredon Hill were square root transformed to achieve normal distributions. This data was then used in a paired t-test to identify differences in average moisture levels between the wooden boxes with and without fertiliser added to the contents.

Moisture conditions within different box treatments compared to tree hollows

The average moisture levels in real tree hollows were compared with those the bottom compartments of the different grouped beetle box treatments at Windsor Forest using measurements taken on 17/08/2022. This analysis was not carried out for Bredon Hill, as the number of trees that could be sampled there were not equivalent to the number of boxes of each treatment on site.

These average moisture data from the tree hollows and beetle boxes at Windsor Forest were tested for normal distributions and outliers using histograms, Shapiro-Wilk tests and boxplots. The average moisture data did not meet the requirements for a parametric test. Because of this, moisture levels were tested for differences between tree hollows and box treatments using a Friedman test. The average moisture differences between tree hollows and individual box treatments at Windsor Forest were then further investigated using paired Wilcoxon signed-rank tests.

Moisture changes in the boxes over time

The average moisture levels in the bottom compartments of the boxes were analysed for significant differences between measurements taken at two different times of year (late summer and late spring) for each box type in the grouped experiments at both sites. The average moisture levels measured at both dates were checked for normal distributions using histograms and Shapiro-Wilk tests. The data was also checked for outliers using boxplots. Where data lacked outliers and fit a normal distribution, the differences between moisture levels recorded during the different sampling sessions was tested using paired T-tests. Where data was deemed not-normal and could not be fitted to a normal distribution through transformation, Wilcoxon signed-rank tests were used. These tests were chosen as they are both designed for use in situations where measurements are repeatedly taken from the same experimental units.

Moisture conditions in different compartments of the beetle boxes

The average moisture conditions recorded in the top compartments (above the internal shelf) and bottom compartments (below the internal shelf) of each box treatment in the grouped experiment were investigated for significant differences. This was done using data collected on 17/08/2020 for Windsor Forest and 10/08/2020 for Bredon Hill. The moisture data for the top and bottom compartments were tested for normality and outliers using histograms, Shapiro-Wilk tests and boxplots. Where the data was normally distributed, paired T-tests were used. Where data did not fit a normal distribution, it was either log- or square root- transformed to fit a normal distribution and then tested using paired T-tests. When a normal distribution could not be achieved, data was tested using non-parametric Wilcoxon signed-rank tests.

Checking for differences in canopy cover over the different box treatments

The levels of canopy cover over different grouped box types were tested for any significant differences that may have influenced the results. This was done by first checking the data for normality and outliers using histograms, Shapiro-Wilk tests and boxplots. As all canopy cover data fulfilled the requirements for parametric tests, the canopy covers for the three box types at Windsor Forest were tested for differences using an ANOVA test, whilst a T-test was used for the two treatments at Bredon Hill.

3.3. Results

Overall, 52 species of beetles were recorded within the beetle boxes at Winsor Forest and Bredon Hill. Of these, 15 were saproxylic, 13 were woodland-associated and 24 had no associations to deadwood (Tables 3.3, 3.4 & 3.5). Of the saproxylic species, 4 (26.7%), had a conservation status (table 3). None of the woodland associated species or non-deadwood associated species were of conservation concern.

The saproxylic beetle species recorded from beetle boxes included two with known strong associations to ancient tree hollows (*Ptenidium turgidum*, *Stenichnus godarti* (Figure 3.10)) and three species with more generalist links to tree hollow habitats (*Oligota apicata*, *Cryptophagus distinguendus, Acrotrichis montandonii*) (Alexander, 2002; Käfer Europas, 2009; Duff, 2020). Two of the species found (*Plegaderus dissectus and Abraeus perpusillus*) are associated with ancient woodland pasture (Alexander, 2002) (Tables 3.3 & 3.4).

Figure 3.10. An image of the *Stenichnus godarti* specimen collected from a beetle box wood mould sample.

At Windsor Forest, 32 species of beetle were found inside beetle boxes, 13 of which were saproxylic, 9 were woodland-associated and 10 had no association to deadwood (Tables 3.3, 3.4 & 3.5). At Windsor Forest, 6 species of beetle were also recorded from real hollows in ancient trees. Of the species found in trees, all but one were also found inside beetle boxes, with the only species not found in both being the non-deadwood-associated, *Rugilus rufipes*.

At Bredon Hill, 27 beetle species were recorded from the beetle boxes, including 6 saproxylic species, 6 woodland-associated species and 15 species that had no association to deadwood (Tables 3.3, 3.4 & 3.5). No beetle species were recorded from wood mould samples taken from real ancient tree hollows at Bredon Hill.

Table 3.2. A summary of the most recorded beetle species in each box treatment at Bredon Hill and Windsor Forest respectively.

Box treatment	1st most common beetle species	2nd most common beetle species	3rd most common beetle species
Bredon Hill			
Wooden boxes with oak sawdust and fertiliser (n=6)	*Orthoperus aequalis* (n=67)	*Ptilium horioni* (n=21)	*Ptinella aptera* (n=12)
Wooden boxes with oak sawdust, without fertiliser (n=6)	*Ptinella aptera* (n=3)	*Micropeplus staphylinoides* (n=2) *Orthoperus aequalis* (n=2)	All other species (n=1)
Windsor Forest			
Plastic boxes with oak sawdust and fertiliser (n=6)	*Cryptophagus distinguendus* (n=59)	*Acrotrichis insularis* (n=39)	*Dienerella clathrata* (n=27)
Wooden boxes with oak sawdust and fertiliser (n=6)	*Clambus punctulum* (n=32)	*Ptinella aptera* (n=21)	*Achrotrichis insularis* (n=6)
Wooden boxes with oak sawdust, without fertiliser (n=6	*Geostibia circellaris* (n=3)	*Cephennium gallicum* (n=2) *Dinerella clathrata* (n=2) *Tasgius moritisans* (n=2)	All other species (n=1)
Wooden boxes with beech sawdust and fertiliser (n=2):	*Ptinella simsoni* (n=44)	*Clambus punctulum* (n=12)	*Othius subuliformis* (n=6)

Table 3.3. Saproxylic beetle species found in samples of wood mould collected from beetle boxes and real tree hollows.

Species	**Status**	**Guild**	**Presence at sites** (W – Windsor Forest, BH – Bredon Hill)	**Total number of specimens found (average per sample)**				
				Wooden box, oak sawdust, without fertiliser (n=12, sampled twice)	**Wooden box, oak sawdust, with fertiliser** (n=12, sampled twice)	**Wooden box, beech sawdust, with fertiliser** (n=2, sampled twice)	**Plastic box, oak sawdust, with fertiliser** (n=6, sampled twice)	**Real tree hollow** (n=9, sampled once)
Histeridae								
Abraeus perpusillus		Predator	W	0 (0)	2 (0.08)	0 (0)	1 (0.08)	0 (0)
Plegaderus dissectus		Predator	BH	1 (0.04)	0 (0)	0 (0)	0 (0)	0 (0)
Ptiliidae								
Ptenidium turgidum	RDB K	Fungivore	W	0 (0)	0 (0)	0 (0)	2 (0.17)	1 (0.11)
Pteryx suturalis		Fungivore	W	0 (0)	1 (0.04)	0 (0)	0 (0)	0 (0)
Ptinella aptera		Fungivore	W + BH	3 (0.13)	33 (1.38)	3 (0)	0 (0)	0 (0)
Ptinella errabunda		Fungivore	W + BH	0 (0)	5 (0.21)	0 (0)	4 (0.33)	2 (0.22)
Staphylinidae								
Atrecus affinis		Predator	W	0 (0)	3 (0.13)	0 (0)	0 (0)	1 (0.11)
Euplectus karstenii		Predator	BH	1 (0.04)	3 (0.13)	0 (0)	0 (0)	0 (0)
Oligota apicata	Notable	Predator	W	0 (0)	0 (0)	0 (0)	2 (0.17)	0 (0)
Stenichnus godarti	RDB 3	Predator	W	1 (0.04)	0 (0)	0 (0)	0 (0)	0 (0)
Elateridae								
Panspaeus guttatus		Unknown	W	1 (0.04)	0 (0)	0 (0)	1 (0.08)	0 (0)
Ptinidae								
Hemicoelus fulvicornis		Xylophagous	W	1 (0.04)	0 (0)	0 (0)	0 (0)	0 (0)
Corylophidae								
Orthoperus aequalis	RDB K	Fungivore	W + BH	2 (0.08)	68 (2.83)	1 (0.25)	18 (1.5)	0 (0)
Curculionidae								

Acalles misellus		Xylophagous	W	1 (0.04)	0 (0)	0 (0)	0 (0)	0 (0)
Euophryum confine		Xylophagous	W + BH	1 (0.04)	4 (0)	1 (0.25)	2 (0.17)	0 (0)

Table 3.4. Woodland-associated beetle species found in samples of wood mould collected from beetle boxes and real tree hollows.

Species	**Stat-us**	**Guild**	**Presence at sites** (W – Windsor Forest, BH – Bredon Hill)	**Total number of specimens found (average per sample)**				
				Wooden box, oak sawdust, without fertiliser (n=12, sampled twice)	**Wooden box, oak sawdust, with fertiliser** (n=12, sampled twice)	**Wooden box, beech sawdust, with fertiliser** (n=2, sampled twice)	**Plastic box, oak sawdust, with fertiliser** (n=6, sampled twice)	**Real tree hollow** (n=9, sampled once)
Ptiliidae								
Acrotrichis insularis		Saprophagous	W	0 (0)	6 (0.25)	1 (0.25)	39 (3.25)	0 (0)
Acrotrichis montandonii		Saprophagous	W	0 (0)	0 (0)	0 (0)	1 (0.08)	0 (0)
Acrotrichis rugulosa		Saprophagous	BH	0 (0)	3 (0.13)	0 (0)	0 (0)	0 (0)
Ptilium horioni		Saprophagous	BH	0 (0)	21 (0.88)	0 (0)	0 (0)	0 (0)
Staphylinidae								
Atheta vaga			BH	0 (0)	1 (0.04)	0 (0)	0 (0)	0 (0)
Cephennium gallicum		Predator	W	2 (0.08)	0 (0)	0 (0)	0 (0)	2 (0.22)
Geostiba circellaris		Unknown	W	3 (0.13)	0 (0)	0 (0)	0 (0)	0 (0)
Mycetoporus rufescens		Saprophagous	W	0 (0)	1 (0.04)	0 (0)	0 (0)	0 (0)
Quedius cruentus		Predator	BH	0 (0)	1 (0.04)	0 (0)	0 (0)	0 (0)
Clambidae								
Clambus punctulum		Saprophagous	W + BH	0 (0)	41 (1.71)	12 (3)	25 (2.08)	0 (0)

Cryptophagidae								
Cryptophagus distinguendus		Fungivore	W + BH	0 (0)	11 (0.46)	0 (0)	59 (4.92)	0 (0)
Latridiidae								
Dienerella clathrata		Saprophagous	W	2 (0.08)	1 (0.04)	0 (0)	18 (1.5)	0 (0)
Dienerella vincenti		Saprophagous	W	0 (0)	0 (0)	0 (0)	8 (0.67)	0 (0)

Table 3.5. Non-deadwood-associated beetle species found in samples of wood mould collected from beetle boxes and real tree hollows.

Species	**Status**	**Guild**	**Presence at sites** (W – Windsor Forest, BH – Bredon Hill)	**Total number of specimens found (average per sample)**				
				Wooden box, oak sawdust, without fertiliser (n=12, sampled twice)	**Wooden box, oak sawdust, with fertiliser** (n=12, sampled twice)	**Wooden box, beech sawdust, with fertiliser** (n=2, sampled twice)	**Plastic box, oak sawdust, with fertiliser** (n=6, sampled twice)	**Real tree hollow** (n=9, sampled once)
Carabidae								
Clivina fossor		Predator	BH	1 (0.04)	0 (0)	0 (0)	0 (0)	0 (0)
Paradromius linearis		Predator	BH	1 (0.04)	0 (0)	0 (0)	0 (0)	0 (0)
Ptiliidae								
Acrotrichis thoracica		Saprophagous	BH	0 (0)	1 (0.04)	0 (0)	0 (0)	0 (0)
Ptenidium laevigatum		Saprophagous	BH	0 (0)	1 (0.04)	0 (0)	0 (0)	0 (0)
Ptenidium pusillum		Saprophagous	BH	0 (0)	2 (0.08)	0 (0)	0 (0)	0 (0)
Ptinella simsoni		Fungivore	W	0 (0)	0 (0)	44 (11)	0 (0)	0 (0)
Staphylinidae								
Aleochara sp.		Predator	W + BH	0 (0)	1 (0.04)	0 (0)	0 (0)	1 (0.11)

Heterothops praevius		Predator	BH	0 (0)	1 (0.04)	0 (0)	0 (0)	0 (0)
Micropeplus staphylinoides		Saprophagous	BH	2 (0.08)	0 (0)	0 (0)	0 (0)	0 (0)
Mycetoporus lepidus		Predator	W	1 (0.04)	0 (0)	0 (0)	0 (0)	0 (0)
Ocypus olens		Predator	W	1 (0.04)	0 (0)	0 (0)	0 (0)	0 (0)
Oligota sp.		Predator	BH	0 (0)	2 (0.08)	0 (0)	0 (0)	0 (0)
Othius punctulatus		Predator	W	1 (0.04)	0 (0)	0 (0)	0 (0)	0 (0)
Othius subuliformis		Predator	W + BH	0 (0)	1 (0.04)	6 (1.5)	0 (0)	0 (0)
Rugilus rufipes		Predator	W	0 (0)	0 (0)	0 (0)	0 (0)	1 (0.11)
Tachyporus dispar		Predator	BH	1 (0.04)	0 (0)	0 (0)	0 (0)	0 (0)
Tasgius ater		Predator	W	0 (0)	1 (0.04)	0 (0)	0 (0)	0 (0)
Tasgius morsitans		Predator	W	2 (0.08)	0 (0)	0 (0)	0 (0)	0 (0)
Xantholinus longiventris		Predator	BH	0 (0)	1 (0.04)	0 (0)	0 (0)	0 (0)
Coccinellidae								
Propylea quatuordecimpunctata		Predator	W	0 (0)	1 (0.04)	0 (0)	0 (0)	0 (0)
Corylophidae								
Sericoderus brevicornis		Fungivore	W	0 (0)	1 (0.04)	0 (0)	0 (0)	0 (0)
Latridiidae								
Adistemia watsoni		Saprophagous	BH	0 (0)	1 (0.04)	0 (0)	0 (0)	0 (0)
Latridius porcatus		Saprophagous	BH	0 (0)	11 (0.46)	0 (0)	0 (0)	0 (0)
Chrysomelidae								
Aphthona nonstriata		Herbivore	BH	0 (0)	1 (0.04)	0 (0)	0 (0)	0 (0)
Phyllotreta atra		Herbivore	W	1 (0.04)	0 (0)	0 (0)	0 (0)	0 (0)

Saproxylic species

The number of saproxylic species was not found to be significantly different in wooden boxes with added fertiliser and wooden boxes without fertiliser at Bredon Hill (t(5) = 2.24, p = 0.08) (Figure 3.11). Similarly, no significant differences were found in the number of saproxylic species found in any of the three box and fertiliser treatment combinations in the main grouped experiment at Windsor Forest (X^2(2) = 3.52, p = 0.17) (Figure 3.12).

The average abundance of specimens of saproxylic species found within boxes also showed no significant difference between the two box treatments at Bredon Hill (t(5) = 2.18, p = 0.08), or the three box treatments in in the grouped experiment at Windsor Forest (X^2(2) = 4.45, p = 0.11) (Figures 3.11 & 3.12).

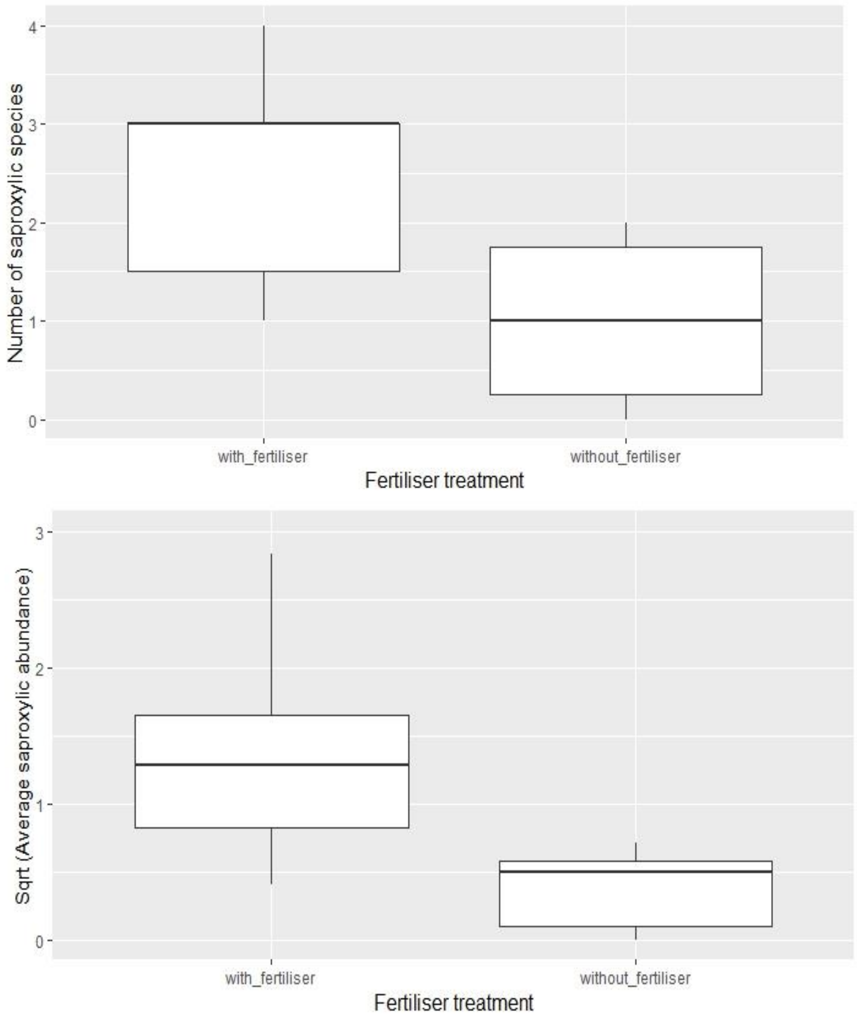


Figure 3.11. Boxplots comparing in the richness (top) and the average abundance (bottom) of saproxylic beetle species in the different box treatments in Bredon Hill (wooden boxes with and without fertiliser).

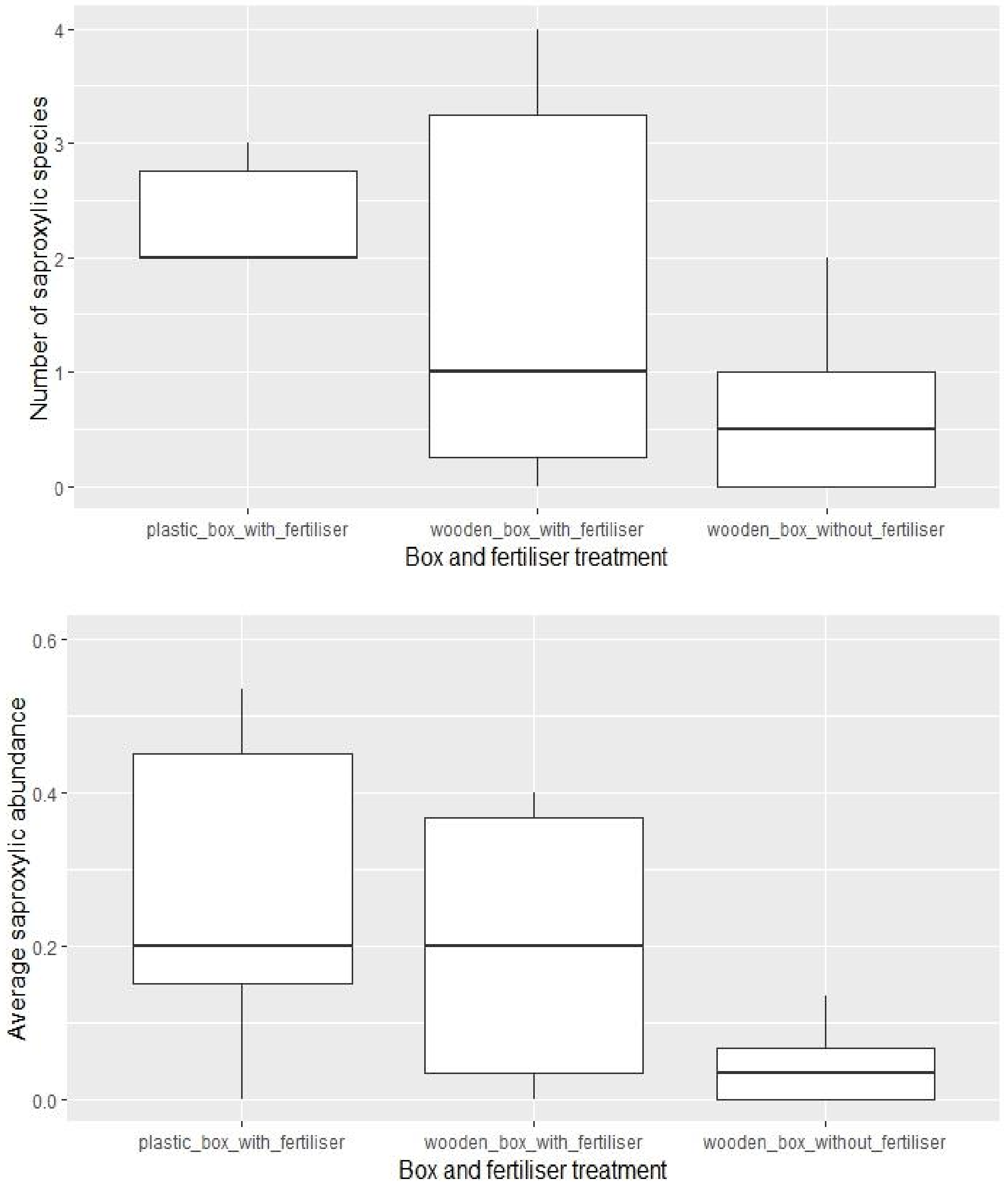


Figure 3.12. Boxplots comparing in the richness (top) and the average abundance (bottom) of saproxylic beetle species in the different box treatments in Windsor Forest (plastic boxes with fertiliser, wooden boxes with fertiliser and wooden boxes without fertiliser).

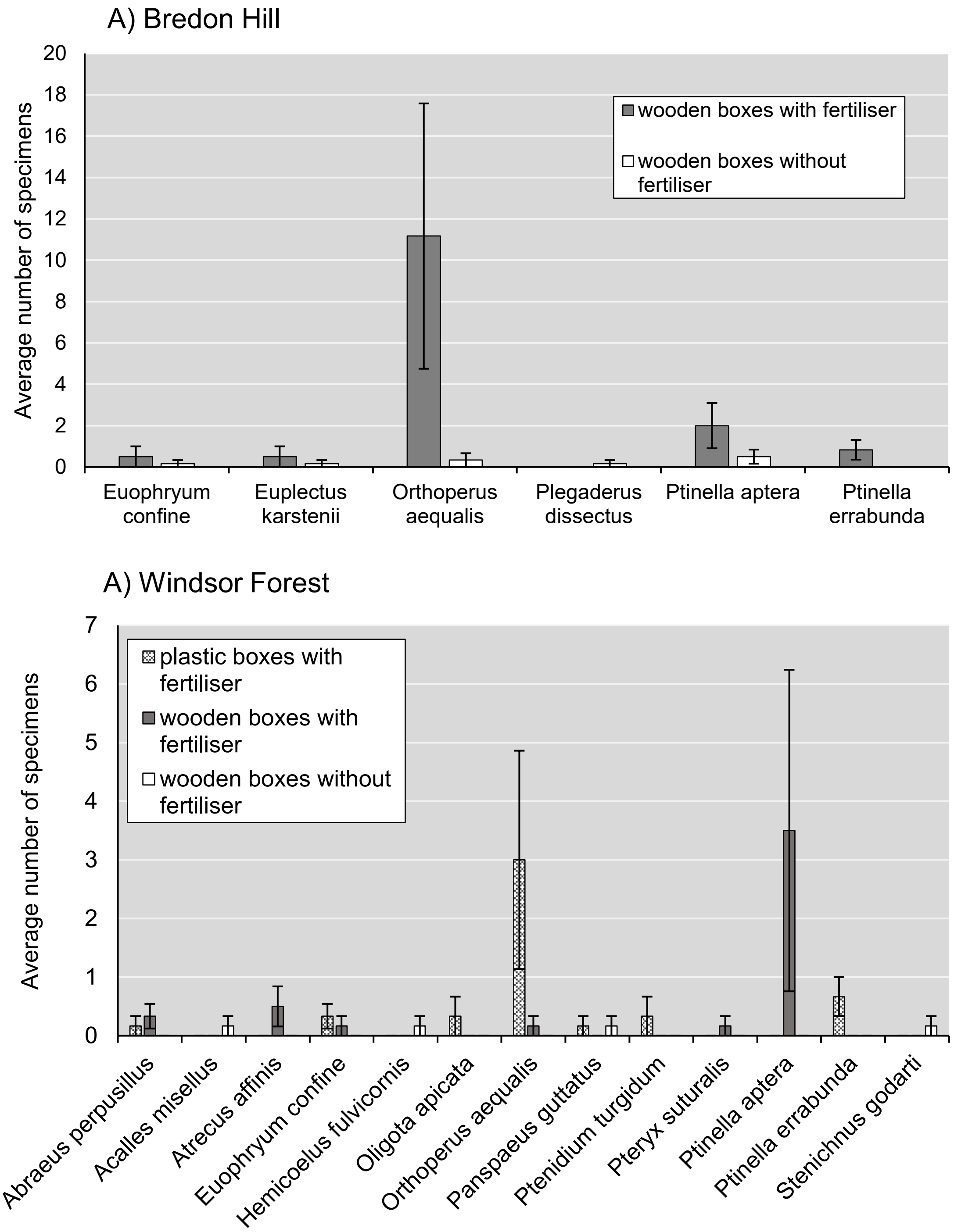


Figure 3.13. Bar graphs showing the average abundances of the saproxylic beetle species found in the different box treatments at Bredon Hill and Windsor Forest.

Woodland-associated species

The number of woodland associated species was not found to differ significantly between wooden boxes with and without fertiliser at Bredon Hill (V = 15, p = 0.06), or between any of the different box treatments at Windsor Forest ($X^2(2)$ = 4.10, p = 0.13) (Figures 3.14 & 3.15). Similarly, a significant difference was not achieved between the average abundance of woodland associated species found in wooden boxes with and without added fertiliser at Bredon Hill (V = 15, p = 0.06) (Figure 3.14).

In contrast, a significant difference was identified in the average abundance of woodland-associated species in the different box treatments at Windsor Forest box treatments ($X^2(2)$ = 8.09, p = 0.02). Further investigation with Wilcoxon signed-rank tests detected that wooden boxes with added fertiliser contained significantly higher average abundances of woodland-associated beetle specimens than wooden boxes without added fertiliser (V = 8, p = 0.03). However, no statistically significant differences were found between the plastic boxes with added fertiliser and either wooden boxes with (V = 0, p = 0.56), or without (V = 0, p = 0.06) added fertiliser (Figure 3.15).

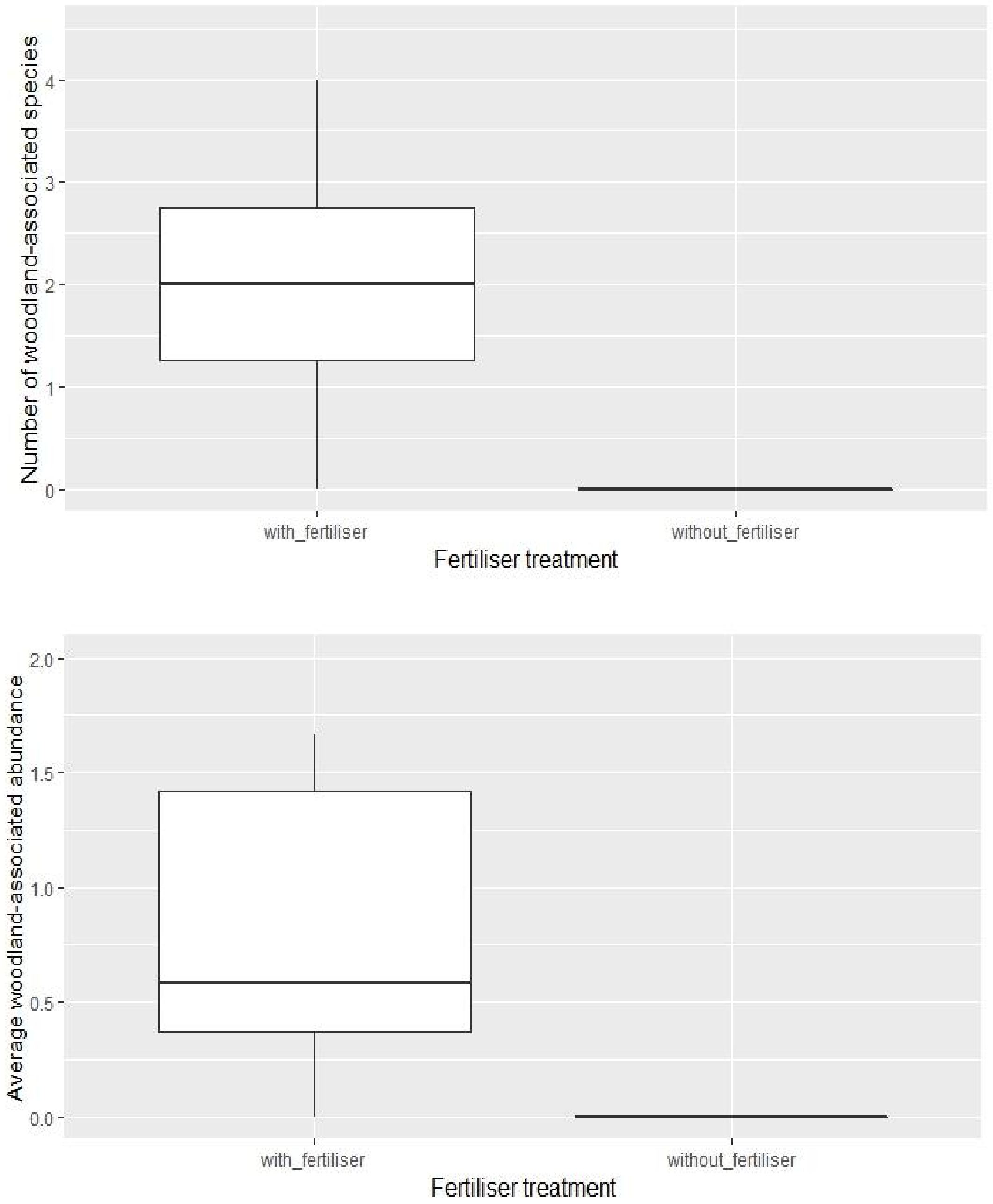


Figure 3.14. Boxplots comparing in the richness (top) and the average abundance (bottom) of woodland-associated (those with links to tree-decay habitats whilst not being strictly saproxylic) beetle species in the different box treatments in Bredon Hill (wooden boxes with and without fertiliser).

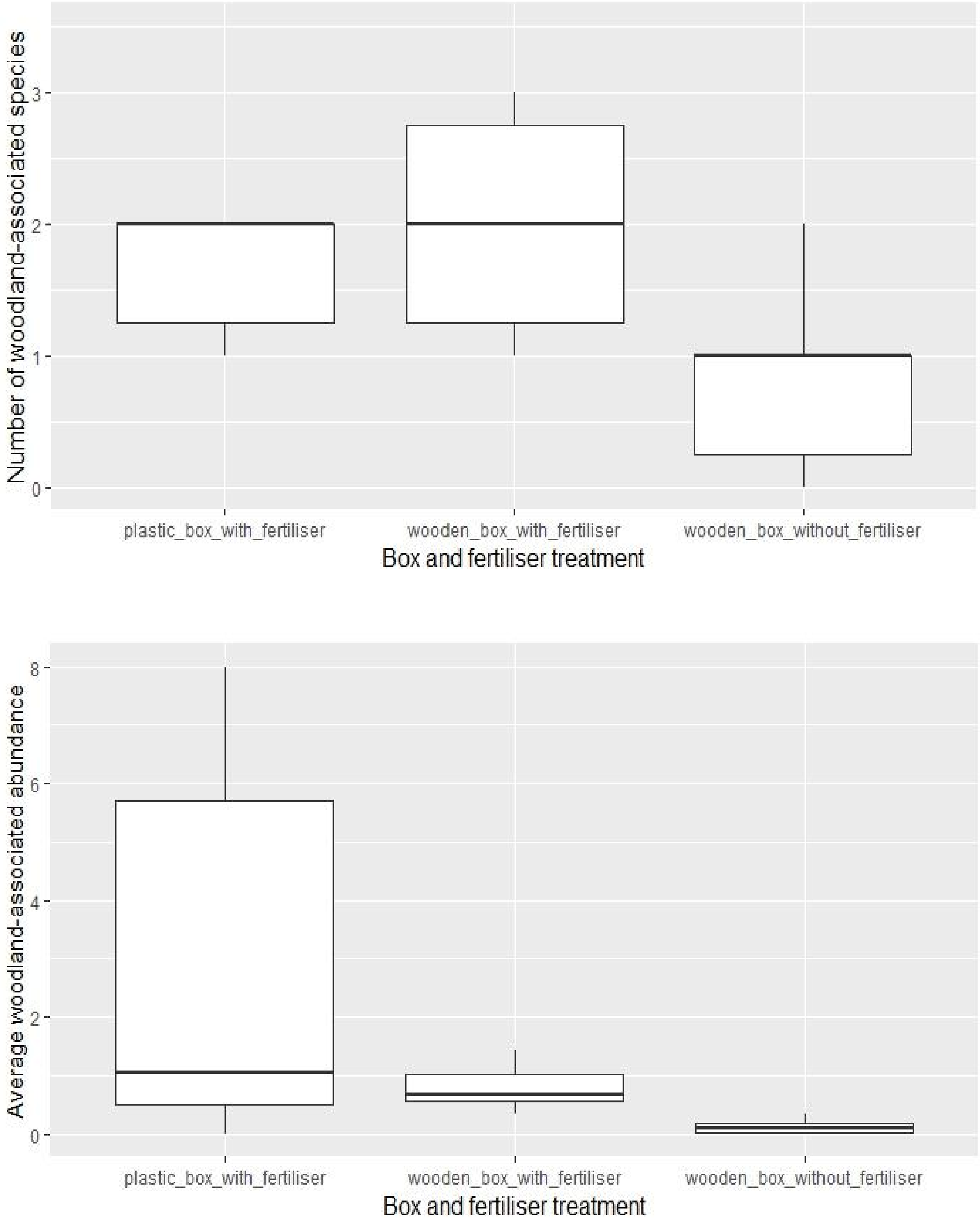
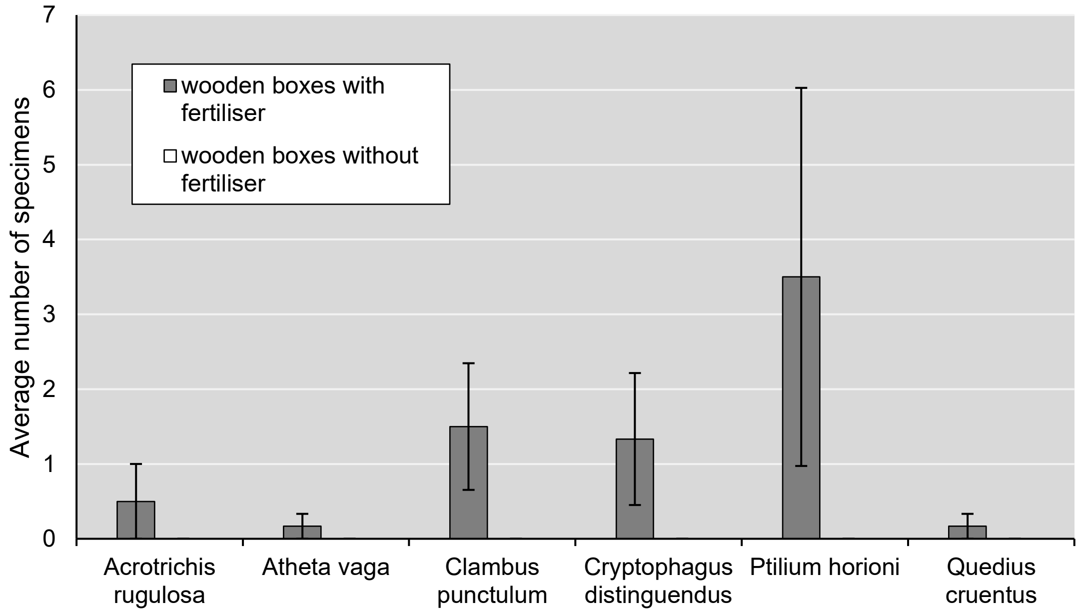


Figure 3.15. Boxplots comparing in the richness (top) and the average abundance (bottom) of woodland-associated (those with links to tree-decay habitats whilst not being strictly saproxylic) beetle species in the different box treatments in Windsor Forest (plastic boxes with fertiliser, wooden boxes with fertiliser and wooden boxes without fertiliser).

A) Bredon Hill



B) Windsor Forest

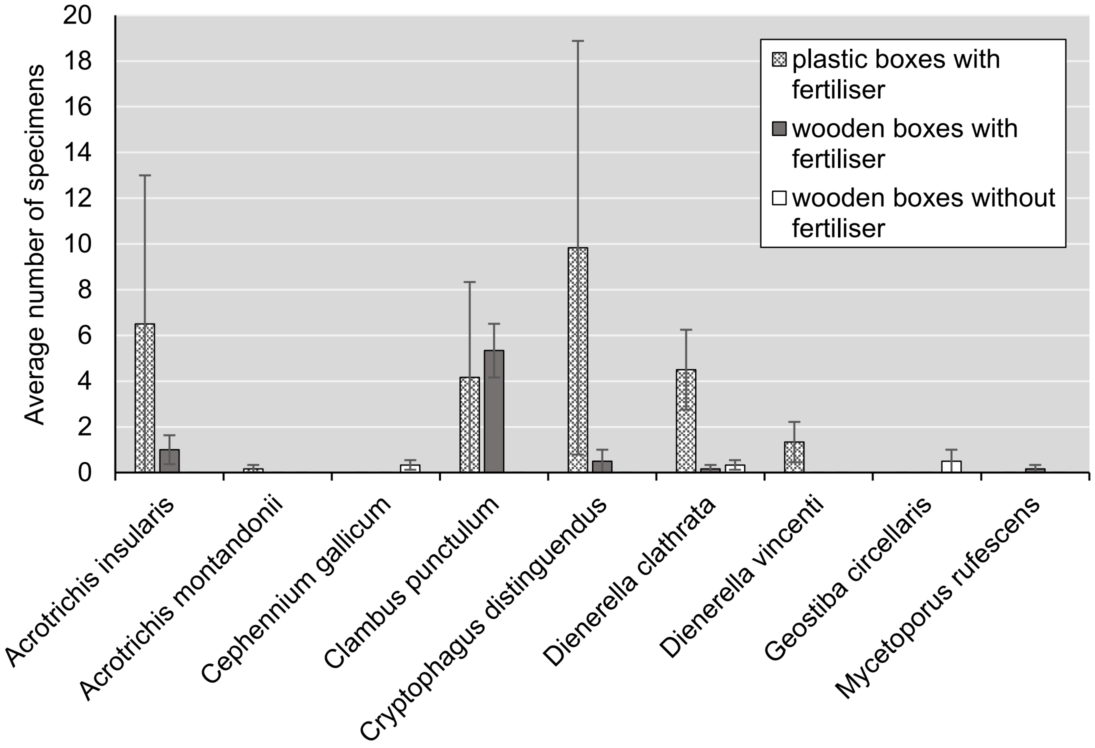


Figure 3.16. Bar graphs showing the average abundances of the woodland-associated beetle species found in the different box treatments at Bredon Hill and Windsor Forest.

Saproxylic and woodland associated species combined

The combined number of saproxylic and woodland-associated species was significantly higher in wooden boxes with added fertiliser than in those without fertiliser at Bredon Hill ($t(5) = 3.22$, $p = 0.02$) (Figure 3.17). Despite this, the average abundance of saproxylic and woodland associated species combined were not found to exhibit significant differences between box types at Bredon Hill ($t(5) = 2.57$, $p = 0.0501$) (Figure 3.17).

No statistically significant differences were observed in the number of combined saproxylic and woodland-associated species ($X^2(2) = 5.73$, $p = 0.057$) between any of the three box treatment variations at Windsor Forest (Figure 3.18).

A significant difference in average abundances of combined saproxylic and woodland associated species was identified in the box treatments at Windsor Forest ($X^2(2) = 8.09$, $p = 0.018$). Wilcoxon signed-rank tests showed that the average abundances were significantly higher in wooden boxes with added fertiliser than in wooden boxes without fertiliser ($V = 0$, $p = 0.036$) (Figure 3.18). No further significant differences were found in the average abundance of combined saproxylic and woodland associated species between the plastic boxes and the wooden boxes with fertiliser ($V = 14$, $p = 0.56$) or between the wooden boxes with and without fertiliser ($V = 15$, $p = 0.06$) (Figure 3.18).

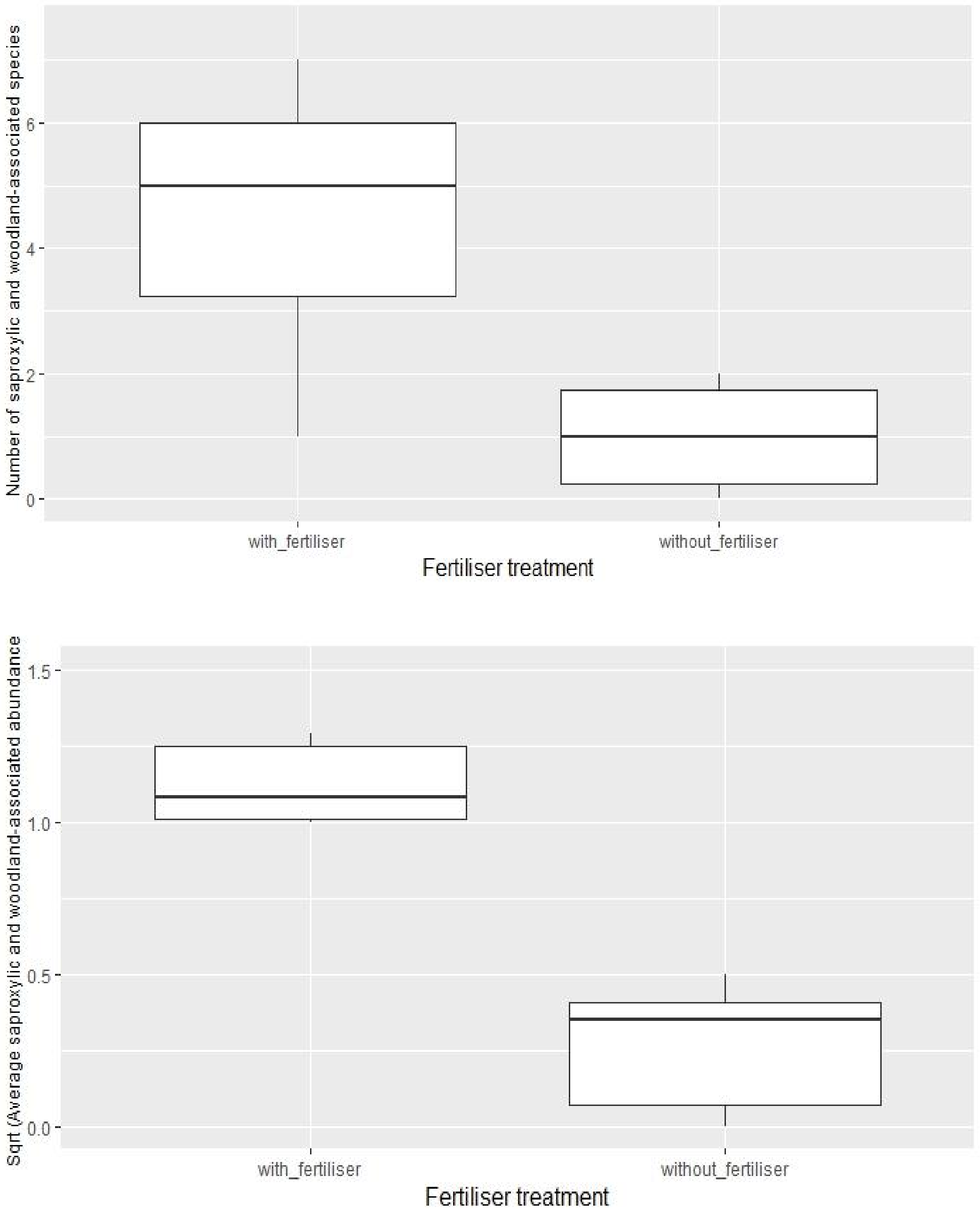


Figure 3.17. Boxplots comparing in the richness (top) and the average abundance (bottom) of a combined measure of saproxylic and woodland-associated beetle species in the different box treatments in Bredon Hill (wooden boxes with and without fertiliser).

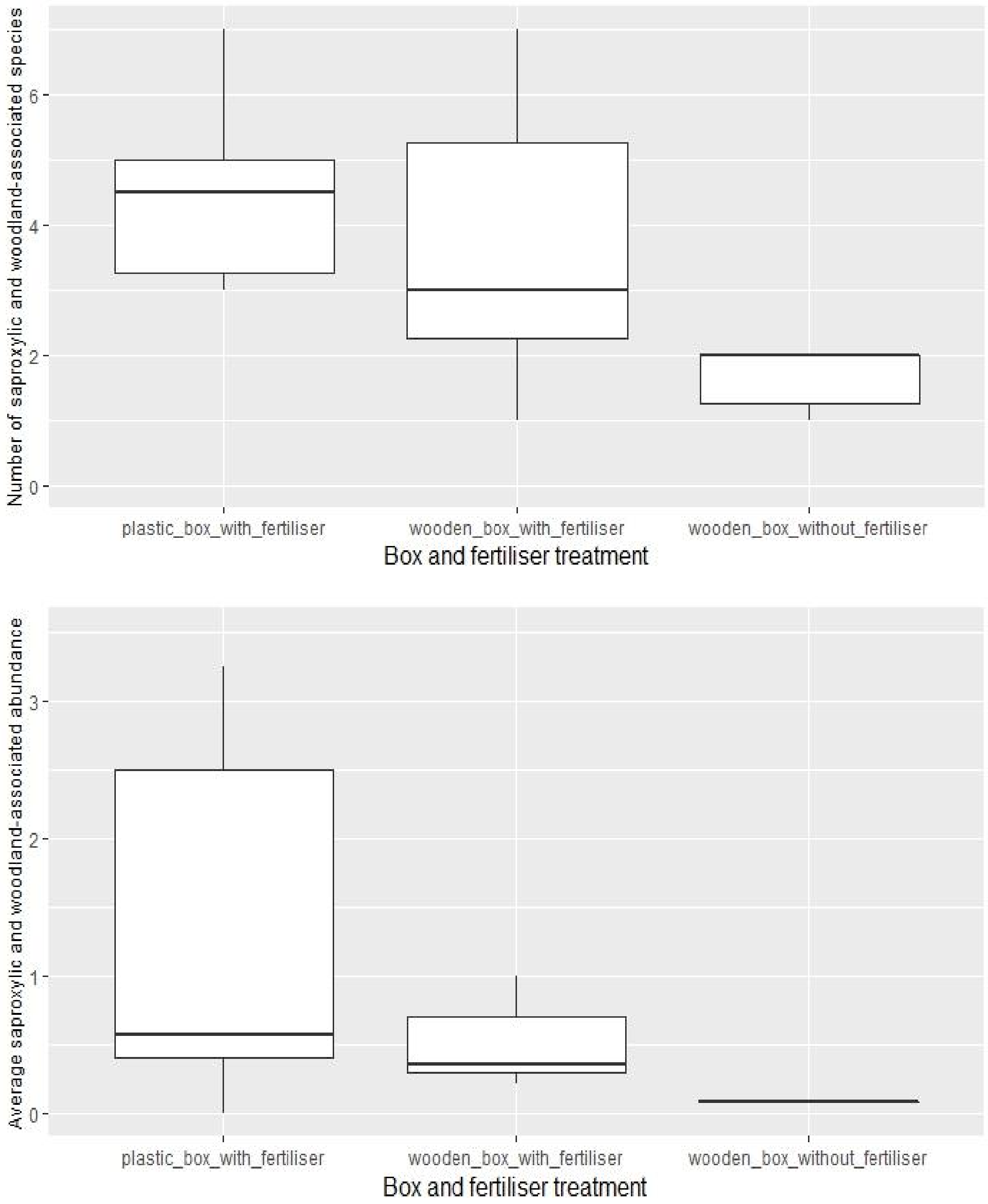


Figure 3.18. Boxplots comparing in the richness (top) and the average abundance (bottom) of a combined measure of saproxylic and woodland-associated beetle species in the different box treatments in Windsor Forest (plastic boxes with fertiliser, wooden boxes with fertiliser and wooden boxes without fertiliser).

Non-deadwood-associated Species

No significant difference was observed between the number of non-deadwood-associated species found in beetle boxes with and without fertiliser at Bredon Hill (t(5)= 1.42, p = 0.22) (Figure 3.19). In contrast, a significant difference was identified in the number of non-deadwood-associated beetle species found in the treatments at Windsor Forest ($X^2(2) = 6.13$, p = 0.047). Pairwise Wilcoxon signed rank tests between groups revealed that the numbers of non-deadwood-associated species were significantly higher in wooden boxes without fertiliser than in plastic boxes with fertiliser at Windsor Forest (V = 0, p = 0.048) (Figure 3.20) No significant differences were found between plastic boxes and wooden boxes with fertiliser (V = 0, p = 0.37) or wooden boxes with and without fertiliser (V = 8, p = 0.35) (Figure 3.20).

No significant difference was found between the average abundance of non-deadwood-associated beetles between wooden boxes with and without fertiliser at Bredon Hill (t(5) = 1.25, p = 0.27) (Figure 3.19). A significant difference was found between the average abundances of non-deadwood-associated beetle species found in the various box treatments at Windsor Forest ($X^2(2) = 6.13$, p = 0.047). The average abundance of non-deadwood-associated species were found to be significantly higher in wooden boxes without fertiliser than in plastic boxes with fertiliser at Windsor Forest (V = 0, p = 0.048) (Figure 3.20) No significant differences were found between plastic boxes and wooden boxes with fertiliser (V = 0, p = 0.37) or between wooden boxes with and without fertiliser (V = 8, p = 0.35) (Figure 3.20).

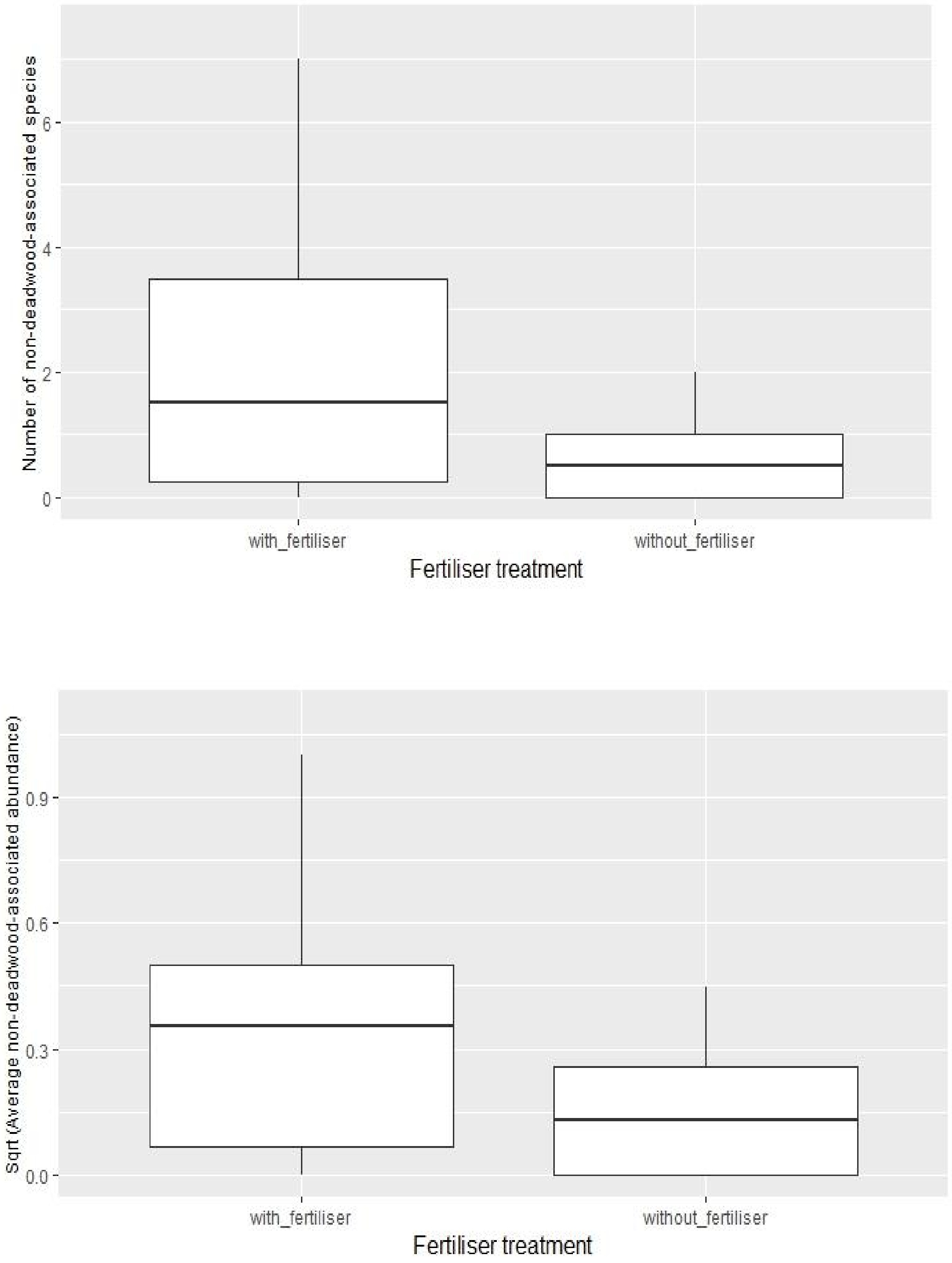
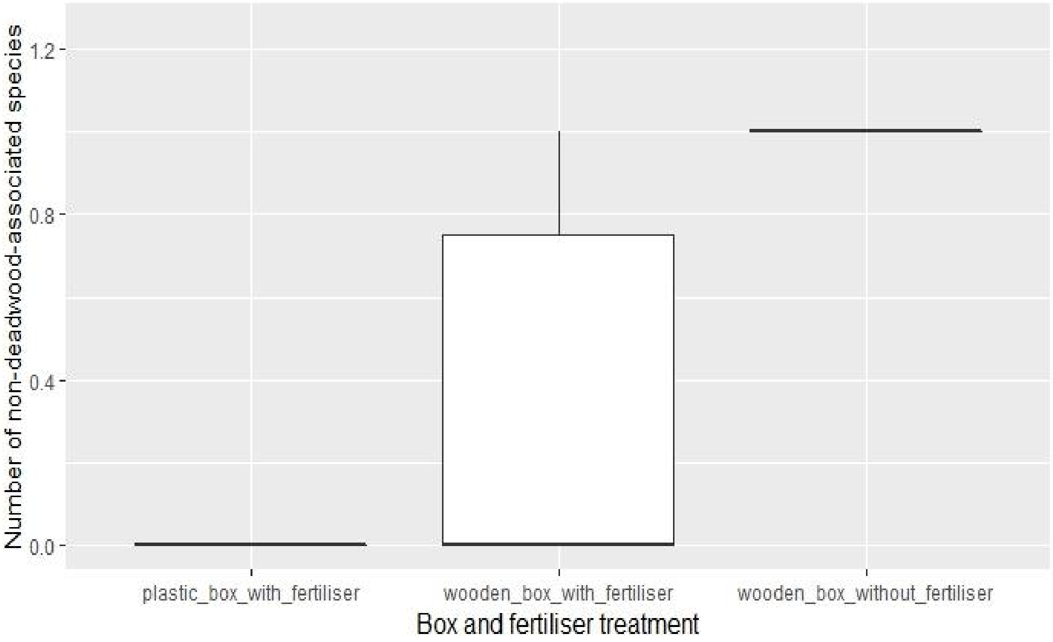


Figure 3.19. Boxplots comparing in the richness (top row) and the average abundance (bottom row) of beetle species with no saproxylic tendencies (non-deadwood-associated) in the different box treatments in Bredon Hill (wooden boxes with and without fertiliser).



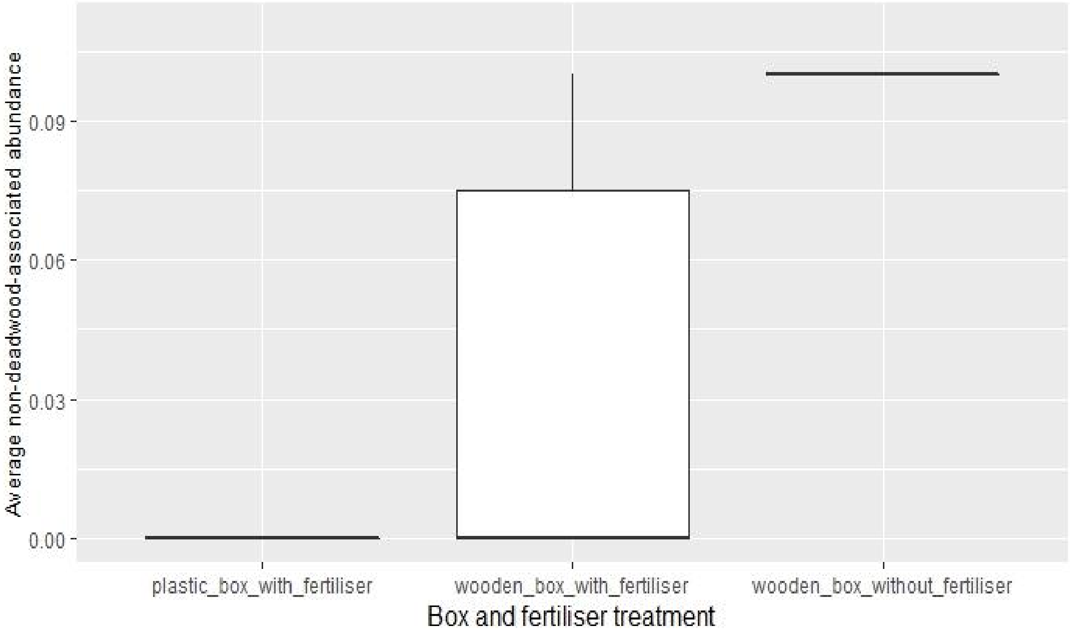
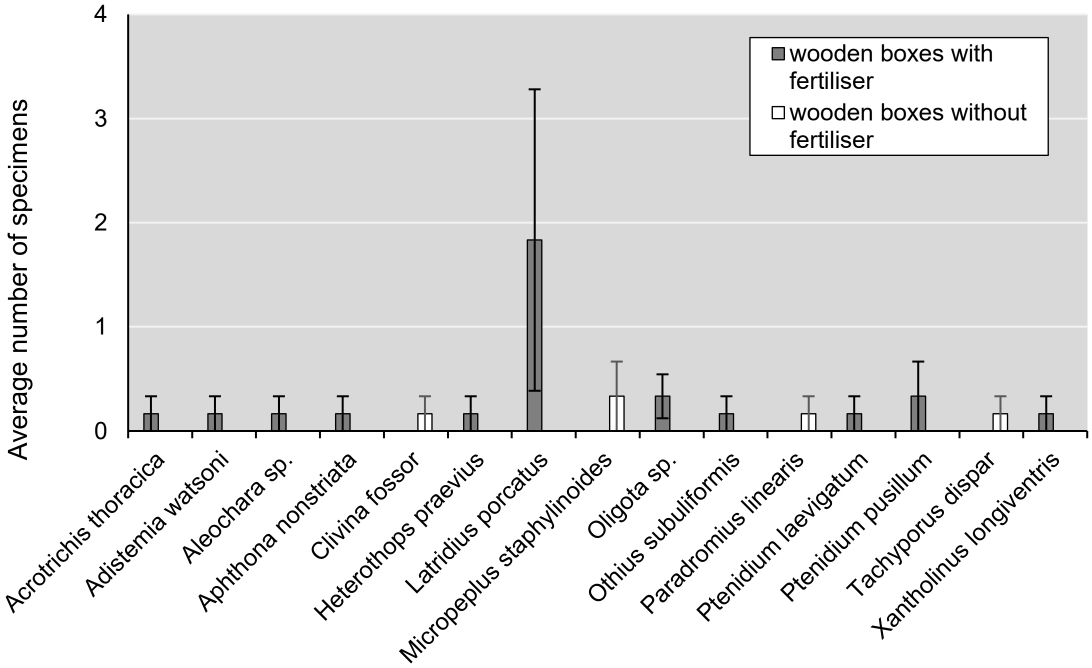


Figure 3.20. Boxplots comparing in the richness (top) and the average abundance (bottom) of beetle species with no saproxylic tendencies (non-deadwood-associated) in the different box treatments in Windsor Forest (plastic boxes with fertiliser, wooden boxes with fertiliser and wooden boxes without fertiliser).

A) Bredon Hill



B) Windsor Forest

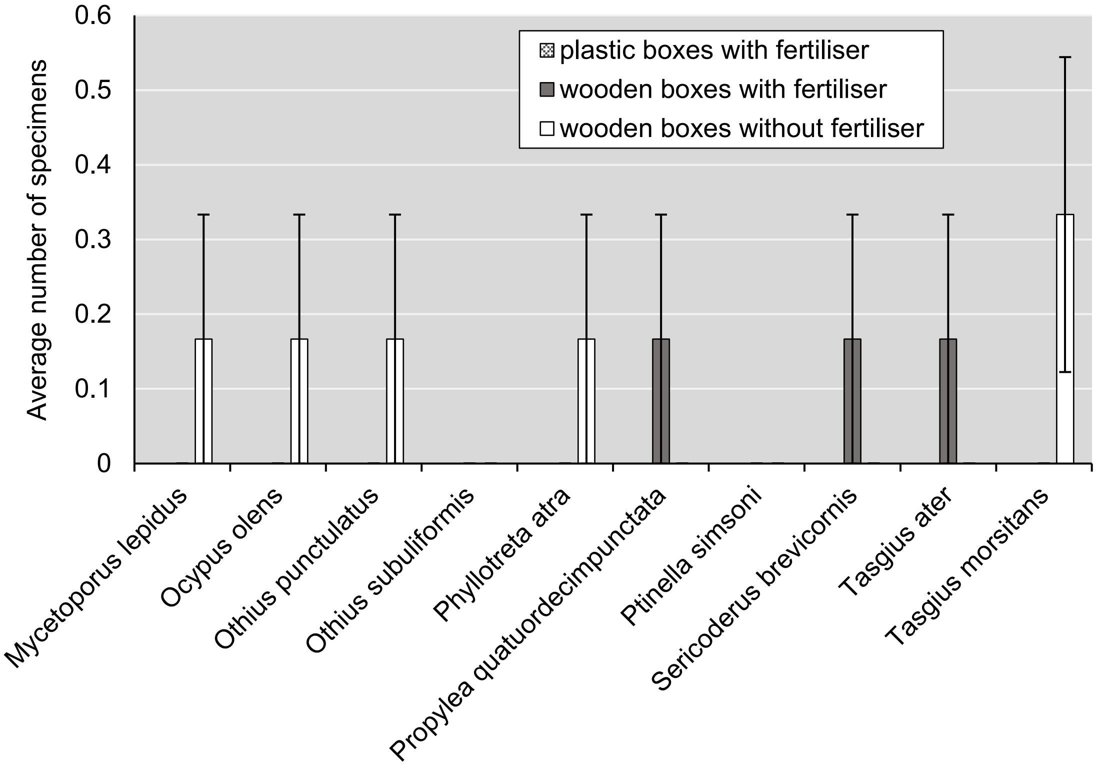


Figure 3.21. Bar graphs showing the average abundances of the non-deadwood-associated beetle species found in the different box treatments at Bredon Hill and Windsor Forest.

The results of the tests investigating the differences in different beetle assemblages between box types presented above are summarised in Table 3.6.

Table 3.6. A summary of the statistical tests investigating the differences in beetle communities between different beetle box treatments. *, $P<0.05$; **, $P<0.01$.

Species assemblage(s)	Site	Measurement	Box types	Test	Statistics
Saproxylic	Bredon Hill	Species richness	Wood with fertiliser/ wood without fertiliser	Paired t test	$t(5) = 2.24$, $p = 0.08$
		Sqrt (Average abundance of specimens per species)	Wood with fertiliser/ wood without fertiliser	Paired t test	$t(5) = 2.18$, $p = 0.08$
	Windsor Forest	Species richness	Plastic with fertiliser/ wood with fertiliser/ wood without fertiliser	Friedman test	$X^2(2) = 3.52$, $p = 0.17$
		Average abundance of specimens per species	Plastic with fertiliser/ wood with fertiliser/ wood without fertiliser	Friedman test	$X^2(2) = 4.45$, $p = 0.11$
Woodland-associated	Bredon Hill	Species richness	Wood with fertiliser/ wood without fertiliser	Wilcoxon signed-rank test	$V = 15$, $p = 0.06$
		Average abundance of specimens per species	Wood with fertiliser/ wood without fertiliser	Wilcoxon signed-rank test	$V = 15$, $p = 0.06$

	Windsor Forest	Species richness	Plastic with fertiliser/ wood with fertiliser/ wood without fertiliser	Friedman test	$X^2(2) = 4.10$, p = 0.13
		Average abundance of specimens per species	Plastic with fertiliser/ wood with fertiliser	Wilcoxon signed-rank test	V = 0, p = 0.56
			Plastic with fertiliser/ wood without fertiliser	Wilcoxon signed-rank test	V = 0, p = 0.06
			Wood with fertiliser > wood without fertiliser	**Wilcoxon signed-rank test**	**V = 8,** **p = 0.03***
Saproxylic & woodland associated combined	Bredon Hill	**Species richness**	**Wood with fertiliser > wood without fertiliser**	**Paired t test**	**t(5) = 3.22,** **p = 0.02***
		Sqrt (Average abundance of specimens per species)	Wood with fertiliser/ wood without fertiliser	Paired t test	t(5) = 2.57, p = 0.0501
	Windsor Forest	Species richness	Plastic with fertiliser/ wood with fertiliser/ wood without fertiliser	Friedman test	$X^2(2) = 5.73$, P = 0.057
		Average abundance of specimens per species	Plastic with fertiliser/ wood with fertiliser	Wilcoxon signed-rank test	V = 14, p = 0.56
			Plastic with fertiliser/ wood without fertiliser	Wilcoxon signed-rank test	V = 15, p = 0.06
			Wood with fertiliser > wood without fertiliser	**Wilcoxon signed-rank test**	**V = 0,** **p = 0.036***

Non-deadwood-associated	Bredon Hill	Species richness	Wood with fertiliser/ wood without fertiliser	Paired t test	t(5)= 1.42, p = 0.22
		Sqrt (Average abundance of specimens per species)	Wood with fertiliser/ wood without fertiliser	Paired t test	t(5) = 1.25, p = 0.27
	Windsor Forest	Species richness	Plastic with fertiliser/ wood with fertiliser	Wilcoxon signed-rank test	V = 0, p = 0.37
			Plastic with fertiliser < wood without fertiliser	**Wilcoxon signed-rank test**	**V = 0, p = 0.048***
			Wood with fertiliser/ wood without fertiliser	Wilcoxon signed-rank test	V = 8, p = 0.35
		Average abundance of specimens per species	Plastic with fertiliser/ wood with fertiliser	Wilcoxon signed-rank test	V = 0, p = 0.37
			Plastic with fertiliser < wood without fertiliser	**Wilcoxon signed-rank test**	**V = 0, p = 0.048***
			Wood with fertiliser/ wood without fertiliser	Wilcoxon signed-rank test	V = 8, p = 0.35

Elateridae larvae

Due to low light conditions on site and a lack of time whilst sampling, some Elaterid larvae were not able to be definitively identified. As the larvae of *L. violaceus* are similar to those of the much more common related genus *Athous*, it was often not possible to definitively distinguish them in the field. However, one advanced-stage larva collected from a tree hollow was identified by its ninth abdominal segment as being a potential *L. violaceus* individual. (Figure 3.22) Several larvae found within beetle boxes and real tree hollows were identified using the structure of their ninth abdominal segments to be a species of the genus, *Melanotus* (Etzler, 2013) (Figure 3.23).

Figure 3.22. An Elateridae larva identified as a potential *Limoniscus violaceus*, found at Bredon Hill on 29/06/2020 in a basal tree hollow.

Figure 3.23. The ninth abdominal segment of an Elateridae larvae showing structures characteristic of *Melanotus*. Specimen found at Windsor Forest on 17/08/2020 in a wooden beetle box with oak sawdust and added fertiliser.

Table 3.7. A summary of Elateridae larvae observations from tree hollows and beetle boxes at Bredon Hill and Windsor Forest. Identified using Etzler, 2013 & Whitehead, 2003)

Date of observation	Site found	Situation found	Number found	Tentative identification
29/06/2020	Bredon Hill	Wooden box containing oak sawdust and added fertiliser	1	*Ampedus* sp.
29/06/2020	Bredon Hill	Wooden box containing oak sawdust without added fertiliser	1	*Athous* sp.
29/06/2020	Bredon Hill	Real basal tree hollow	2	*Athous* sp.
29/06/2020	Bredon Hill	Real basal tree hollow	1	Potential *Limoniscus violaceus*
06/07/2020	Windsor Forest	Real basal tree hollow	3	*Melanotus* sp.
06/07/2020	Windsor Forest	Wooden box containing oak sawdust and added fertiliser	1	Unidentified
10/08/2020	Bredon Hill	Wooden box containing oak sawdust without added fertiliser	1	*Athous* sp.
17/08/2020	Windsor Forest	Wooden box containing oak sawdust and added fertiliser	2	*Melanotus* sp.
17/08/2020	Windsor Forest	Wooden box containing oak sawdust without added fertiliser	1	*Melanotus* sp.

Other immature beetle observations from wood mould samples

Several of the Coleoptera larvae collected from wood mould during this study were not identified due time limitations and difficulties in examination resulting from their small size. However, those that were identified included individuals from the decaying-wood associated genus, *Pediacus*. The genus, *Acrotrichis*, was also represented which contains several woodland-associated species (Table 3.8).

Table 3.8. A summary of beetle larvae not belonging to the Elateridae that were retrieved from wood mould samples taken from beetle boxes and real basal tree hollows.

Life stage	Identification	Total number of specimens found (average per sample)				
		Wooden box, oak sawdust, without fertiliser (n=12, sampled twice)	**Wooden box, oak sawdust, with fertiliser** (n=12, sampled twice)	**Wooden box, beech sawdust, with fertiliser** (n=2, sampled twice)	**Plastic box, oak sawdust, with fertiliser** (n=6, sampled twice)	**Real tree hollow** (n=9, sampled once)
Larvae	Unidentified Coleoptera	5 (0.21)	36 (1.5)	2 (0.5)	20 (1.67)	6 (0.67)
	Carabidae	0 (0)	1 (0.04)	0 (0)	0 (0)	0 (0)
	Staphylinidae	2 (0.08)	7 (0.29)	0 (0)	0 (0)	1 (0.11)
	Curculionidae	1 (0.04)	1 (0.04)	0 (0)	0 (0)	0 (0)
	Pediacus sp.	0 (0)	1 (0.04)	0 (0)	0 (0)	0 (0)
	Cryptocephalus sp.	0 (0)	1 (0.04)	0 (0)	0 (0)	0 (0)
	Total Coleoptera Larvae	8 (0.33)	47 (1.96)	2 (0.5)	20 (1.67)	7 (0.78)
Pupae	*Acrotrichis* sp.	0 (0)	0 (0)	0 (0)	1 (0.08)	0 (0)
	Quedius sp.	0 (0)	0 (0)	0 (0)	1 (0.08)	0 (0)
	Pediacus sp.	0 (0)	1 (0.04)	0 (0)	0 (0)	0 (0)

Beetle fragments

A single elytron that was identified as having belonged to a *L. violaceus* individual was retrieved from a real basal tree hollow at Bredon Hill. Wood mould extracted from real tree hollows at Windsor Forest contained fragments of beetles including *Euophryum* sp. and *Synchita variegata*. A pronotum of *Silvanus bidentatus* was found in a wooden beetle box containing oak sawdust and added fertiliser at Windsor Forest.

Other invertebrates in beetle boxes and tree hollows

Table 3.9. A summary of all non-coleopteran invertebrates retrieved from wood mould samples from beetle boxes and real tree hollows.

Identification	Total number of specimens found (average per sample)				
	Wooden box, oak sawdust, without fertiliser (n=12, sampled twice)	**Wooden box, oak sawdust, with fertiliser** (n=12, sampled twice)	**Wooden box, beech sawdust, with fertiliser** (n=2, sampled twice)	**Plastic box, oak sawdust, with fertiliser** (n=6, sampled twice)	**Real tree hollow** (n=9, sampled once)
Oligochaeta					
Aporrectodea rosea	2 (0.08)	0 (0)	0 (0)	0 (0)	0 (0)
Bimastos eiseni	1 (0.04)	4 (0.17)	3 (0.75)	0 (0)	0 (0)
Bimastos rubidus	2 (0.08)	4 (0.17)	1 (0.25)	0 (0)	0 (0)
Dendrobaena attemsi	4 (0.17)	0 (0)	0 (0)	0 (0)	0 (0)
Lumbricus castaneus	0 (0)	0 (0)	0 (0)	0 (0)	1 (0.11)
Lumbricus rubellus	1 (0.04)	0 (0)	0 (0)	0 (0)	0 (0)
Immature/ unidentified	97 (4.04)	97 (4.04)	29 (7.25)	1 (0.08)	39 (4.33)
Total	107 (4.46)	105 (4.38)	33 (8.25)	1 (0.08)	40 (4.44)
Gastropoda – Snails					
Carychiinae	1 (0.04)	0 (0)	0 (0)	0 (0)	0 (0)
Cochlicopa cf. *lumbricella*	1 (0.04)	0 (0)	0 (0)	0 (0)	0 (0)
Vertigo pygmaea	0 (0)	1 (0.04)	0 (0)	0 (0)	0 (0)
Discus rotundatus	0 (0)	0 (0)	0 (0)	2 (0.17)	0 (0)
Euconulus fulvus	0 (0)	1 (0.04)	0 (0)	0 (0)	0 (0)
Zonitoides excavatus	2 (0.08)	0 (0)	0 (0)	1 (0.08)	2 (0.22)
Oxychilus sp.	1 (0.04)	1 (0.04)	2 (0.5)	0 (0)	0 (0)
Oxychilus alliarius	1 (0.04)	1 (0.04)	2 (0.5)	0 (0)	0 (0)

Unidentified	1 (0.04)	0 (0)	0 (0)	0 (0)	4 (0.44)
Total	7 (0.29)	4 (0.17)	4 (1)	3 (0.25)	6 (0.67)
Gastropoda – Slugs					
Total	2 (0.08)	0 (0)	0 (0)	0 (0)	0 (0)
Diplopoda					
Glomeris marginata	1 (0.04)	0 (0)	0 (0)	0 (0)	0 (0)
Polydesmus angustus	0 (0)	0 (0)	0 (0)	0 (0)	1 (0.11)
Polydesmus denticulatus	1 (0.04)	0 (0)	0 (0)	0 (0)	0 (0)
Proteroiulus fuscus	0 (0)	0 (0)	0 (0)	0 (0)	5 (0.56)
Cylindroiulus punctatus	6 (0.25)	5 (0.21)	5 (1.25)	0 (0)	5 (0.56)
Immature/ unidentified Polydesmida	114 (4.75)	84 (3.5)	0 (0)	0 (0)	16 (1.78)
Immature/ unidentified Blaniulidae	0 (0)	0 (0)	0 (0)	0 (0)	1 (0.11)
Immature/ unidentified Julidae	11 (0.46)	18 (0.75)	3 (0.75)	1 (0.08)	1 (0.11)
Total	133 (5.54)	107 (4.46)	8 (2)	1 (0.08)	29 (3.22)
Chilopoda					
Schendyla nemorensis	0 (0)	0 (0)	0 (0)	1 (0.08)	0 (0)
Strigamia crassipes	0 (0)	2 (0.08)	0 (0)	0 (0)	0 (0)
Geophilus carpophagus/easoni	0 (0)	0 (0)	0 (0)	1 (0.08)	0 (0)
Geophilus flavus	0 (0)	1 (0.04)	0 (0)	0 (0)	0 (0)
Geophilus truncorum	0 (0)	9 (0.38)	0 (0)	1 (0.08)	0 (0)
Cryptops hortensis	26 (1.08)	12 (0.5)	19 (4.75)	1 (0.08)	12 (1.33)
Lithobius crassipes	3 (0.13)	0 (0)	0 (0)	0 (0)	0 (0)
Lithobius forficatus	2 (0.08)	4 (0.17)	2 (0.5)	0 (0)	0 (0)
Lithobius microps	15	7 (0.29)	1 (0.25)	0 (0)	2 (0.22)
Lithobius variegatus	0 (0)	0 (0)	0 (0)	0 (0)	2 (0.22)
Immature /unidentified Geophilomorpha	0 (0)	2 (0.08)	0 (0)	1 (0.08)	1 (0.11)
Immature /unidentified *Cryptops* sp.	3 (0.13)	0 (0)	0 (0)	0 (0)	1 (0.11)
Immature /unidentified *Lithobius* sp.	17 (0.71)	9 (0.38)	1 (0.25)	0 (0)	2 (0.22)
Total	66 (2.75)	66 (2.75)	23 (5.75)	5 (0.42)	20 (2.22)
Pauropoda					

Total	2 (0.08)	0 (0)	0 (0)	0 (0)	0 (0)
Symphyla					
Total	0 (0)	0 (0)	1 (0.25)	0 (0)	0 (0)
Oniscoidea					
Haplophthalmus danicus	3 (0.13)	7 (0.29)	1 (0.25)	0 (0)	249 (27.67)
Trichoniscus pusillus agg.	3 (0.13)	18 (0.75)	0 (0)	0 (0)	7 (0.78)
Philoscia muscuorum	2 (0.08)	0 (0)	0 (0)	1 (0.08)	0 (0)
Oniscus asellus	17 (0.71)	17 (0.71)	2 (0.5)	7 (0.58)	13 (1.44)
Porcellio scaber	44 (1.83)	289 (12.04)	7 (1.75)	404 (33.67)	7 (0.78)
Armadilidium vulgare	2 (0.08)	11 (0.46)	0 (0)	0 (0)	0 (0)
Immature /unidentified *Porcellio* sp./ *Oniscus* sp.	144 (6)	224 (9.33)	31 (7.75)	228 (19)	19 (2.11)
Immature /unidentified *Armadillidium* sp.	0 (0)	14 (0.58)	0 (0)	0 (0)	0 (0)
Total	215 (8.96)	580 (24.17)	41 (10.25)	640 (53.33)	295 (32.78)
Diplura					
Total	2 (0.08)	0 (0)	1 (0.25)	0 (0)	4 (0.44)
Collembola					
Total	259 (10.79)	521 (21.71)	19 (4.75)	474 (39.5)	27 (3)
Opiliones					
Paroligolophus agrestis	1 (0.04)	0 (0)	0 (0)	0 (0)	0 (0)
Dicranopalpus ramosus agg.	1 (0.04)	0 (0)	0 (0)	0 (0)	0 (0)
Leiobunum rotundum	0 (0)	2 (0.08)	0 (0)	0 (0)	0 (0)
Juvenile/unidentified	0 (0)	0 (0)	0 (0)	1 (0.08)	0 (0)
Total	2 (0.08)	2 (0.08)	0 (0)	1 (0.08)	0 (0)
Acari					
Total	890 (37.08)	929 (38.71)	93 (23.25)	408 (34)	193 (21.44)
Pseudoscorpiones					
Chthonius ischnocheles	13 (0.54)	4 (0.17)	0 (0)	1 (0.08)	0 (0)
Chernes cimicoides	0 (0)	6 (0.25)	0 (0)	0 (0)	0 (0)
Lamprochernes chyzeri	0 (0)	1 (0.04)	0 (0)	0 (0)	0 (0)
Allochernes wideri	0 (0)	0 (0)	0 (0)	1 (0.08)	0 (0)
Pselaphochernes scorpioides	0 (0)	1 (0.04)	0 (0)	2 (0.17)	0 (0)
Lamprochernes savignyi	0 (0)	1 (0.04)	0 (0)	0 (0)	0 (0)
Juvenile/unidentified	0 (0)	2 (0.08)	0 (0)	0 (0)	0 (0)
Total	13 (0.54)	15 (0.63)	0 (0)	4 (0.33)	0 (0)

Aranae					
Total	8 (0.33)	21 (0.88)	2 (0.5)	21 (0.88)	3
Psocoptera					
Total	0 (0)	0 (0)	0 (0)	1 (0.08)	1 (0.11)
Hemiptera					
Aphidoidea	4 (0.17)	8 (0.33)	0 (0)	0 (0)	1 (0.11)
Coccomorpha	0 (0)	0 (0)	0 (0)	0 (0)	2 (0.22)
Unidentified	8 (0.33)	10 (0.42)	0 (0)	1 (0.08)	0 (0)
Total	12 (0.5)	18 (0.75)	0 (0)	1 (0.08)	3 (0.33)
Thysanoptera					
Total	22 (0.92)	26 (1.08)	0 (0)	0 (0)	9 (1)
Hymenoptera					
Formicidae	104 (4.33)	12 (0.5)	1 (0.25)	5 (0.42)	0 (0)
Alloxysta victrix	1 (0.04)	0 (0)	0 (0)	0 (0)	0 (0)
Mymaromma anomalum	0 (0)	0 (0)	0 (0)	1 (0.08)	0 (0)
Vespa germanica	1 (0.04)	0 (0)	0 (0)	0 (0)	0 (0)
Unidentified	9 (0.38)	17 (0.71)	2 (0.5)	4 (0.33)	1 (0.11)
Total	115 (4.79)	29 (1.21)	3 (0.75)	10 (0.83)	1 (0.11)
Diptera					
Chrysopilus laetus	0 (0)	0 (0)	0 (0)	0 (0)	2 (0.22)
Unidentified	8 (0.33)	24 (1)	2 (0.5)	20 (1.67)	6 (0.67)
Total	8 (0.33)	24 (1)	2 (0.5)	20 (1.67)	8 (0.89)
Siphonaptera					
Total	0 (0)	1 (0.04)	0 (0)	0 (0)	0 (0)

Immature insect observations (non – beetles)

Table 3.10. A summary of immature insects (not including Coleoptera) retrieved from wood mould samples taken from beetle boxes and real tree hollows.

Life stage	**Identification**	**Total number of specimens found (average per sample)**				
		Wooden box, oak sawdust, without fertiliser (n=12, sampled twice)	**Wooden box, oak sawdust, with fertiliser** (n=12, sampled twice)	**Wooden box, beech sawdust, with fertiliser** (n=2, sampled twice)	**Plastic box, oak sawdust, with fertiliser** (n=6, sampled twice)	**Real tree hollow** (n=9, sampled once)
Larvae	**Neuroptera**					
	Total	1 (0.04)	0 (0)	0 (0)	0 (0)	0 (0)
	Hymenoptera					
	Formicidae	10 (0.42)	0 (0)	0 (0)	0 (0)	0 (0)
	Lepidoptera					
	Total	5 (0.21)	44 (1.83)	0 (0)	2 (0.17)	0 (0)
	Diptera					
	Unidentified	7 (0.29)	19 (0.79)	0 (0)	7 (0.58)	2 (0.22)
	Sciaridae	1 (0.04)	2 (0.08)	0 (0)	0 (0)	0 (0)
	Stratiomyidae	0 (0)	16 (0.67)	1 (0.25)	0 (0)	1 (0.11)
	Chloromyia sp.	0 (0)	1 (0.04)	0 (0)	0 (0)	0 (0)
	Faniidae	1 (0.04)	1 (0.04)	0 (0)	1 (0.08)	0 (0)
	Chrysopilus laetus	0 (0)	0 (0)	0 (0)	0 (0)	1 (0.11)
	Total	9 (0.38)	39 (1.63)	1 (0.25)	8 (0.67)	4 (0.44)
Pupae	**Lepidoptera**					
	Total	0 (0)	1 (0.04)	0 (0)	0 (0)	2 (0.22)

Incidental observations

Beetles

On several occasions, beetles were observed in the crevice where the lid rests upon the top rim of the box. This crevice, where two pieces of wood are tightly adpressed together mimics the conditions found between the bark of trees and the sapwood beneath it.

- On 12/08/2019 several individuals of *Silvanus bidentatus* were found in this crevice on a box rim, which is a species commonly observed under tree bark (Alexander, 2002).

- On 13/10/2021, the saproxylic species *Ampedus elongatulus* was found to have formed a pupal cell in compacted sawdust on the box rim. At the time of observation, the adult beetle was inside the cell, with the larval skin discarded behind it indicating that it had completed its development there (Figure 3.24). Next to the *A. elongatulus*, an adult of the saproxylic tenebrionid, *Nalassus laevioctostriatus* was also found (Figure 3.24). Additionally, another Elaterid larva was observed nestled within compacted wood-mould on the lid of another box during this visit (Figure 3.20).

Figure 3.24. A series of photographs showing observations of beetles found on the rims of wooden beetle boxes at Windsor Forest. The photographs on the left and centre showing an *Ampedus elongatulus* individual that was found in a pupal cell on the rim of a wooden beetle box, having completed its larval development. The larval skin can be seen discarded behind the adult beelte. An adult *Nalassus laevioctostriatus* is also shown next to the *A. elongatulus* in the left picture. The right-hand picture shows an Elaterid larva that was found among compacted wood mould on the rim of a different wooden beetle box.

Other fauna

In addition to beetles, other organisms were observed using beetle boxes as habitat. Some utilised the previously mentioned space between the box lid and the box rim, whilst several were found inside the main structure of the boxes. One particularly prominent observation was that individuals of the common house spider (*Tegenaria domestica*) were present in the majority of boxes surveyed throughout the study.

- On 29/06/2020, ants were observed using the space between a box rim and a box lid as a nesting site (Figure 3.25). The ants had taken advantage of compacted wood mould, that had been compressed under the box lid to build their nest structure.

Figure 3.25. A photograph showing an ants' nest that was found on the rim of a wooden beetle box at Bredon Hill.

- On 29/06/2020 a Peacock butterfly (*Aglais io*) was observed sheltering on the underside of the internal shelf in a wooden beetle box at Bredon Hill.
- On 25/05/2021, the shell of an old wasps' nest was found inside the lid of a wooden beetle box at Windsor Forest (Figure 3.26).

Figure 3.26. A photograph of the remains of an old wasp nest found inside a wooden beetle box at Windsor Forest.

- On 13/10/2021, several pale tussock moth caterpillars (*Calliteara pudibunda*) were observed inside the lids of beetle boxes at Windsor Forest (Figure 3.27). Of these, some had formed pupal cases attached to the box lid (Figure 3.27).

Figure 3.27. Photographs depicting a caterpillar and a pupal case of *C. pudibunda*, both of which were found inside wooden beetle boxes at Windsor Forest.

- On 13/10/2021, a common field mouse (*Apodemus sylvaticus*) was observed inside the top compartment of one of the plastic boxes at Windsor Forest (Figure 3.28). On the same visit, a store of nuts was found inside the central entrance of one of the wooden boxes (a variant containing beech sawdust) (Figure 3.28). The nuts were hollowed in a way that indicated that it had been done by a mouse (Wainhouse – pers. comm.).

Figure 3.28. Photographs depicting an individual of *A. sylvaticus* observed inside a plastic beetle box and a nut store of a mouse found inside the entrance of a wooden beetle box at Windsor Forest.

Moisture

The average moisture level recorded from all real tree hollows at Bredon Hill (n=3) was 48.68 %vol with average moisture levels per hollow ranging from 34.07 %vol and 59.10 %vol (recorded on 10/08/20). For the real tree hollows at Windsor Forest (n=6), the average moisture level across all hollows was 35.38%vol with average moisture levels per hollow ranging from 19.47 %vol and 55.43 %vol (recorded on 17/08/20).

Table 3.11. A summary of average moisture measurements taken from top and bottom box compartments during two sampling sessions.

	Average moisture in the bottom compartments of boxes (%vol)			**Average moisture in the top compartments of boxes (%vol)**
Box treatment	**first sampling session (Bredon Hill: 10/08/20, Windsor Forest: 17/08/20)**	**Second sampling session (Bredon Hill: 02/06/21, Windsor Forest: 24/05/21)**	**Average across both sampling sessions**	**first sampling session (Bredon Hill: 10/08/20, Windsor Forest: 17/08/20)**
Bredon Hill				
wooden boxes with oak sawdust and fertiliser (n=6)	9.37	30.57	15.26	6.42
wooden boxes with oak sawdust, without fertiliser (n=6)	14.03	21.16	22.30	2.54
Windsor Forest				
plastic boxes with oak sawdust and fertiliser (n=6)	8.96	8.97	8.97	2.00
wooden boxes with oak sawdust and fertiliser (n=6	28.22	24.47	26.34	30.52
wooden boxes with oak sawdust, without fertiliser (n=6)	23.57	34.64	29.10	20.78

wooden boxes with beech sawdust and fertiliser (n=2)	17.43	22.30	19.87	22.25

Moisture levels in the main compartment of different box treatments

No significant differences were found between average moisture levels in the main compartment of the wooden boxes with and without added fertiliser at Bredon Hill (t(5) = 1.24, p = 0.27) (Figure 3.29).

Significant differences were identified within the three box treatments in the grouped experiment at Windsor Forest ($X^2(2) = 9.33$, p = 0.009). Pairwise Wilcoxon signed rank test between groups showed that the average moisture content of plastic boxes with fertiliser was significantly lower than in both wooden boxes without fertiliser (V = 0, p = 0.03) and wooden boxes with fertiliser (V = 0, p = 0.03) (Figure 3.30). The wooden boxes with and without fertiliser did not have significantly different average moisture content of the wood mould within their main cavities (V = 7, p = 0.56) (Figure 3.30).

Figure 3.29. A box plot showing the average moisture content (% vol) in the bottom compartments of the two different beetle box treatments (wooden boxes with fertiliser added to the contents, wooden boxes without fertiliser added to the contents) at Bredon Hill averaged over data gathered on 10/08/2021 and 02/06/2021.

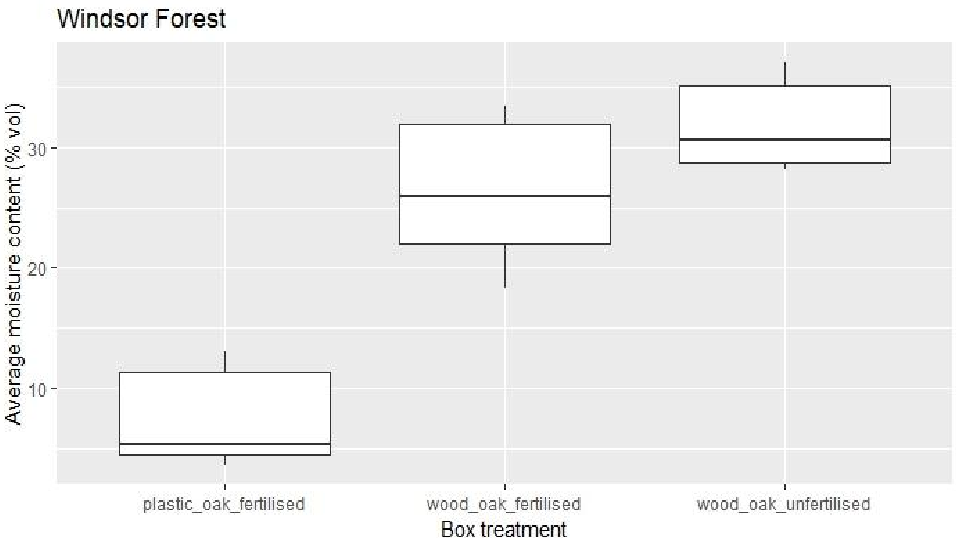


Figure 3.30. A box plot showing the average moisture content (% vol) in the bottom compartments of beetle boxes of three different treatments (plastic boxes with fertiliser added to the contents, wooden boxes with fertiliser added to the contents, wooden boxes without fertiliser added to the contents) at Windsor Forest averaged over data gathered on 17/08/2020 and 24/05/2021.

Comparison of moisture levels in beetle boxes to those in real basal tree hollows

A pairwise Wilcoxon signed rank test including average moisture data taken from real tree hollows and the bottom compartments of beetle boxes at Windsor Forest on 17/08/2020 showed a significant difference between groups ($X^2(3) = 12.6$, p = 0.006) (Figure 3.31). When the differences between moisture levels in specific beetle box treatments and real tree hollows were investigated, they were not found to be significant for wooden boxes without fertiliser (V = 1, p = 0.06) and wooden boxes with fertiliser (V = 6, p = 0.44) (Figure 3.31). However, moisture levels were found to be significantly lower in plastic boxes than in real tree hollows (V = 0, p = 0.03) (Figure 3.31).

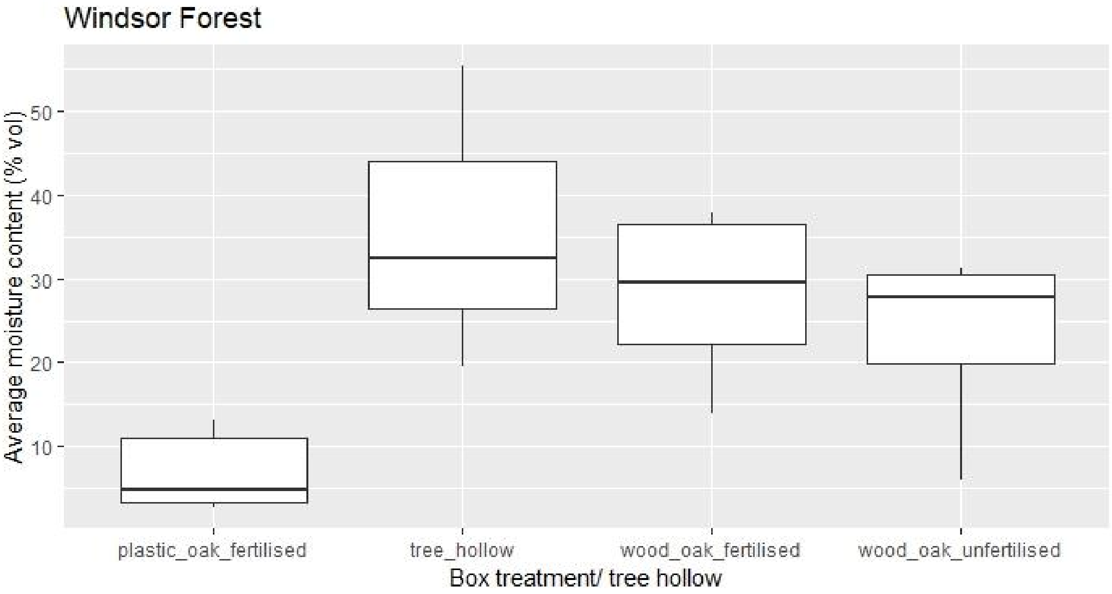


Figure 3.31. A box plot showing the average moisture content (% vol) in real tree hollows and in the bottom compartments of beetle boxes of three different treatments (plastic boxes with fertiliser added to the contents, wooden boxes with fertiliser added to the contents, wooden boxes without fertiliser added to the contents) at Windsor Forest from data gathered on 17/08/2020.

Differences in moisture levels in bottom box compartments of beetle boxes at different times of year

At Bredon hill, moisture levels significantly increased between the sampling session in late summer (10/08/2020) and in late spring (02/06/2021) in wooden boxes with added fertiliser (t(5)= -5.56, p = 0.003), and in wooden boxes without added fertiliser(t (5) = -3.63, p = 0.02) (Figure 3.32).

At Windsor Forest, A significant increase was found in moisture levels in the bottom compartments of wooden boxes without added fertiliser between sampling sessions in late spring (24/05/2021) and late summer (17/08/2020) (V = 21, p = 0.03) (Figure 3.33). In contrast, no significant differences were found between the average bottom compartment moisture levels recorded in late summer and late spring for plastic boxes with added fertiliser (V = 10, p = 1) and for wooden boxes with added fertiliser (V = 4, p = 0.22) at Windsor Forest (Figure 3.33).

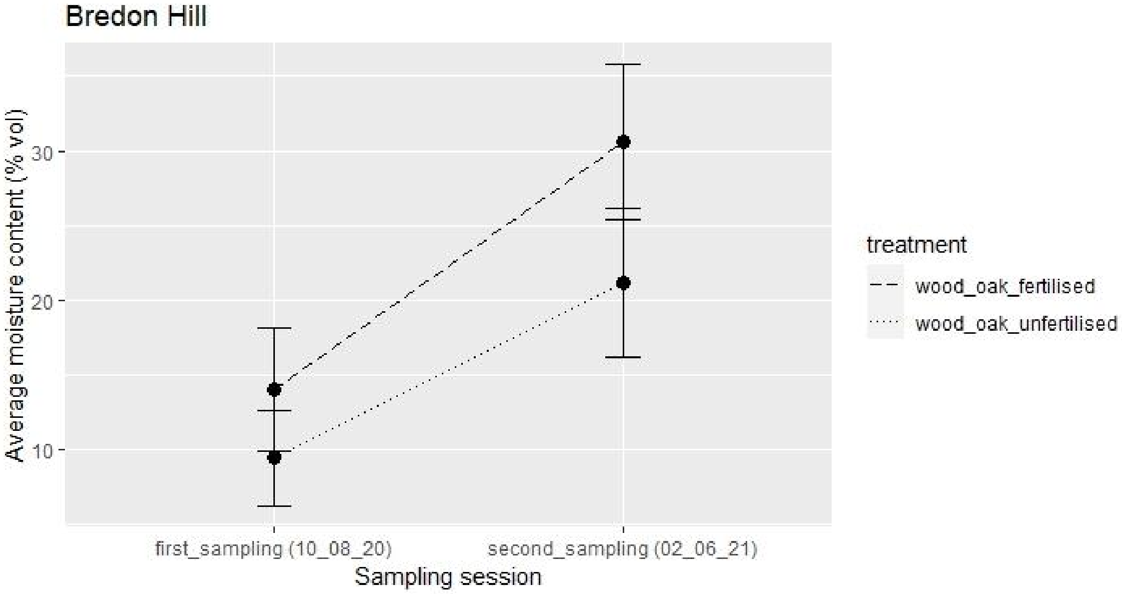


Figure 3.32. A dot plot showing the change in average moisture content (% vol) in the central cavity of different beetle box treatments at Bredon Hill between sampling sessions made on 10/08/2021 and 02/06/2021.

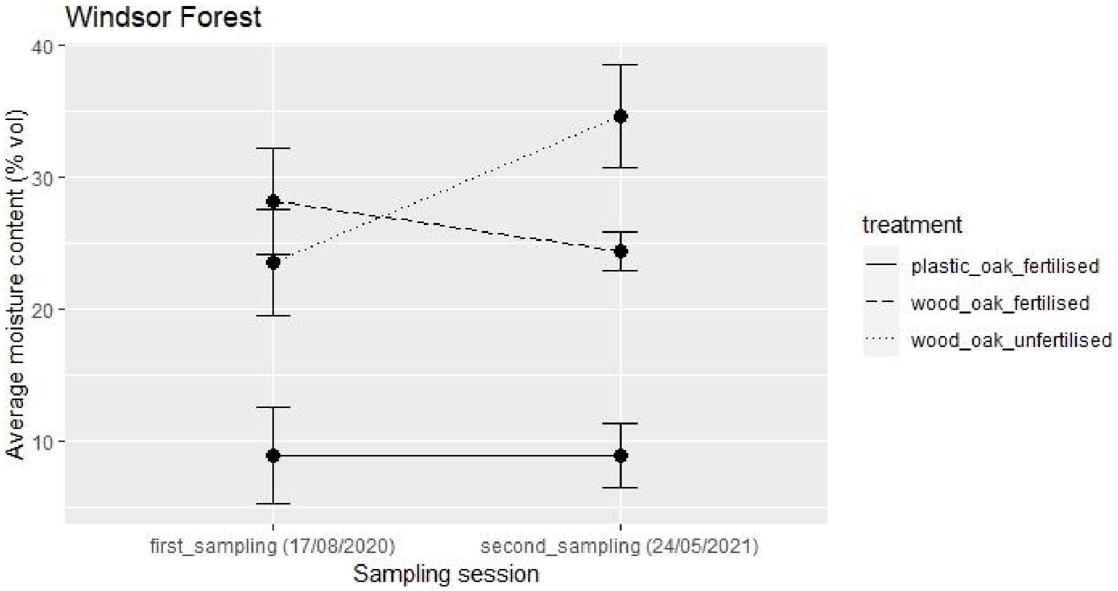


Figure 3.33. A dot plot showing the change in average moisture content (% vol) in the central cavity of different beetle box treatments at Windsor Forest between sampling sessions made on 17/08/2021 and 24/05/2021.

Differences in the average moisture content of the wood mould in the top and bottom compartments of different beetle box treatments

At Bredon Hill, moisture levels in the bottom compartment of wooden boxes without added fertiliser were significantly higher than moisture levels in the top compartment ($t(5) = -3.18$, p-value = 0.02) (Figure 3.34). No significant differences were found between the moisture levels in the top and bottom compartments of the wooden boxes with added fertiliser at Bredon Hill ($t(5) = -2.43$, p-value = 0.06) (Figure 3.34).

The average moisture levels in the bottom compartment (below the internal shelf) of plastic beetle boxes at Windsor Forest were found to be significantly higher than the moisture levels in the top compartment (above the internal shelf) ($t(5) = 8.36$, p-value = 0.0004) (Figure 3.35). In contrast, moisture levels were not found to be significantly different between the top and bottom compartments of the wooden boxes with added fertiliser ($V = 8$, $p = 0.69$), or the wooden boxes without added fertiliser ($V = 13$, $p = 0.69$) at Windsor Forest (Figure 3.35).

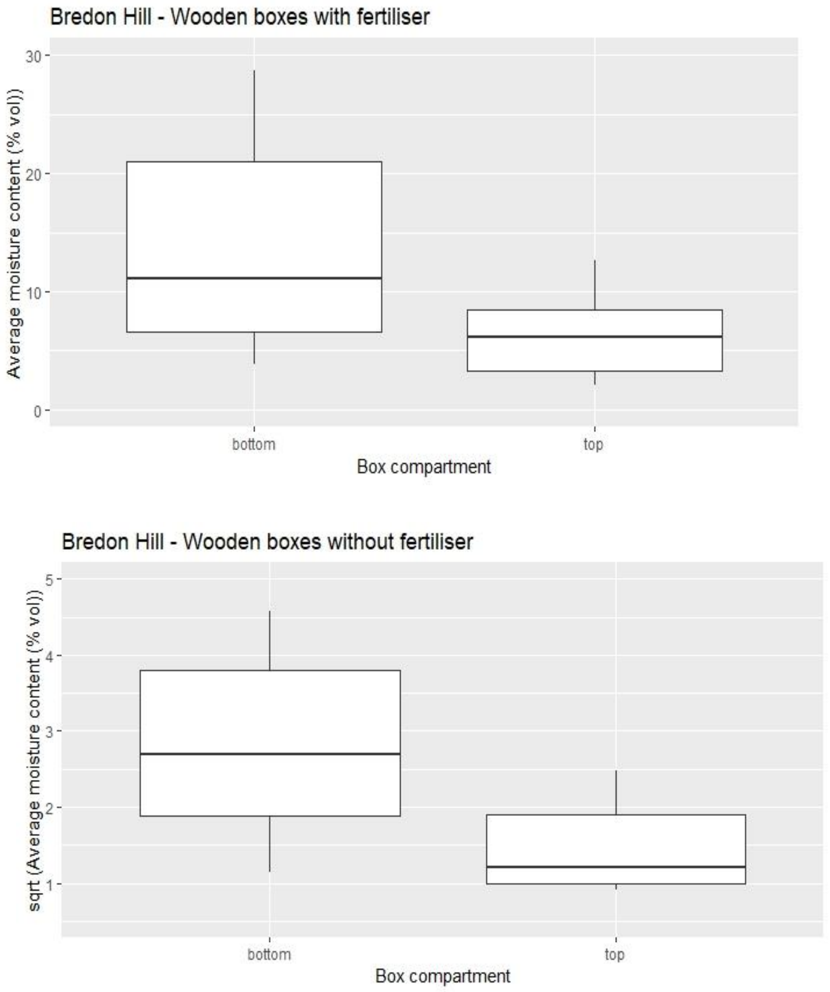


Figure 3.34. Boxplots showing the moisture levels in the top and bottom compartments of different beetle box treatments at Bredon Hill.

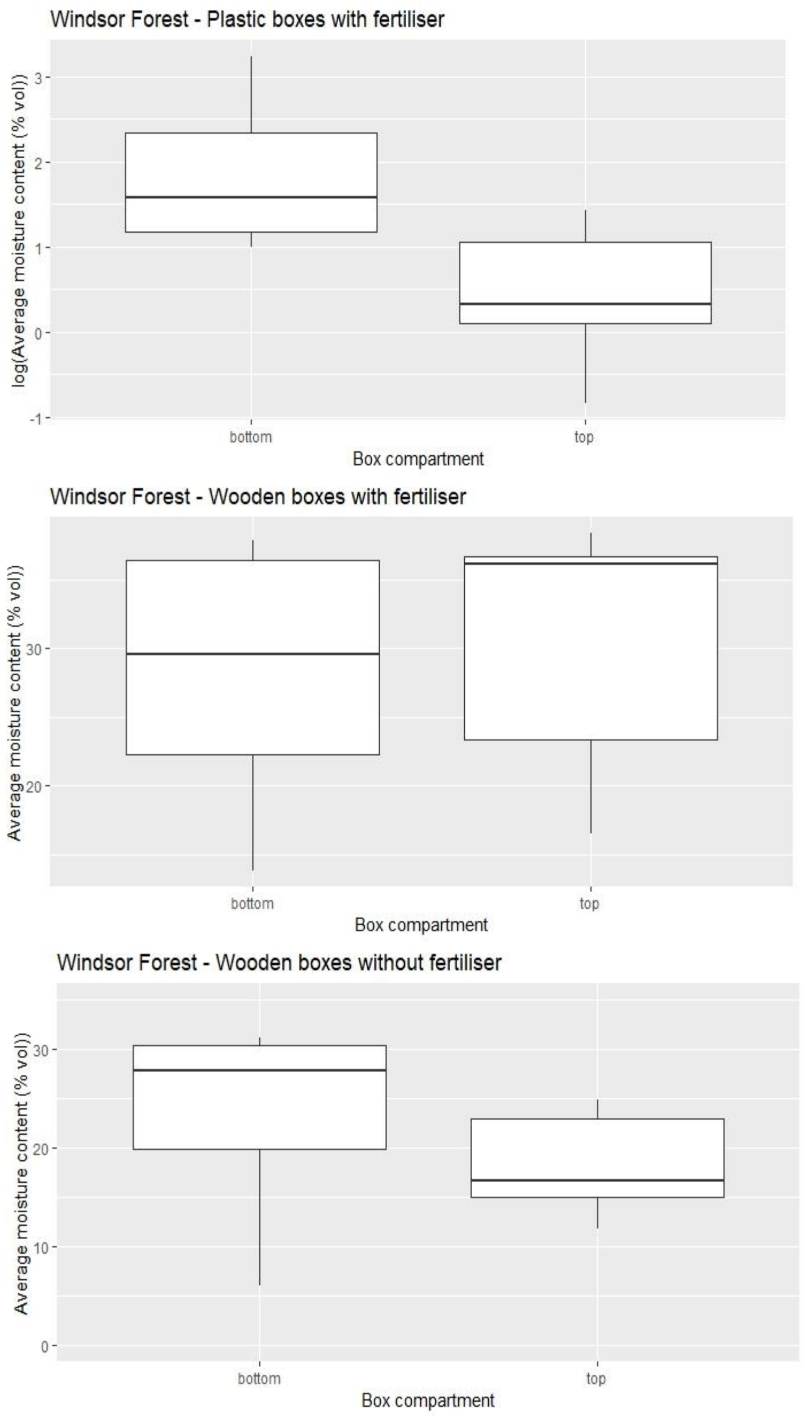


Figure 3.35. Boxplots showing the moisture levels in the top and bottom compartments of different beetle box treatments at Windsor Forest.

Canopy cover

No significant differences were found between the percentage canopy cover over the different box treatments at Windsor Forest (F(2)=0.58, p=0.57) or Bredon Hill (t(6.04)= -0.80, p-value = 0.46)

3.4. Discussion

Overall observations

A key aim of this research was to investigate the potential of ground level beetle boxes as a conservation tool to support saproxylic beetle species through periods of resource scarcity. The results from this study have shown that beetle boxes can provide habitat for saproxylic beetles, including rare and tree-hollow specialist species. Two of the species recorded from beetle boxes in this study, *Ptenidium turgidum* and *Stenichnus godarti*, are rarities that are known to live in the moist, crumbly wood mould inside broadleaved tree cavities (Alexander, 2002). As this was the intended habitat that the beetle boxes were designed to replicate, the presence of these beetles indicates that the beetle boxes were able to successfully recreate the conditions in tree hollows. This is consistent with evidence from previous studies investigating trunk-mounted beetle boxes, which also demonstrated the attractiveness of beetle boxes as a habitat for several tree-hollow specialist beetles (Jansson, Ranius, *et al*., 2009; Hilszczańsk *et al*., 2014; Carlsson *et al*., 2016).

Breeding of beetles inside beetle boxes

Incidences of large numbers of individuals of the same species occurring in the same box, as well as the presence of teneral individuals and beetle larvae provide evidence that saproxylic beetles were able to breed within the beetle boxes during the present study. This supports the findings of Hilszczański *et al*. (2014), who found that saproxylic beetle larvae were able to complete their lifecycle within beetle boxes. Many of the beetle larvae observed within the beetle boxes were small and difficult to identify. As a result, the investigation of beetle larvae present in beetle boxes in the present study was limited. However, some families and genera containing saproxylic species were identified among the immature beetles found. Future analysis of beetle box contents would benefit from a greater focus on the breeding activities of beetle species within them. If the boxes are found to be used by *L. violaceus* in the future, a study of the larval development of this species within boxes would be especially valuable.

Beetle boxes as habitat corridors

The weevil, *Acalles misellus* was found in a beetle box at Windsor Forest during the present study (Figure 3.36). Weevils in the *Acalles* genus are flightless and therefore limited in their ability to disperse over large areas (Buse, 2012). They are considered relict species of ancient woodland and are highly threatened by the loss and fragmentation of habitat patches (Buse, 2012). The presence of dispersal-limited beetles such as *A. misellus* within beetle boxes supports the idea that they may be used as habitat steppingstones to promote movement of restricted species into new habitat patches.

Figure 3.36. An image of the *Acalles misellus* specimen found in a Windsor Forest beetle box.

New rot-hole species interaction observations

The investigation of wood mould fauna in the present study found several species interacting with wood mould in a way that has not previously been highlighted in their habitat descriptions. Descriptions of the habitat of *Ptinella* species indicate that they reside largely under the close-fitting bark of dead trees (Alexander, 2002). Only *Ptinella aptera* is mentioned to inhabit general decaying wood in addition to bark habitats (Duff, 2012). The extent to which *Ptinella* species were found within the beetle box wood-mould substrates may demonstrate that tree hollows are of greater importance to this genus than previously considered.

Similarly, *Orthoperus aequalis* is listed as preferring the microhabitats of fungoid bark and bracket fungi (Duff, 2020). However, the fact that *O. aequalis* was the dominant species found within the beetle boxes shows that this species can thrive in a tree-hollow equivalent situation. The large numbers of specimens collected included several teneral individuals, indicating that *O. aequalis* was using the wood mould for breeding, thus reinforcing that rot-hole habitats promote the reproduction and persistence of *O. aequalis*. Examples such as these demonstrate that beetle boxes provide opportunities to gather valuable data on invertebrate habitat requirements.

Use of beetle boxes by the wider woodland fauna

Outside of the decaying wood mould niche, the beetle boxes were also observed to provide habitat for a range of non-target organisms. All types of beetle boxes were heavily used by *T. domestica*, which built webs inside both the upper and lower compartments of the boxes. Beetle boxes were used by *C. pudibunda* caterpillars as sheltered pupation sites, and one box was used by wasps for nesting. Such opportunistic use of boxes was not limited to invertebrates, with observations of a field mouse and a mouse food-store inside beetle boxes. These findings demonstrate that sheltered spaces are in high demand by various members of the woodland fauna, reinforcing the value of tree-hollow habitat in woodland ecosystems. It also shows that artificial hollow habitat provided by structures such as beetle boxes can benefit the wider woodland ecology in addition to specialist saproxylic and decay-associated invertebrates.

Limoniscus violaceus

A motivation for the present research was to investigate the ability of a new, partially buried beetle box design to mimic the basal tree hollow habitat of the endangered *L. violaceus* and thus provide this species with conservation support. No *L. violaceus* individuals were observed in the beetle boxes during the present study, meaning that the conclusions that can be drawn on the applicability of beetle boxes for *L. violaceus* are limited at this time. The larvae of *L. violaceus* require at least two years to develop (Whitehead, 2003). As a result, it is unsurprising that no adult *L. violaceus* were found within the box wood mould during the sampling of the present study, which took place after one year of box deployment. In addition to this, wood mould developed from sawdust in beetle boxes is increasingly inhabited by tree-hollow specialist species when it has been left to mature for longer lengths of time (Carlsson *et* *al*., 2016). To illustrate this, the observation of *L. violaceus* larvae in a metal bin and plastic bag filled with wood mould were made by Ted Green after the containers had been left in the field for approximately six years (Whitehead, 1998, 2003). Consequently, it is possible that the wood mould in the boxes of the present study has not yet reached a state of maturity at which it is suitable for *L. violaceus* inhabitation. For this reason, continued monitoring of beetle boxes for *L. violaceus* is advised, as discussed in the 'Recommendations for future research' section at the end of this chapter.

Overall average moisture levels recorded from tree hollows during late summer in 2020 were higher than the average moisture levels recorded for any of the beetle box treatments during the same recording sessions. This difference was found to be statistically significant for the plastic box treatment. High moisture content of wood mould is a characterising feature of optimal habitat for *L. violaceus* (Cuff, Müller, *et al*., 2021). Therefore, the moisture content of wood mould in beetle boxes (particularly plastic ones) may have limited the potential for them to be used as habitat by *L. violaceus.* The 'Recommendations for future research' section highlights how beetle boxes could be adapted to increase the amounts of moisture entering the wood mould to address this discrepancy for future trials.

It is possible that adult *L. violaceus* present in tree hollows or beetle boxes could have been missed due to the choice of sampling techniques used in the present study. Hand sorting and sieving of wood mould has previously proven to be a suitable method of finding *L. violaceus* (Henshall *et al*., 2015). However, previous studies using this method extracted a greater volume of wood mould (5-10 litres) than that taken in the present study (2 litres) (Henshall *et al*., 2015). Smaller volumes were taken during the present study to minimise disturbance to the tree hollow habitat, to avoid excessive emptying of the beetle boxes, and to ensure that sample sorting would be possible within limited study timescales. It is possible that the lower volumes of wood mould taken were not sufficient to encapsulate *L. violaceus* populations present. Future research targeted specifically towards *L. violaceus* could adapt surveying methods to maximise chances of finding any individuals of this species present in beetle boxes, as discussed in the 'Recommendations for future research' section.

The ability of beetle boxes to replicate basal tree hollows

Other than *L. violaceus*, little is known about the invertebrate fauna that preferentially inhabits tree hollows at the base of trees as opposed to hollows higher up in tree trunks and branches. On surveying basal hollows for *L. violaceus*, Gouix & Brustel (2012) identified a range of notable beetle species from these habitats. However more research is needed to understand how the basal nature of hollows impacts their attractiveness to different beetle species. Some tree hollow-specialist beetle species, such as *Ampedus cardinalis, Elater ferrugineus, Prionychus ater* and *Liocola marmorata*, have been found at higher abundances in tree hollows that are situated higher up in the tree (Ranius, 2002). However, tree hollow height above ground has been found to negatively correlate with the richness of saproxylic species found within them (Schauer *et al*., 2018; Henneberg *et al*., 2021). From these findings, it is possible that boxes placed close to the ground such as those investigated in the present study may have overall benefits for saproxylic diversity, whilst carrying the trade-off of being less suitable for certain species. This is an area that would benefit from further study, as mentioned in the 'Recommendations for future research' section.

The present study sought to broaden understanding of basal hollow beetle communities by investigating samples of species present in them. Through this, this study aimed to construct comparisons of the beetle communities inhabiting ground level beetle boxes to those in the target basal tree hollow habitat. Of the beetles found in wood mould samples collected from real tree hollows, all the saproxylic and woodland-associated species were also found in the beetle boxes. The only species that was found in tree hollows and not in beetle boxes was the non-deadwood-associated Staphylinid, *Rugilus rufipes*. The high level to which the identified tree hollow fauna was represented in beetle boxes further supported the finding that beetle boxes can develop similar habitats to those found in hollows.

A single elytron of the nationally scarce, saproxylic Zopherid beetle, *Synchita variegata* was found in a tree hollow but was not represented in the boxes. This is unsurprising, as *S. variegata* is associated with fungal growth on recently dead *Fagus* wood (Alexander, 2002). As the target habitat of the beetle boxes was extensively decayed wood mould, they are not suitable for *S. variegata*. In addition, species that colonise recently dead trees tend to be more specialised, so it is unlikely that *S. variegata* would be attracted to the oak-based wood mould in the majority of the beetle boxes, even if it were at an appropriate state of decay.

Several beetle species occurred at greater average abundances in beetle boxes than in tree hollows. This may be a result of the differing stages of decay in beetle boxes in comparison to tree hollows. The first year of leaf litter decay is characterised by a rapid breakdown of cellulose (Voříšková & Baldrian, 2013). Fungal biomass also increases during the first 21 months of leaf litter decay (Osono & Takeda 2001). As the material in the beetle boxes was still in an early stage of decay at the time of invertebrate sampling, it is likely that greater decay rates in the beetle box wood provided more available resources to inhabiting beetles than that found in tree hollows. A longer-term study incorporating annual sampling to assess the beetle and fungal abundance changes and the proportions of beetles in different guilds could allow greater insight into to the reasons behind these trends.

The present study found a limited assemblage of beetle species in the tree hollows compared to other studies of similar habitats (Gouix *et al*., 2009; Gouix & Brustel, 2012). Species found within beetle boxes that were also found through emergence trapping of tree hollows by Gouix *et al* (2009) included *Euplectus karstenii*, *Clambus punctulum*, *Quedius cruentus*, and *Othius punctulatus*. Most notable from these are *E. karstenii*, which lives in old, decaying wood, and *Clambus punctulum*, which feeds upon slime moulds in decaying material (Alexander, 2002; Schmidl & Bußler, 2004). Overall, these species constitute a very small proportion of the beetle fauna collected by Gouix *et al* (2009). The short time given by the present study for wood mould to mature and for beetles to colonise the boxes is likely partially responsible for this. Additionally, differences in sampling methods used by Gouix *et al* (2009) and the present study may have contributed to this finding.

Chrysopilus laetus

Although the majority of beetle species found in real tree hollows were also represented in beetle boxes in the present study, one notable difference was found in the Diptera inhabitants. Sampling of wood mould from real tree basal hollows yielded several adult and larval specimens of *Chrysopilus laetus*. This is a specialist species of ancient tree hollows containing rotten heart wood, having been recorded from both Beech (*Fagus* sp.) and Poplar (*Populus* sp.) trees (Stubbs & Drake, 2014; Drake, 2017). Windsor Forest was historically the only site in England in which this fly species was found, although it has experienced recent range expansions into various counties across the country (Drake, 2017). Prior to 2007, *C. laetus* was consistently categorised as endangered (RDB1) in Great Britain; however, due to its expansion, it currently holds conservation status of Nationally Scarce in Great Britain, with an IUCN status of Near Threatened (Drake, 2017).

Despite beetle boxes being located near both trees in which *C. laetus* was found, no observations of *C. laetus* were made from them. This may indicate that the wood mould in the boxes does not yet possess qualities required for the breeding of *C. laetus*, or that not enough time has passed to allow *C. laetus* populations to become established within the boxes. Additionally, Diptera generally require wetter substrates for their larval development than many beetles (Ulyshen, 2018). Therefore, it is also possible that lower average moisture levels of the wood mould in the plastic beetle boxes than in real tree hollows contributed to the lack of observations of this species within this box treatment. Should beetle boxes at Windsor Forest be subject to future monitoring surveys, *C. laetus* is a key species that could be monitored for as a measure of success in replicating basal tree hollow habitat.

Haplophthalmus danicus

Another notable difference between beetle boxes and tree hollows, was that the woodlouse, *Haplophthalmus danicus*, was found in considerably higher abundances in tree hollows than in beetle boxes. The typical habitat of *H. danicus* is damp deadwood in woodlands, but it is also found in a range of other habitats that are characterised by particularly high moisture levels, such as fens and river flood plains (Gregory, 2009). As average moisture levels recorded from real tree hollows was higher than that recorded in the beetle box treatments, with a statistically significant difference found for the plastic boxes, it is likely that the preference of *H. danicus* for particularly moist habitats is the reason that it was more abundant in real tree hollows than in beetle boxes. This further highlights the importance of considering wood mould moisture content in accurately replicating tree hollow habitats.

Comparison to other beetle box studies

Species found in the present beetle box study that were also found in beetle boxes investigated by Carlsson, *et al*. (2016) included, *Euplectus karstenii, Quedius cruentus* and *Stenichnus godarti*. Similar to the comparison made with tree hollow emergence trapping, this represents only a small proportion of the species found by Carlsson, *et al*. (2016). This is presumed to also result from differing amounts of time that the boxes were left to mature and differing sampling techniques used by Carlsson, *et al*. (2016) and the present study.

A study of tree-mounted beetle boxes in Wytham Woods, sampled after 6 months of exposure using a temperature/humidity gradient extraction trap found 78 adult beetle specimens of 13 species, although differences in the volume of wood mould sampled mean that these numbers are not comparable with the present study (Elbourne, 1970). The only beetle species that the beetle boxes in the present study and those investigated by Elbourne (1970) had in common is *Ptinella aptera*.

The body-size of beetles inhabiting beetle boxes

The beetle fauna retrieved from beetle boxes during this study consisted largely of species with small body-sizes (under 5mm). This is consistent with the findings of Elbourn (1970) who sampled the wood mould inside their box structures after they had been left in the field (Wytham woods, UK) for six months using extraction trapping. In contrast, Jansson, Ranius, *et al*. (2009) and Carlsson, *et al*. (2016) found a higher proportion of saproxylic species with larger body sizes in beetle boxes in Sweden. Jansson, Ranius, *et al*. (2009) sampled the boxes after four years, whilst Carlsson, *et al*. (2016) sampled after a minimum of nine years, with both studies using pitfall trapping and emergence trapping for invertebrate extraction. This suggests that the lack of larger beetle species within beetle boxes in the present study could have been a result of the chosen sampling method or the shorter amount of time that boxes had been left in the field. The presence of larvae of beetle genera containing beetles with larger body sizes such as *Melanotus* in the beetle boxes supports the hypothesis that larger beetle species will be represented in beetle boxes to a greater extent over time.

The rot types occurring in beetle boxes

Previous beetle box studies have noted an absence of red rot associated beetle species among the colonisers (Jansson, Ranius, *et al*., 2009). The likely explanation for this in the context of the decay processes of natural tree hollows was discussed in the introduction to this chapter. Due to the anticipated lack of red rot in beetle boxes, the finding of three *Melanotus* larvae in wooden beetle boxes at Windsor Forest was unexpected, as saproxylic members of this genus preferentially develop in red-rotten wood (Alexander, 2002). Similarly, the presence of an *Ampedus* sp. larva in a beetle box at Bredon Hill and an individual of *Ampedus elongatulus* pupating on the rim of a beetle box at Windsor Forest were surprising, as red-rotten wood is presumed to be required for the larvae of several *Ampedus* species, including A*. elongatulus* to develop (Alexander, 2002). These findings suggest that red-rotting fungi are not a strict requirement for the completion of the lifecycles of *Melanotus* and *Ampedus*. Previously observed links of these species to red rot may be incidental, as result of their preferences for the conditions in tree hollows that foster red rot, rather than the red rotten wood itself. Alternatively, the *Melanotus* and *Ampedus* specimens observed in the boxes during this study may have made use of nearby sources of red rot in surrounding decaying trees before moving to the beetle boxes in which they were found. Further investigation into the impact of particular rot processes on saproxylic beetle development is needed to fully understand the relationship of tree hollow fauna to red rotting fungi.

Effects of experimental manipulation of boxes on beetle communities

Effects of different box construction materials

A key aim of the present study was to investigate whether invertebrates interact with beetle boxes made of plastic in different ways to those made of wood. This is the first study of its kind to form a direct comparison of different beetle box construction materials. A driver for this aspect of the research is optimising the longevity of beetle boxes, so that they can provide a more consistent habitat. This is important as real tree hollows can persist in the landscape for hundreds of years (Woodland Trust, 2021a). As a result, the invertebrate fauna that inhabit hollows are adapted to rely on this consistency through strategic breeding strategies and low dispersal tendencies (Ranius & Hedin, 2001).

The influence of construction material on the moisture content of beetle boxes

The average moisture levels in the bottom compartments were lower in plastic boxes than in wooden boxes. This is unsurprising considering the impermeability of plastic to water and the fact that plastic boxes do not develop the same gaps and fissures in their walls through environment-induced warping. The plastic boxes did have holes in their lids to encourage the maintenance of a moist internal environment, however the thin nature of the plastic meant that channels to encourage water to enter these holes were could not be crated in the same way as for the wooden boxes, further limiting the tendency for water to enter the plastic boxes. Low moisture levels are linked to slower wood decay (Crockatt & Bebber, 2014). Therefore, it is likely that the lower moisture levels in plastic boxes caused the wood mould inside them to decay at a lower rate than for that in wooden boxes.

The average moisture levels in the wood mould of plastic boxes were found to be significantly lower than the average moisture levels recorded from tree hollows. Higher moisture levels have been linked to *L. violaceus* inhabitants of tree hollows (Cuff, Müller, *et al*., 2021). Therefore, plastic boxes currently have lower likelihood of providing suitable *L. violaceus* habitat than the wooden boxes. This may be addressed by enhancing drainage features future designs of plastic boxes trialled for *L. violaceus* conservation, as highlighted in the ‘Recommendations for future research’ section of this chapter.

The influence of plastic construction material on beetle communities inhabiting beetle boxes

No significant differences were found in any of the beetle categories between beetle diversity or abundance in plastic boxes with added fertiliser compared to wooden beetle boxes with added fertiliser. This suggests that construction material was not as important as the composition of the wood mould contents in the overall biodiversity of beetle inhabitants. It also suggests that the lower moisture levels observed in plastic boxes in comparison to wooden boxes does not have a detrimental effect on the attractiveness of the internal wood mould to a range of colonising beetles.

Despite the lack of general trends in the different groups of beetles, there were some beetle species that seemed to exhibit preferences for plastic boxes. These included *Achrotrichis insularis*, *Cryptophagus distinuendus*, *Dienerella clathrata* which were on average more abundant in plastic boxes than in wooden boxes. In addition to this, *Ptenidium turgidum*, *Ptinella errabunda*, *Oligota apicata* and *Dienerella vincenti* were only recorded from plastic boxes. As previously mentioned, *P. turgidum* is a species with particular association to tree-hollow wood mould (Alexander, 2002). Reflecting this, *P. turgidum* was one of the species that the present study also retrieved from the real tree hollows at Windsor Forest. Therefore, its presence in plastic boxes suggests that the use of a less natural construction material does not prevent the formation of the target tree-hollow habitat for less high-moisture-dependant species.

Figure 3.37. Images of *Dienerella clathrata* and *vincenti* specimens found in wood mould of beetle boxes. The lower images illustrate the characteristic differences in elytral apices between these two species.

Several of the differences in beetle communities between plastic and wooden boxes are likely to be a result of the moisture differences between the box types. Cateau et al., (2016) found that *Dienerella clathrata* was more abundant in samples collected after extensive periods of fine weather, inferring that this species is more readily collected from drier substrates. As a result, it is unsurprising that *Dienerella* species preferred the plastic boxes, as these were found to contain significantly dryer wood mould than other box types trialled in the present study (Figure 3.37). In contrast, *Acalles misellus* was found to prefer more humid conditions, being encountered specifically when sampling was preceded by extensive rainfall (Cateau et al., 2016). In agreement with this, *A. misellus* was only encountered in a wooden box during the present study, which had significantly higher moisture levels than the plastic boxes. The differences in species composition between plastic and wooden boxes suggests that variation in wood-mould moisture inside beetle boxes might allow them to cater to a wider range of species needs and thus promote increased beetle diversity inhabiting boxes. This presents a trade-off between catering to high diversity, or tailoring boxes to moisture-associated species such as *L. violaceus*.

Beetles inhabiting crevices in the boxes

One difference between beetle boxes made of plastic and wood was that the external structure of wooden boxes seemed to provide additional niches that were not present in plastic boxes. The finding of several species of beetle and other insects in the crevice between the box rim and the lid of the wooden boxes indicates that these incidental areas of adpressed wood provided an additional habitat resource. This niche was used as a protected pupal development site for an individual of *Ampedus elongatulus*.

This finding may have implications for the further improvement of the box design for the breeding of other rare elaterids including *L. violaceus*. Gioux *et al*. (2012) notes that *L. violaceou*s females lay their eggs into fissures in the tree cavity wall. After hatching, the larvae then seek out moist, compacted clumps of wood mould for pupation (Gioux *et al*.,2012). Both of these conditions are replicated in the compacted sawdust on the box rim where the *Ampedus* was found. With this in mind, a potential new feature for the beetle boxes could be to screw small planks of wood into the interior surface of beetle boxes with some compacted sawdust trapped beneath, artificially providing potential new pupation niches.

It had previously been assumed that the aforementioned breeding niche would naturally be formed through general compaction of the wood mould and, in the wooden boxes through the incidental inconsistencies in the wood grain. Since Ted Green MBE (a founder of the Ancient Tree Forum) has previously found the larvae of *L. violaceus* inside a plastic bin filled with wood mould, it was presumed that cavity wall texture may not be essential for this breeding. However, with the above evidence of the use of sawdust compacted between two pieces of wood by saproxylic beetle species indicates that a wooden construction material may provide additional benefits that are not present in plastic boxes.

Observations of other invertebrate groups in plastic and wooden beetle boxes

There was a notable absence of Oligochaeta and Diplopoda in the samples collected from plastic boxes. This is likely due to the significantly drier conditions found in the plastic boxes in comparison to wooden boxes. Worms are key ecosystem engineers of decaying soil-like substrates (Desie *et al*., 2020). Additionally, the removal of key macrofauna including millipedes has been shown to significantly decrease the decomposition rate of wood-mould within beetle boxes (Wetherbee *et al*., 2021). Therefore, the low occurrence of these groups in plastic boxes is likely to have impeded the decomposition processes of the wood mould within them. The lack of worms in the plastic box wood mould may have resulted in the conditions in plastic boxes being more like that of an aerial tree hollow, which are not directly connected to the soil and are therefore likely to exhibit lower representation of soil fauna. This supports the idea that, in order for plastic boxes to more effectively replicate the specific conditions in basal tree hollows, it would be beneficial to add additional features to promote increased moisture in the boxes and encourage and increased presence of soil macrofauna.

Effects of the addition of fertiliser to box contents

The influence of fertiliser addition on the moisture content of beetle boxes

At Windsor Forest, only boxes without added fertiliser showed a significant change in moisture level in the wood mould of the main box compartment over time. This lack of moisture stability in wood mould without fertiliser may be a result to lower levels of mycorrhizal fungi in the wood mould in these boxes. Mycorrhizal fungal growth changes the structure and improves water retention of soils (Augé *et al*., 2001; Wu *et al*., 2008). Fungal activity has been found to be promoted by increased nitrogen levels (Bebber *et al*., 2011). Therefore, lower levels of fungal growth in boxes without added nitrogen-rich fertiliser component may have caused the wood mould in these boxes to be less able to retain moisture.

The influence of fertiliser addition on beetle communities in beetle boxes

The results of this study showed that the addition of poultry manure fertiliser to beetle box contents is positively linked to the abundances of woodland-associated species found in the resultant wood mould after one year of box deployment. For the boxes at Windsor Forest, this trend was statistically significant, with greater abundances of beetle specimens from the woodland-associated category being found in wooden boxes with oak sawdust and added fertiliser than in those without the fertiliser component in their wood mould. This trend was also evident at Bredon Hill, as all the woodland-associated beetles collected from beetle box samples at this site were found in boxes with fertiliser added to their contents. Despite this clear difference, the results from this group did not achieve statistical significance. This is likely a result of the low replication of the experiment causing a single box with added fertiliser in which no woodland associated species were found to have a strong influence upon the paired analysis of Bredon Hill data. Despite the lack of statistical significance, evidence from the data convincingly supports the positive link between woodland associated beetle abundance and the addition of fertiliser to wood mould.

The present study did not quantify the effects of adding poultry manure to wood mould on the chemical composition of the resultant wood mould as chemical analysis was outside the scope of the study. However, the addition of fertiliser was expected to increase the nitrogen content of the wood mould (Hara, 2001). This reflects conditions found in natural tree hollows (Kelner–Pillault, 1974; Jönsson *et al*., 2004). Nitrogen is thought to be a limiting factor of wood-decay, as the enzymes responsible for this process are composed of a high proportion of nitrogen (Sterner & Elser, 2002; Cornwell *et al*., 2009). To support this, higher nitrogen concentrations in angiosperm wood is linked to faster wood decomposition in forests across the world (Weedon *et al*., 2009). Further, the experimental addition of nitrogen increases the rate of beech wood decay by fungi (Bebber *et al*., 2011). In a similar way, the fungal decomposition of leaf litter is also thought to be aided through increased levels of nitrogen (Purahong, *et al*., 2016). As a result of this, it is likely that the addition of nitrogen to wood mould in beetle boxes increased the decomposition rate of the sawdust and leaf litter components through the activity of fungi.

In addition to this, manure application to soils has been found to significantly increase the phospholipid-derived fatty acid (PLFA) content of soils, indicating that it positively influences overall microbial biomass (Lazcano *et al*., 2013). This was found to be a result of increases in bacterial communities (Lazcano *et al*., 2013). Bacteria play a role in wood decomposition, for example through acting to increase the permeability of wood (Greaves, 1971; Clausen, 1996). Complex communities of bacteria also contribute to the decomposition of leaf litter (Purahong *et al*, 2016). As a result, it is possible that higher nitrogen levels in the wood mould of beetle boxes achieved through the addition of poultry fertiliser may have influenced the rate of bacterial decomposition in addition to that of fungi.

Increased rates of wood and leaf litter decomposition resulting from the addition of poultry fertiliser to beetle box wood mould is a probable factor in the higher abundances of woodland associated beetles observed in these boxes during the present study. The majority of woodland-associated species identified in the present study were classified as saprophagous, meaning that they feed upon decaying organic matter and would therefore benefit from its increased rate of progression. Benefits of high nitrogen levels in tree cavities for saprophagous invertebrates has previously been observed in tree cavities, as the larval growth of *Myathropa floraea* is positively influenced by the presence of nutrient rich frass of Cetoniine beetles (Sánchez-Galván *et al*., 2014)

When saproxylic and woodland-associated species were combined in analysis to test the responses of all species with any behavioural link to decaying wood to added fertiliser in wood mould, average species abundances continued to show significant differences between wooden boxes with fertiliser and wooden boxes without at Windsor Forest. An additional significant trend emerged for the data at Bredon Hill, showing that the species diversity of saproxylic and woodland-associated beetles was significantly higher in wooden boxes with fertiliser than wooden boxes without fertiliser. Saproxylic beetles found in the beetle boxes included several fungivorous and xylophagous species that are likely to also benefit from the aforementioned presumed increases in fungal presence and decay rates associated with higher nitrogen levels.

Despite overall trends, it is interesting to note that the rare saproxylic beetle species, *Stenichnus godarti,* which has a particular association to tree-hollow habitats, was only recorded in a wooden box that did not have fertiliser added to its contents. This suggests that an added fertiliser component is not a requirement for the boxes to provide suitable conditions for rare specialist beetles. However, as this observation is based on a single observation, further investigation is required to understand how rare, tree hollow-associated species respond to nitrogen levels.

In contrast to the trends found in the present study, Jansson, Ranius, *et al*. (2009) did not find poultry manure to produce any significant effect on the saproxylic beetle communities inhabiting beetle boxes. This may have been a result of differing volumes of manure used, with Jansson, Ranius, *et al*. (2009) adding one litre of poultry manure to beetle boxes, whilst the present study added a total of four litres of poultry manure. Also, the present study used poultry manure in pelletised form, whereas that used by Jansson, Ranius, *et al.* (2009) was in a raw form (Jansson 2018, pers. comm.). Pelletised manure contains nutrients in a more concentrated form and releases these nutrients into soil at a slower rate than unprocessed manure (Hara, 2001). This is likely to have resulted in a more consistent addition of nitrogen to the wood mould substrate over a longer period of time in the beetle boxes of the present study in comparison to those studied by Jansson, Ranius, *et al.* (2009).

Although Jansson, Ranius, *et al*. (2009) found no effects of manure on wood mould beetle communities, they did find that the addition of poultry carrion was beneficial for overall saproxylic species, whilst boxes containing high protein lucerne flour and oat flakes contained higher numbers of red listed species (Jansson, Ranius, *et al*., 2009). However, whilst these differences were evident after four years, content-associated trends were no longer significant in subsequent sampling after ten years of box deployment (Carlsson *et al*., 2016). This suggests that, without continuous additions of the nutrient-rich ingredients the wood mould, the benefits deplete over time. Despite this lack of long-term benefit from added nutrients, beetle box wood mould was found to contain higher numbers of hollow-specialist beetle species after longer periods of time in the field (Carlsson *et al*., 2016). This may mean that, whilst added nutrient components can initiate an initial boost in decay-related beetle communities, this becomes less important over time as natural tree-hollow dynamics (including animal defecation and death) progress within the boxes.

The influence of fertiliser addition on other invertebrate groups

Similar average numbers of Oligochaeta and Diplopoda specimens were found in the wooden boxes with wood mould containing oak sawdust with and without additional fertiliser in their contents. Both groups play important roles in the decomposition of woody substrates (Hendrix, 1996; Wetherbee *et al*., 2022). Therefore, it is considered unlikely that the addition of fertiliser greatly influences the aspects of decay driven by microorganism activity.

Combined effects of beetle box construction materials and fertiliser addition

An unexpected trend found in the data was that non-deadwood associated beetles had significantly higher species richness and average abundance in wooden beetle boxes without added fertiliser than in plastic boxes with fertiliser at Windsor Forest. As this group did not contain many saprophagous or fungivorous species it is likely that the trends within this group were driven by factors other than fungal growth. It is likely that, without the influence of box content, the moisture level in the boxes was a driving factor for the presence of these species. Wooden boxes without fertiliser were also found to contain significantly more moisture than plastic boxes (Figure 3.26). Staphylinidae were the most diverse beetle family among non-deadwood associated group. The abundance and diversity of Staphylinidae is positively associated with higher substrate moisture levels (Nasir *et al*., 2012; Irmler & Lipkow, 2018). It has been suggested that this is a result of their smaller elytra providing a lower resilience to desiccation than in other beetle groups with full elytra where a large sub-elytral space buffers moisture loss (Chown *et* al., 2011; Dolson *et al*., 2021). It is also thought that higher substrate moisture levels provide greater protection against the desiccation of Staphylinid eggs (Nasir *et al*., 2012).

Because of this, it is likely that Staphylinidae avoided the dryer conditions in the wood mould of plastic boxes.

Influence of sawdust species on beetle box colonisation

This is the first study to investigate the impacts of using sawdust from different tree species in wood mould on inhabiting invertebrate communities. Specifically, it investigated whether using sawdust from the tree species with the most dominant tree-hollow presence on site enhanced the value of beetle boxes installed there for the local deadwood fauna.

The influence of sawdust species on the moisture content of beetle boxes

Due to the lower replication of the box treatment containing beech sawdust, statistical analysis was deemed not to be appropriate in comparing the moisture levels within them to those of the other box treatments. The average percentage volume of moisture in the bottom compartments of the boxes containing beech were slightly lower than in the wooden box treatments at Windsor Forest in which wood mould contained oak sawdust. The overall average moisture recorded from the top compartment of beech-containing beetle boxes was higher than that found in wooden boxes with oak sawdust and without fertiliser, but it was lower than that in wooden boxes containing oak sawdust and fertiliser at Windsor Forest. The moisture in wood mould containing beech sawdust may have been influenced by the decay process and fungal content of this wood type. The wood of *Fagus* trees has a higher rate of decay than that of *Quercus* (Kahl *et al*., 2017; Bari *et al*., 2020). The lower resistance of *Fagus* wood to fungal activity is a contributing factor to this (Bari *et al*., 2020). Higher resultant fungal growth in *Fagus*-based wood mould may contribute to higher moisture retention (Augé *et al*., 2001). However, as the average moisture levels for this box treatment were calculated from only two boxes, it is likely that the levels of rainfall experienced at the locations of the boxes had a strong influence on the resultant values. Further investigations into fungal colonisation of wood mould incorporating different species of wood could further elucidate their role in the moisture dynamics occurring within.

The influence of fertiliser addition on the beetle communities inhabiting beetle boxes

The majority of beetle species that were found in the beetle boxes containing *Fagus* sawdust were also found in other box types that contained *Quercus* sawdust during the study. These included *Ptinella aptera*, *Orthoperus aequalis*, *Euophryum confine*, *Acrotrichis insularis*, *Clambus punctulum* and *Othius subuliformis*. This supports the hypothesis that beetle communities that use extensively decayed wood as their habitat tend to be generalists between different tree species (Stokland *et al*., 2012).

Despite the general similarity of beetle species occurring in *Fagus*- and *Quercus*-based sawdust, one notable difference was observed. The fourth most common beetle species found during this study was *Ptinella simsoni*, of which 44 specimens were found. All these specimens were collected from a single wooden box containing beech sawdust and added fertiliser. As *P. simsoni* is believed to be fungivorous, its presence only in a box containing *Fagus* sawdust may be explained by differences in fungal species present in *Fagus*- and *Quercus*- based wood mould. Saprotrophic fungal communities have been found to differ between deadwood of these two tree species, supporting this theory (Purahong *et al*., 2018). Alternatively, it is possible that the box within which *P. simsoni* was found was located in an area of forest with particularly strong source populations of this species, causing the high level of colonisation observed. Further investigation of the distributions of *P. simsoni* in Windsor Forest and its attraction to different fungal species would be required to better understand this finding.

Little is known about the ecology of *P. simsoni* and this is reflected in inconsistencies in the literature. Duff (2012) lists decaying grass heaps as the preferred habitat of *P. simsoni* and it is not listed as saproxylic by Alexander (2002). However, the Pantheon system produced a habitat description of heart-rot in hollow tree cavities for this species (Webb *et al*., 2018). These inconsistencies demonstrate that there is still much to learn about the habitat requirements of saproxylic species, particularly those that are infrequently found or belong to lesser studied families such as the Ptiliidae.

Comparison of species found in beetle boxes at different sites

The composition of beetle species inhabiting the same box types appeared to vary between the two experimental sites. At Bredon Hill, the clearly dominant species found in wooden boxes with fertiliser was *Orthoperus aequalis.* Despite this species also being present a Windsor Forest, it did not inhabit the wooden boxes with fertiliser to the same extent. This may have been because *O. aequalis* preferentially colonised the plastic boxes in the grouped experiment at Windsor Forest, being the fifth most abundant species found in this box type. It may also have performed well at Bredon Hill due to a preference for the more open, pasture landscape in which the beetle boxes at this site were positioned.

Similarly, the most abundant beetle species in wooden boxes with fertiliser at Windsor Forest was *Clambus punctulum*, which occurred in the same box type at Bredon Hill to a lesser extent. This species is known to feed upon slime moulds (Alexander, 2002). Slime moulds exhibit photophobic behaviours to avoid UV radiation, heat and aridity that may result in their dehydration (Latty & Beekman, 2010; Smith-Ferguson & Beekman, 2020). The cooler, more shaded conditions found in the enclosed beech woodland at Windsor Forest may have provided a more hospitable matrix to allow the colonisation of the boxes by slime moulds in comparison to the open, exposed Bredon Hill.

Study limitations

It is possible that some trends in beetle diversity and average species abundance were not identified as significant due to the low level of replication of the present study. For example, the present study did not find any significant influence of box treatment on the diversity and average abundance of saproxylic species when analysed in isolation from woodland associated species. However, visual inspection of graphs for saproxylic species indicate potential positive links of diversity average abundance to plastic construction and fertiliser addition to wood mould, which may have proven significant under a higher level of replication. The funding, time, and workforce available for this work were the key limiting factors that prevented the incorporation of a greater number of box replicates.

Another limiting factor of the current research was that field conditions in the woodlands cannot be controlled. This meant that there was a possibility that the invertebrate inhabitancy of the boxes was influenced by factors outside of the independent variables controlled by researchers. For example, the control group of wooden boxes without fertiliser added to their contents may have accumulated additional nitrogen during the study through other means, such as the defecation of small mammals inside the boxes. However, any affects on box nitrogen through processes such as this are deemed unlikely to have considerably influenced the results of this study, as the initial addition of fertiliser to the wood mould in the respective beetle box treatments was large enough that it would take considerable time for such a level of nitrogen to accumulate through natural means. It is also important that beetle boxes are trialled under such uncontrolled natural conditions, as these are the environments in which they are intended to be employed as conservation measures. The observations made under these conditions are therefore most informative for real-world applications of the beetle boxes.

It is possible that the grouped nature of the experimental design influenced the extent to which different box treatments were inhabited by invertebrates. A potential example of this can be seen in *Orthoperus aequalis*, which exclusively inhabited beetle boxes with added fertiliser, apart from a single exception in which two *O. aequalis* specimens were found in a wooden box without added fertiliser. This box was paired with the box within which the second-highest abundance of *O. aequalis* at was recorded in the present study. This could be a sign that the grouped arrangement of the boxes resulted in a source-sink interaction, in which the *O. aequlis* in the fertilised box reproduced to an extent that competition drove dispersal to surrounding habitat patches, even if the immediately surrounding habitat (the unfertilised box) was sub-optimal (Kristan, 2003). The grouped experimental design was considered the most appropriate design for the present experiment, as it provided minimised the extent to which the results were influenced by the variable abiotic conditions in different areas of a heterogenous woodland landscape. Despite the potential that the experimental design influenced the results, the trends observed between box types remained strong enough to infer meaningful conclusions on the variables studied during this work.

The present study was limited in the investigation techniques that could be used to identify the presence of *L. violaceus* in the beetle boxes. Previous studies have found success in surveying *L. violaceus* populations using emergence trapping (Gioux *et al*., 2009; Gouix & Brustel, 2012). Pitfall trapping is also a potentially successful method for *L. violaceus* detection in wood mould (Gouix & Brustel, 2012; Cuff, Müller, *et al*., 2021). These methods were not used as part of the present study as *L. violaceus* is protected by the Wildlife and Countryside Act (1981) in the UK. Because of this, lethal trapping methods were not an option for the recent study. Emergence and pitfall trapping could have been carried out without killing-fluid in the collection vessels to avoid killing for *L. violaceus* specimens. However, non-lethal trapping would have required frequent emptying of the traps to minimise the potential of *L. violaceus* being trapped for too long. This would have been very labour intensive and likely impossible due to Covid-19 restrictions at the time of sampling. In addition, live trapping would still have presented a high risk of mortality to any caught *L. violaceus* specimens through predation or drowning. The sieving and extraction sampling techniques used by the present study was deemed to be the most effective alternative to the above methods, whilst also safeguarding local *L. violaceus* populations.

The analysis of the beetle fauna inhabiting beetle boxes was limited by the fact that ecological associations of beetle species are often not fully understood, an example of which has been discussed in the section on *P. simsoni*. As a result of such uncertainties, the species categorisations of ‘saproxylic’, ‘woodland-associated’ and ‘non-deadwood associated’ used in the present study should be considered as somewhat flexible and open to future change as new information is uncovered. Nevertheless, it was considered that enough information is presently available on the majority of species found in this study, that meaningful distinctions could be made between these categories for the analysis of the results of this study.

Summary of aims

Nitrogen content

This study aimed to gather data on the influence of added nitrogen in artificially created wood mould on the invertebrates that use it as a habitat. It is clear that the addition of fertiliser gives an initial boost to the attractiveness of the wood-mould habitat to saproxylic and woodland associated beetles, as significant, positive links were found for these groups. It is likely that these links are due to increased decay rates linked to the nitrogen limitation of wood-decaying enzymes (Sterner & Elser, 2002; Cornwell *et al*., 2009). However, despite the positive links found, the observation of the RDB 3 tree hollow specialist, *S. godarti*, in a beetle box that did not contain added nitrogen indicates that, although nitrogen benefits saproxylic occupancy of beetle boxes as a whole, it is not necessarily a requirement for beetle boxes to be able to mimic tree hollow habitats effectively.

It is possible that the trends found to be associated with the addition of fertiliser would decrease over time. For example, the effects of the addition of various components of wood-mould on the beetle communities inhabiting beetle boxes by Jansson, Ranius, *et al*. (2009) were no longer evident after an additional five to six years of deployment when they were later re-visited by Carlsson *et al*. (2016). This may be a result of nutrients building up in the boxes over time through natural processes. Continued monitoring of the boxes in the present study would therefore be worthwhile, as outlined in the ‘recommendations for future research’ section.

Longevity of beetle boxes

Boxes made of plastic were trialled during the present study as a more durable alternative to the commonly used wooden boxes. Plastic showed potential as a resilient construction material for beetle boxes, containing saproxylic and woodland associated beetle communities that did not differ significantly in diversity or abundance from those in wooden boxes with added fertiliser. A plastic box was also found to contain the tree-hollow specialist beetle, *P.turgidum*, indicating that the box design had been successful in providing conditions that were analogous to those in tree-hollows. Despite this, plastic boxes lacked the additional incidental niche that was provided by areas of adpressed wood between the rim and the lid of wooden boxes.

The wood mould in the plastic boxes was significantly dryer than that in wooden boxes. As a result, the wood mould in the plastic boxes was more suitable to a slightly different assemblage of beetles than those found in wooden boxes. This shows that incorporating areas of dryer wood mould such as that found in plastic boxes alongside areas of more moist mould can increase the diversity of species inhabiting beetle boxes. However, the dryness of the mould in the plastic boxes in their current form will likely limit their suitability for providing habitat for species that prefer particularly moist wood mould such as *L. violaceus*. Ways in which this might be addressed are highlighted in the 'Recommendations for future research' section.

Basal design of beetle boxes

All saproxylic and woodland associated beetle species recorded from real basal tree hollows during this study were also represented within beetle box fauna. This suggests that beetle boxes replicated the conditions within their target habitat successfully enough to cater to several key tree hollow beetle species. Observations of the specialist species, *Ptenidium turgidum* and *Stenichnus godarti* also support this conclusion. No *L. violaceus* adults were found within the ground level beetle boxes, while a potential larva and elytron were observed within real tree hollows during this study, indicating that beetle boxes are not yet providing habitat for this species. However, this may have been due to the early stage at which sampling was carried out in the present research. Proposals for the future monitoring of the interactions of *L. violaceus* with beetle boxes are outlined in the 'Recommendations for future research' section.

Sampling time

The present study has identified a suite of species that can be expected in the early stages of box deployment, contributing to the understanding of community succession in decaying wood. The beetle fauna recorded in the beetle boxes during the present study was limited in comparison to that found in previous studies (Jansson, Ranius, *et al*., 2009; Carlsson *et al*., 2016). This is likely due in part to the early sampling time of the present work. As some beetle genera were identified in their immature stages that were not present as adults in the wood mould (e.g. *Pediacus* sp.) it is likely that the fauna in the boxes will continue to expand and change over time.

Recommendations for future research

Fungi

It is evident that fungal communities within the boxes play an important role in shaping the beetle communities inhabiting the internal wood mould. It would be beneficial to further explore this through characterising fungal communities present in the wood mould of both real tree hollows and beetle boxes. This could be done through next-generation sequencing (NGS) (Soliman *et al.*, 2017). This methodology would allow comparisons to be drawn between beetle boxes and their target habitat and enabling the identification of missing fungal components in beetle box wood mould.

Compressed wood mould microhabitats

Based on incidental observations of beetles making use of the space between the box lid and the box rim as a habitat and a pupation site, it may be beneficial to explore this concept further in future beetle box designs. Additional areas of wood adpressed together with compressed sawdust between them could be attached to the box walls to increase bark-mimicking resources on the boxes. The idea of replicating an under-bark space was partially explored by Elbourn (1970) who investigated the use of a beetle box design with a doubled wall on two sides. However, these gaps were left hollow to approximate loose, peeling areas of bark (Elbourn, 1970). Should these spaces be filled with compacted sawdust such as that found under the lids of some beetle boxes in the present study, this may more effectively provide additional pupation habitat for beetles such as *Ampedus* sp. or even *L. violaceus* during future trials.

Beetle box wood mould moisture content

The present study identified the moisture content of wood mould to be a key influencing factor in shaping the communities of beetles and other invertebrates that inhabit beetle boxes. A greater range of moisture levels in beetle boxes can allow them to cater to a greater diversity of beetle species. However, the wood mould in beetle boxes was found to be generally dryer than that found in real tree hollows. Therefore, for beetle boxes to provide habitat to tree-hollow specialist invertebrate species that prefer particularly moist conditions such as *L. violaceus* and *C. laetus*, the addition of more effective drainage features would be beneficial. This is especially true for the plastic beetle boxes which contained significantly dryer wood mould than tree hollows and wooden boxes. It is therefore recommended that future beetle box designs tailored towards *L. violaceus* should feature larger drainage holes in the lid and a larger entrance hole to allow the infiltration of more water into the wood mould.

Continued monitoring of beetle boxes for *L. violaceus*

Although no *L. violaceus* individuals were found within beetle boxes during the present study, it would be worthwhile to carry out continued monitoring activities to observe whether the boxes become colonised over time. The need for continued monitoring is reinforced by the finding that beetle box habitats become increasingly inhabited by tree-hollow specialist beetle species over time (Carlsson *et al*., 2016).

Monitoring the volatile organic chemicals (VOCs) emitted from beetle boxes would be a useful tool in tracking the potential attractiveness of beetle box habitats to *L. violaceus* over time. Basal tree hollow habitats inhabited by *L. violaceus* have been found to emit certain VOCs that are likely associated with particular decay fungi (Cuff, Müller, *et al*., 2021). If the appropriate VOCs are detected from beetle boxes, this would indicate that the boxes have reached a level of maturity at which a targeted investigation of beetle box colonisation by *L. violaceus* would be worthwhile. Such future investigation of the presence of *L. violaceous* in beetle boxes could be conducted by a more extensive extraction and sieving/sorting of the internal wood mould. Following the methodology of Henshall *et al*. (2015), the extraction of five or more litres of wood mould would give greater chance of finding specimens of finding any *L. violaceous* specimens present. If this search was specifically targeted towards the larger, more readily found *L. violaceous*, processing of samples through extraction traps would not be necessary. Therefore, any mould extracted from boxes could be replaced after sorting, minimising the impact of the survey on the ongoing ability of the boxes to act as supplemental habitat.

Further investigation of variation in wood mould contents

The present study demonstrated the benefits of adding nitrogen-rich fertiliser to wood-mould for some groups of beetles. However, there is potential that addition of other components to wood mould may make it more attractive to *L. violaceus*. Although *L. violaceus* larvae are considered to be predatory on other invertebrates, there is also evidence that they feed on carrion (Gouix, 2012). This has been further supported by observations of *L. violaceus* being attracted to meat-based pet food lures (Heaver, 2021, pers. comm.). As a result, it may be beneficial to include carrion components in the box contents during future trials. This has previously explored in in a preliminary trial, during which wood mould ingredients including small animal corpses were packed into the hollow of a re-erected beech tree (Whitehill, 2003). When this hollow was inspected 5 and 6 years after the initial set-up, adult and larval *L. violaceus* individuals were found (Whitehill, 2003). Although this isolated incidence is not enough to provide definitive proof that the presence of carrion supports *L. violaceus*, it indicates the value of exploring this more in future research. In addition, Jansson, Ranius, *et al*. (2009) found that the addition of poultry carrion to beetle box contents increased the number of beetle specimens found within. This further supports the potential of further beetle box trials incorporating the addition of carrion into their wood mould to increase their conservation potential.

Comparison of basal and trunk-mounted beetle boxes

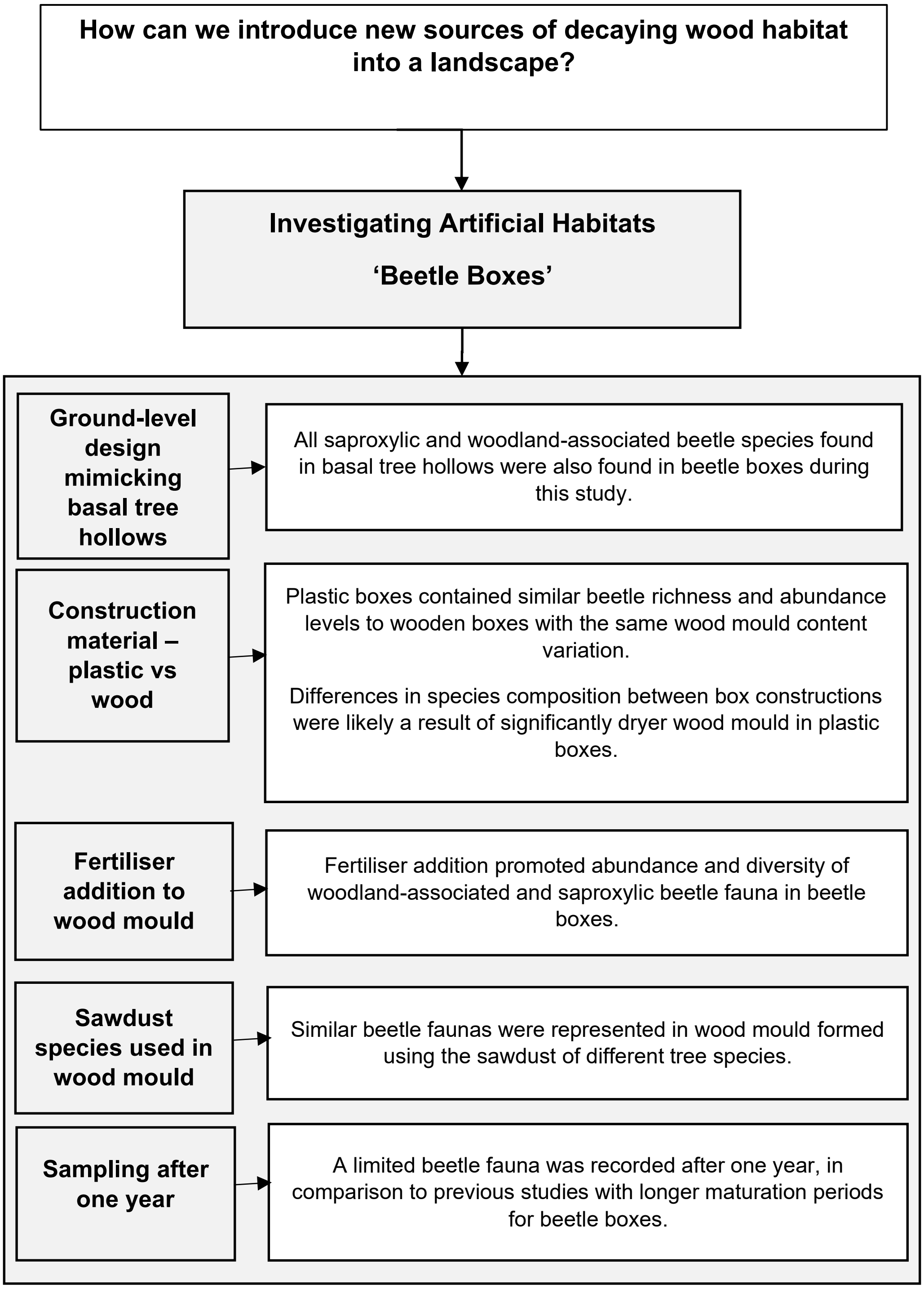
The present study identified a community of beetle species that can inhabit ground-level beetle boxes. In future research, it would be interesting to provide a direct comparison of beetle boxes at ground level and those mounted upon trunks such those used in previous beetle box research (Elbourn, 1970; Jansson, Ranius, *et al*., 2009; Hilszczański *et* al., 2014; Carlsson *et al*., 2016). By incorporating both ground-level and trunk-mounted boxes in the same woodland in future studies, data could be gathered that would allow researchers to better understand how the height of beetle boxes influences how invertebrates interact with them.

Investigation of beetle boxes in new contexts

The present study has presented new findings of beetle box inhabitancy in areas of continuous, high-quality woodland. It would be valuable to expand upon this by investigating the application of beetle boxes in other conservation contexts. For example, beetle boxes may provide beneficial functions to the ‘island of senescence’ concept discussed in section 1.4 of this thesis. Beetle boxes could bring additional deadwood value to plantations, potentially enhancing wood mould habitat within islands designated for decaying wood retention. They may also provide additional connectivity when stationed between existing islands.

Overall summary

The results of this study further demonstrate the potential of beetle boxes as a conservation tool for supporting tree hollow invertebrates. The findings have indicated that moisture and nutrient levels within beetle boxes play key roles in determining the beetle fauna that use them as habitat. This knowledge will prove useful in informing the future applications of beetle boxes for conservation management schemes.



How can we introduce new sources of decaying wood habitat into a landscape?

Investigating Artificial Habitats

'Beetle Boxes'

Ground-level design mimicking basal tree hollows

All saproxylic and woodland-associated beetle species found in basal tree hollows were also found in beetle boxes during this study.

Construction material – plastic vs wood

Plastic boxes contained similar beetle richness and abundance levels to wooden boxes with the same wood mould content variation.

Differences in species composition between box constructions were likely a result of significantly dryer wood mould in plastic boxes.

Fertiliser addition to wood mould

Fertiliser addition promoted abundance and diversity of woodland-associated and saproxylic beetle fauna in beetle boxes.

Sawdust species used in wood mould

Similar beetle faunas were represented in wood mould formed using the sawdust of different tree species.

Sampling after one year

A limited beetle fauna was recorded after one year, in comparison to previous studies with longer maturation periods for beetle boxes.

Figure 3.38. A conceptual framework outlining the key findings on the main research areas that this chapter addressed concerning beetle boxes as artificial habitats.

Chapter 4 - A concrete beetle box as an urban deadwood resource

4.1 - Introduction

Rationale and basis for study

The use of artificially created habitats to support insect populations in urban landscapes has become increasingly popular in the form of bee hotels, since their development in the 1950s (Krombein, 1967; MacIvor & Packer, 2015). In addition to their conservation value, bee hotels facilitate the observation of insect behaviour and can be used as valuable educational tools (Manolis & Manoli, 2021). Such observations have occasionally resulted in new scientific discoveries on behavioural interactions such as parasitism being made (Prendergast & Yeates, 2018). Similarly, bee hotels have been involved in monitoring expanding invertebrate ranges, with new country records occasionally being made through bee hotel surveillance (Ivanov & Fateryga, 2019). The conservation and educational benefits of artificial habitats have the potential to be expanded into other invertebrate groups, such as saproxylic communities.

Despite their extensive diversity, invertebrate faunas of deadwood are underappreciated by the public (Thorn *et al*., 2020) This may be a result of their inaccessibility, as the niches occupied by saproxylic invertebrates (e.g. tree hollows, tunnels in sapwood and the spaces underneath bark) are often less readily observable than those of other invertebrate guilds. It is important that education around saproxylic invertebrates is improved, so that deadwood resources in landscapes can receive more appropriate levels of appreciation and protection. There is potential for beetle boxes, such as those trialled in Chapter 3 of this thesis, to play a role in this. Beetle boxes could be used in urban areas the same way as bee hotels to make saproxylic invertebrates more accessible to the public. In this way they could function as a tool improve education around the importance of saproxylic faunas for natural processes such as decomposition and pollination (Mestre *et al*., 2018; Falk, 2021)

As described in Chapter 3 of this thesis, ground-level beetle boxes were initially designed to provide additional habitat for the specialised invertebrate fauna of basal rot holes in trees, particularly the endangered violet click beetle. This design also has the added benefit of being easier to install than previously trialled trunk-mounted beetle boxes, without the need for specialised tree-climbing equipment. Boxes at ground level are also more accessible for regular monitoring, making them preferable as an educational resource.

Should beetle boxes be employed in urban contexts for educational purposes, it is possible that they could help provide residual conservation benefits by acting as habitat stepping-stones for specialised invertebrate species of tree hollows and creating corridors of dispersal (Jansson, Ranius, *et al*., 2009). This could facilitate the movement saproxylic species across otherwise hostile landscapes to reach new woodland habitat patches containing suitable hollow trees.

Current state of research and knowledge gaps

Beetle boxes as a garden feature

All previous beetle box studies have taken place in woodland contexts (Elbourn, 1970; Jansson, Ranius, *et al*., 2009; Hilszczański *et* al., 2014; Carlsson *et al*., 2016; Mestre *et al*., 2018; Weatherbee *et al*., 2022)., As a result, it is difficult to predict how beetle boxes would perform in other landscape types such as managed gardens. Other decay-rich microhabitats such as compost heaps are known to contribute to garden biodiversity (Smith *et al*., 2006). As a result, it is likely that specialised decaying wood resources such as those in beetle boxes could further improve the diversity of species able to inhabit gardens. Compost heaps have also played a role in the movement and establishment of beetle species in new areas (Ødegaard & Tømmerås, 2000). This supports the idea that beetle boxes in gardens may provide similar benefits for the movement of saproxylic species through urbanised landscapes. However, it is possible that the low dispersal tendencies of some saproxylic species may impede the stepping-stone function of beetle boxes. The diversity of saproxylic species inhabiting beetle boxes has been shown to be negatively affected by increased distances of boxes from a tree-hollow source population (Jansson, Ranius, *et al*., 2009; Mestre *et al*., 2018). This may mean that the usability of beetle boxes in gardens is limited to those with existing deadwood patches in the surrounding area. The present study will further investigate this hypothesis by installing a beetle box into a wildlife garden with some existing deadwood resources, providing an initial insight into a high-potential scenario for garden beetle boxes.

Concrete as a construction material for beetle boxes

Deterioration of wooden beetle boxes over time has been a problem in several previous studies (Hilszczański *et* al., 2014; Carlsson *et al*., 2016). Longevity of beetle boxes is important as their target fauna are adapted to long-lived tree hollow habitats (Ranius & Hedin, 2001; Ranius *et al*., 2009). This is supported by Carlsson *et al*. (2016) who found that beetle boxes become more attractive habitats for hollow specialist species over time. The preference for older wood mould was suggested to be a result of natural successional changes that commonly occur in the saproxylic fauna occupying deadwood resources (Speight, 1989; Carlsson *et al*. 2016). Chapter 3 of this thesis aimed to address the problem of beetle box longevity through trialling beetle boxes made from plastic. The present study seeks to develop this further by investigating the properties of a beetle box constructed from concrete, as discussed in the 'Study aims' section.

Investigation of beetle box sampling methods

Two common methods of sampling the invertebrates in wood mould are hand sorting and extraction trapping using apparatus such as Tullgren or Winkler extraction traps (Krell, Chung, *et al*., 2005; Cuff, Windsor, *et al*., 2021). The live examination of invertebrates through hand sorting of wood mould on site may be preferable from an educational perspective. Because of this, it would be useful to better understand the proportion of the fauna inhabiting beetle boxes that may be effectively examined through this method. Previous studies have evaluated the efficacy of Winkler extraction trapping by hand sorting samples after trapping to extract any remaining invertebrates (Krell, Chung, *et al*., 2005; Ivanov *et al*., 2010). However, there is little research that has reversed this process to better understand the effectiveness of hand sorting wood mould samples.

Study aims

Beetle boxes as a garden feature

This study aims to expand knowledge on the potential applications of beetle boxes by gathering preliminary data on the invertebrate fauna that may be expected to colonise a beetle box in an urban garden setting. Through this, this study aims to evaluate the potential for garden-based beetle boxes to be used as tools for education on deadwood ecology, in addition to the conservation of saproxylic species.

Concrete as a construction material for beetle boxes

This study will address the problem of beetle box deterioration over time by trialling beetle boxes made from concrete, which is expected to be a more durable alternative to the wooden designs used in previous studies. To do this, data on the moisture and invertebrate community dynamics occurring within a concrete beetle box will be gathered. These data will be used to develop a preliminary understanding of how well a concrete box can mimic the stable conditions found in tree hollows. Through this, this study aims to assess the potential for concrete as a viable construction material for future beetle box trials.

Investigation of beetle box sampling methods

An aim of this study is to investigate the effectiveness of hand sorting and Winkler trapping when used in conjunction with one another to extract invertebrates form a wood mould substrate. Data will be gathered on the abundances of specimens from different invertebrate groups that are extracted through these two methods. The patterns identified in this data will further understanding of the biases of sampling methods and inform the methodologies of future beetle box studies.

4.2 - Methods

Study site

This investigation was carried out in a wildlife garden in North London, approximately four miles from the Thames Estuary. The garden had deadwood representation in the form of several mature log-piles and veteran hawthorn trees with some signs of hollowing. There were no larger veteran trees with basal tree hollows on-site. The wildlife garden also featured three ponds. More information about this site can be found in Section 1.5.

Concrete beetle box construction

A concrete beetle box was built by a team of MSc students in the architecture school of the University of East London. It was made in a cylindrical shape (as opposed to the cuboid shape used in previous studies) as an adaptation to the nature of concrete construction. The box was constructed by initially creating a form out of chicken wire which was subsequently coated with concrete. Due to the amount of time and resources required to construct the concrete beetle box, a single box was made. This therefore provides initial observations of the suitability of concrete as an artificial-habitat construction material. Dependant on the performance of the concrete box, these observations can be used as the basis for more extensive trials using concrete for beetle box construction in the future.

Like the beetle boxes trialled in Chapter 3, the base of the concrete beetle box was half open to the soil to allow invertebrate colonisation from the surrounding environment (Figure 4.1). The concrete beetle box also had an entrance hole in the centre to allow crawling and flying invertebrates to enter the bottom box compartment (Figure 4.1). An internal shelf covering half of the box’s circumference was present above the entrance hole to maintain a hollow area and increase the similarity of the internal box conditions to real tree hollows (Figure 4.1). The box lid was concave with four drainage holes to encourage moisture to enter the box, thus promoting consistently moist conditions (Figure 4.1). The drainage holes were 3cm in diameter which is larger than those used in the beetle box designs in chapter three of this thesis (Figure 4.1). The previously used size (0.8cm diameter) produced dryer conditions in plastic beetle boxes than those found in natural tree hollows; therefore, the inclusion of 3cm diameter drainage holes is expected to better encourage increased levels of moisture within the concrete beetle box. A roughened texture was created on the surface of the beetle box by pressing creased plastic onto the walls and subsequently removing it, leaving an irregular impression on the concrete as it dried (Figure 4.1). This was intended to mimic the texture of tree bark to encourage the growth of epiphytes on the beetle box walls. It was hoped that over time, this would give the box a more natural appearance and potentially offer additional niches for invertebrates.

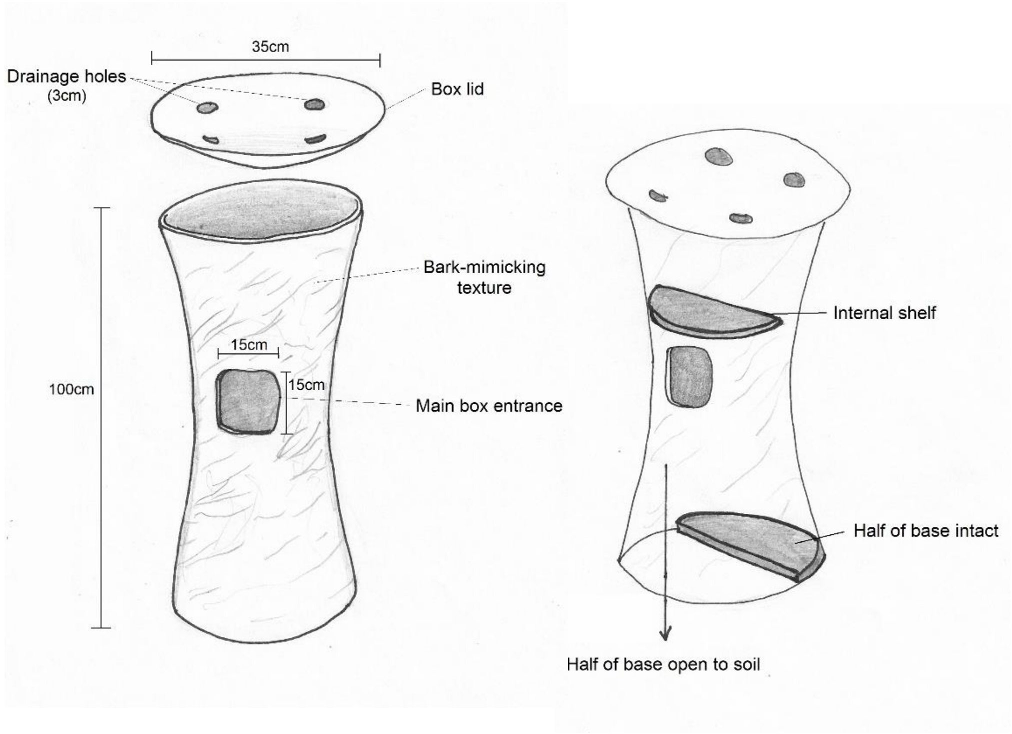


Figure 4.1. Diagrams of the concrete beetle box used in this study, with key features and dimensions labelled.

Beetle box installation

The concrete beetle box was installed on 19/11/2019. Installation involved the box being half-buried in the soil up to the lower edge of the central box opening (Figure 4.2). The box was buried into a plant bed within approximately 20 meters of mature hawthorn trees and a wood pile.

Figure 4.2. A photograph of the concrete beetle box installed in the ground at the wildlife garden.

Beetle box contents

The concrete box was filled with a mixture of untreated, dried sawdust, leaf-litter, soil and poultry manure (pelletised poultry faeces, sourced from Elixir Garden Supplies). The bottom compartment of the box below the internal shelf was filled with a mixture of 12 litres of leaves, 12 litres of oak sawdust, 24 litres of soil, and 2 litres of poultry fertiliser. The top compartment of the box, above the shelf was filled with a mixture of 16 litres of leaves, 16 litres of oak sawdust, 8 litres of soil and 2 litres poultry fertiliser. The differences in the mixtures used in the top and bottom compartment were designed to reflect the transition of wood mould into soil that naturally occurs in tree hollows (Gioux *et al*., 2015). The poultry fertiliser was added to increase the nitrogen content of the wood-mould substrate, reflecting the naturally high nitrogen levels recorded from real tree hollows (Kelner–Pillault, 1974; Ulyshen, 2015). After filling the box, ten litres of water were added to the box to create damp conditions and promote the decay of the wood mould (Rousk & Bååth, 2011).

Invertebrate sampling from the concrete beetle box

Sampling took place on 07/05/2021, 19/07/2021 and 17/09/2021. One litre in volume of wood mould was removed from both the top and the bottom sections of the concrete beetle box using a soil corer (a total of two litres volume removed from the box per sampling session). Preliminary sorting of the samples was undertaken on site, with the removed wood mould being thoroughly sieved in a white tray for 10 minutes with all visible invertebrates being collected using forceps and a pooter. The collected invertebrates were placed into tubes containing a 70% ethanol solution to be identified at a later date. This fluid was chosen as it is known to effectively preserve the morphology of many soil invertebrate groups (Krogmann & Holstein, 2010). The tubes were labelled with the box location, sampling date and the box compartment (top or bottom) from which the specimens were extracted. This labelling was done both internally using pencil on strips of printer paper, and externally using permanent marker on the body of the tube. The preliminary sorting was done to investigate the efficacy of hand sorting and to remove larger invertebrates that may not be able to pass through the mesh bag used in the Winkler traps.

Following preliminary invertebrate extraction, the remaining soil from the samples was placed into plastic pots using a plastic funnel. The samples from the top and bottom compartments of the box were kept separate and placed into their own individual pots. The plastic pots were labelled both internally and externally with the site name, the date of sample collection and the compartment (top or bottom) from which the sample was taken. Internal labels consisted of printer paper marked with pencil and external labelling was done with permanent markers on the base and lid of each collection pot.

Winkler trapping

After being sealed into plastic containers, the wood mould samples were and taken off site. The samples were then transferred into mesh bags with 2mm holes and placed into Winkler extraction traps. The traps were used to extract macro-invertebrates that had not been detected and extracted during hand sorting. Each trap had a collection pot connected to its base containing a 50% propylene glycol, 50% water mixture with an added drop of unscented washing-up liquid. This fluid is a widely recommended entomological killing agent which is low-cost, safe to use and preserves the condition of specimens well (Weeks & McIntyre, 1997; McCravy & Willand, 2007; Weigand *et al.,* 2021). Samples from the top and bottom compartments of the concrete box were placed into separate Winkler traps to observe any differences in the invertebrate fauna inhabiting the different areas of the box.

Samples were left in Winkler traps for eight weeks. This time period was deemed sufficient for extensive extraction as it was a week longer than the seven weeks at which Krell, Chung, *et al*. (2005) observed the abundances of most invertebrate groups caught in Winkler Traps to reach a plateau. To further ensure that the invertebrates in the samples had been extracted to as great an extent as possible, the samples were further visually inspected on removal from the traps after the eight-week period. No invertebrate life was observed in any of the samples during these inspections.

Specimen identification

All invertebrate specimens were extracted from the hand sorting and Winkler trapping samples using a stereo microscope. These were identified at least to order level, with some specimens being identified to family, genus and species level. Identification of specimens was aided by a range of taxonomic keys and photograph resources (Hansen & Solodovnikov, n.d.; UK Beetles, n.d.-j; Blower, 1985; Hopkins, 1991; Barber, 2008; Käfer Europas, 2013; Legg & Farr-Cox, 2016; Duff, 2020).

4.3 - Results

Coleoptera found in the concrete beetle box

Three species of beetle were found from samples taken from the concrete beetle box. Of these, two were fully identified and one (*Carpelimus* sp.) was identified to genus level due to difficulties in species determination. As *Carpelimus* species found in the UK have similar ecological habits, this was not expected to negatively impact the interpretation of the results of this study. One of the beetle species found (*Euplectus karstenii*) was classified as saproxylic and neither of the fully identified species had a conservation status. Several species of *Carpelimus* sp. have been assigned conservation statuses, so it cannot be ruled out that the species found may be of conservation concern. Over the three sampling sessions in May, July and September, *Annomatus diecki* and *Euplectus karstenii* both only appeared singularly in the months that they were found (Table 4.1). In contrast, *Carpelimus* sp. consistently increased in numbers over the four-month sampling period (Table 4.1).

Table 4.1. A summary of the beetle diversity found within the concrete beetle box over the four-month sampling period.

Family	**Genus/ species**			**Number of specimens found**			
		Guild	**Saproxylic**	**07/ 05/ 2021**	**19/ 07/ 2021**	**17/ 09/ 2021**	**Tot al**
Bothrideridae	*Anommatus diecki*	Saprophagous	No	1	0	0	1
Staphylinidae	*Carpelimus* sp.	Saprophagous	No	0	4	20	24
Curculionidae	*Euplectus karstenii*	Predator	Yes	0	1	1	2
Total				1	5	21	27

Table 4.2. A summary of the beetle larvae found within the concrete beetle box over the four-month sampling period.

	Number of specimens found			
Identification	**07/05/2021**	**19/07/2021**	**17/09/2021**	**Total**
Unidentified Coleoptera larvae	1	0	0	**1**
Cryptocephalus larvae	0	1	0	**1**
Athous larva	0	0	1	**1**
Total	1	1	1	**3**

Other invertebrates found in the concrete beetle box

Of the invertebrate groups found in the concrete beetle box, the most abundant were Collembola (n=866), Acari (n=288) and Oniscoidea (n=263) (Table 4.4).

The abundances of Collembola and Acari both peaked on the second sampling session, on 19/07/2021 (Table 4.4). The high abundance of Oniscoidea was largely due to large numbers of the species *Haplophthalmus danicus* (n=222), which increased in numbers over the sampling period, reaching its peak abundance on 17/09/2021(Table 4.4).

Table 4.3. A summary of insects (excluding Coleoptera) found in the concrete beetle box over three sampling sessions.

Identification	**Number of specimens found**			
	07/05/2021	**19/07/2021**	**17/09/2021**	**Total**
Psocoptera				
Total	1	1	1	**3**
Thysanoptera				
Total	0	2	0	**2**
Hymenoptera (Formicidae)				
Total	31	0	0	**31**
Diptera (adult)				
Total	0	7	9	**16**
Diptera (larva)				
Total	23	0	0	**23**

Table 4.4. A summary of invertebrates found in the concrete beetle box over three sampling sessions.

Identification	**Number of specimens found**			
	07/05/2021	**19/07/2021**	**17/09/2021**	**Total**
Oligochaeta				
Total	1	2	9	**12**
Gastropoda (slug)				
Total	0	0	1	**1**
Diplopoda				
Proteroiulus fuscus	1	0	0	**1**
Immature/ unidentified Polydesmida	1	1	7	**9**
Total	2	1	7	**10**
Chilopoda				
Lithobius microps	0	4	0	**4**
Cryptops hortensis	5	10	5	**20**
Immature /unidentified *Lithobius* sp.	1	1	0	**2**
Total	6	15	5	**26**
Oniscoidea				
Haplophthalmus danicus	3	33	186	**222**
Oniscus asellus	1	0	0	**1**
Porcellio pruinosus	0	1	0	**1**
Porcellio scaber	8	0	0	**8**
Armadillidium nasatum	13	8	0	**21**
Armadillidium vulgare	0	1	0	**1**
Immature /unidentified *Porcellio* sp./ *Oniscus* sp.	0	3	1	**4**
Immature /unidentified *Armadillidium* sp.	0	0	5	**5**
Total	25	45	192	**263**
Diplura				
Total	1	2	0	**3**
Collembola				
Total	89	700	77	**866**

Acari				
Total	43	172	73	**288**
Pseudoscorpiones				
Lamprochernes savignyi	0	1	0	**1**
Pselaphochernes scorpioides	0	1	0	**1**
Total	0	2	0	**2**
Aranae				
Linyphiidae	0	0	1	**1**

The influence of different specimen extraction methods

The majority of specimens of the most abundant invertebrate groups (Collembola, Acari and Onicoidea) were collected through Winkler extraction trapping (Figure 4.3). In addition, several groups were only collected through Winkler extraction trapping and were not found through hand sorting, including Gastropoda, Pseudoscorpiones, Aranae, Psocoptera and Thysanoptera) (Figure 4.4). In contrast, hand sorting extracted the majority of specimens of Oligochaeta, Diplopoda, Chilopoda, Diplura and Formicidae (Figure 4.4). Diptera larvae were exclusively collected through hand sorting of wood mould (Figure 4.4).

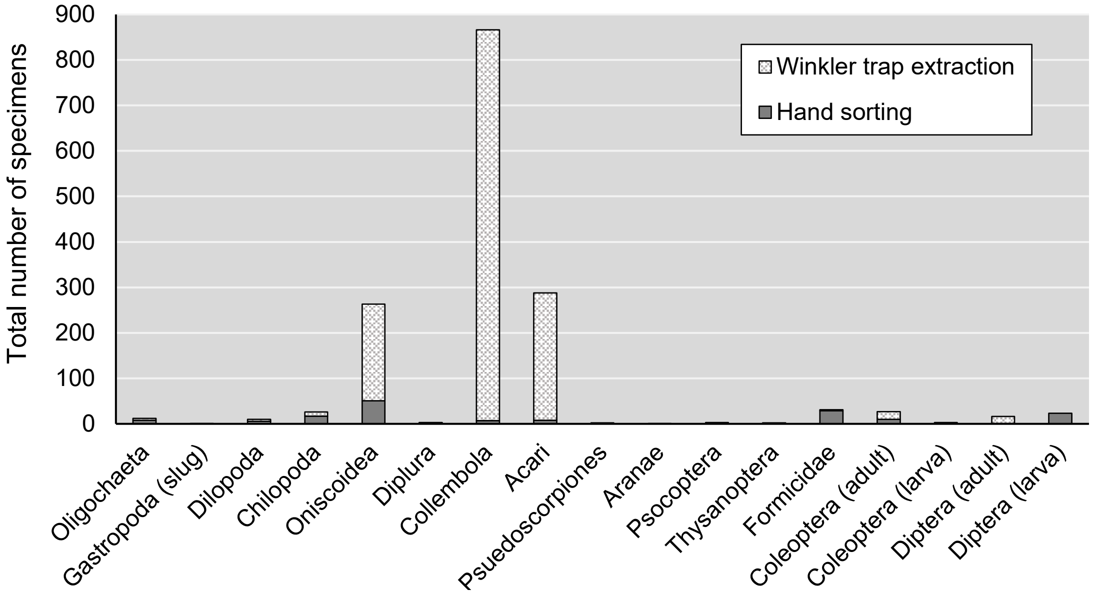


Figure 4.3. A bar graph showing the total number of specimens of the various invertebrate groups found in the concrete beetle box. The bars are separated by shading to indicate the proportion of the total number of specimens that was extracted using either hand sorting (grey) or Winkler extraction trapping (crosshatched).

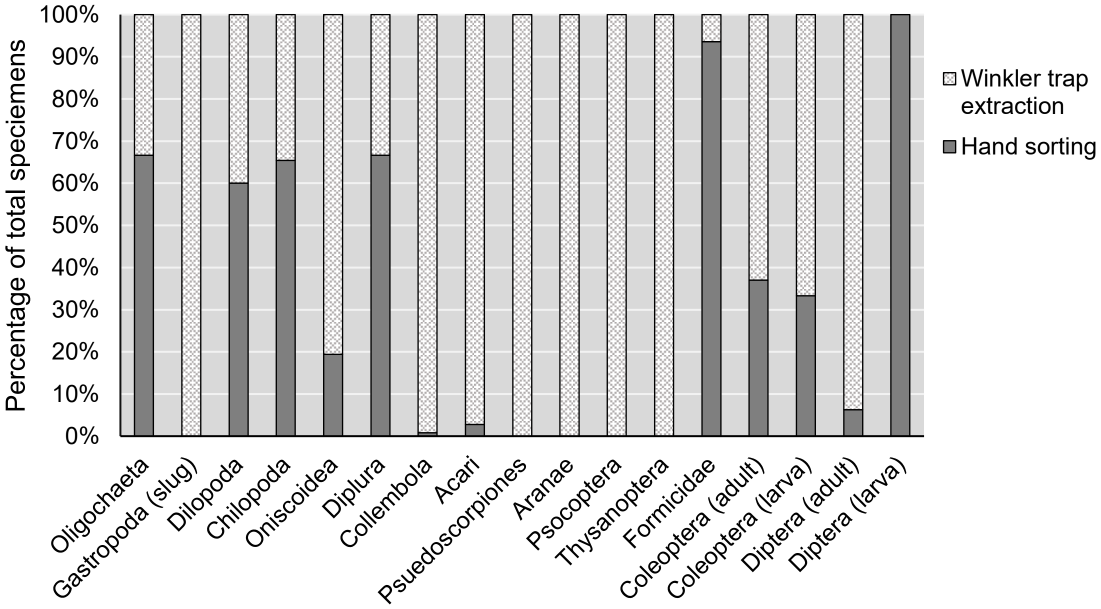


Figure 4.4. A bar graph showing the percentages of the total number of specimens of the various invertebrate groups found in the concrete beetle box that were extracted using hand sorting and Winkler extraction trapping. The bars are separated by shading to indicate percentage of specimens that was extracted using either hand sorting (grey) or Winkler extraction trapping (crosshatched).

Invertebrate group representation in the different box compartments

Two of the most common invertebrate groups, Collembola and Acari were represented to similar extents in the bottom and top compartments of the concrete beetle box (Figure 4.5). Groups including Gastropoda, Diplopoda, Diplura, Thysanoptera and Coleoptera larvae were only found in the bottom compartment of the box (Figure 4.6). Similarly, adult Coleoptera, Oniscoidea, Chilopoda and Formicidae demonstrated a strong bias towards the bottom box compartment (Figure 4.6). The only group found exclusively in the top compartment was Aranae, of which only one specimen was found during this study (Figure 4.6).

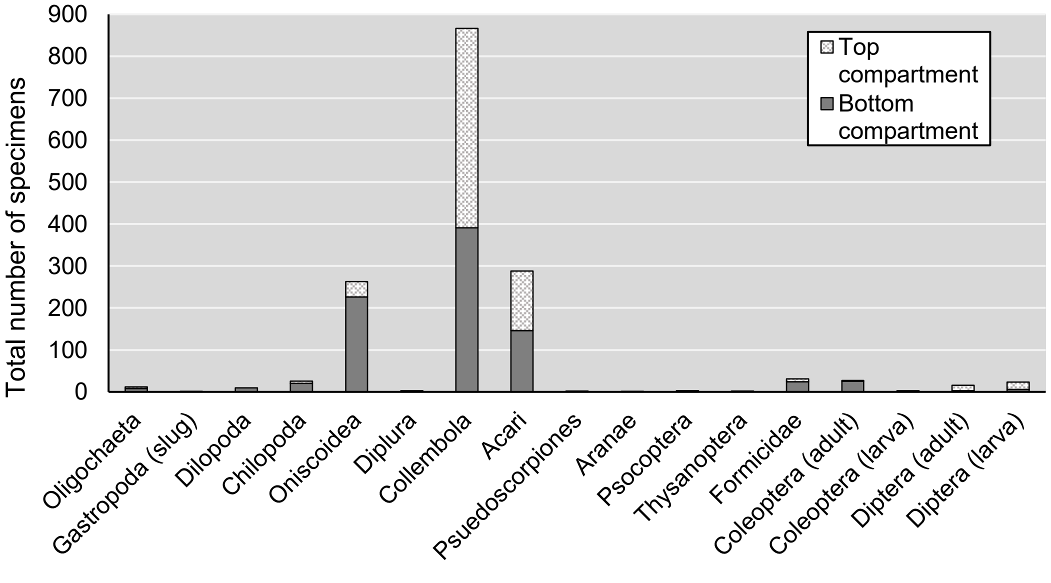


Figure 4.5. A bar graph showing the total number of specimens of the various invertebrate groups that were found in either the top or the bottom compartment of the concrete beetle box. The bars are separated by shading to indicate the proportion of the total number of specimens that was found in either the top (crosshatched) or bottom (grey) compartment of the box.

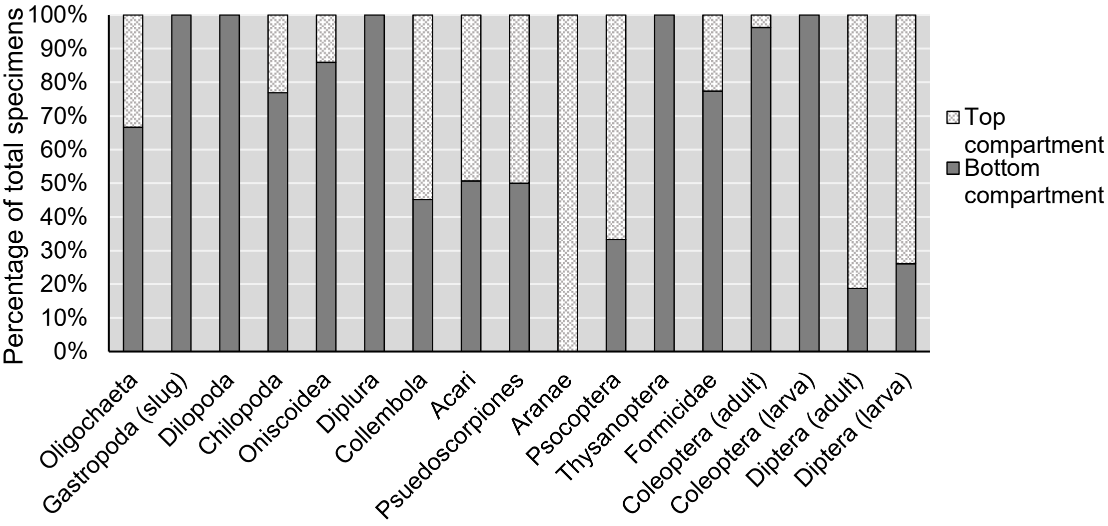


Figure 4.6. A bar graph showing the percentages of the total number of specimens of the various invertebrate groups found in the top and bottom compartments of the concrete beetle box. The bars are separated by shading to indicate percentage of specimens that was found in either the top (crosshatched) or bottom (grey) compartment of the box.

Moisture Content of wood mould in the concrete beetle box

Average moisture levels in both compartments of the concrete beetle box increased over the four-month sampling period (Table 4.5). For the first two sampling sessions, average moisture levels in the bottom compartment of the box were higher than those in the top compartment (Table 4.5). During the final sampling session, a higher moisture reading was recorded in the top compartment than in the bottom; however, as this was a single reading and not the result of an average, these measures are not fully comparable (Table 4.5). The average moisture levels in the bottom compartment of the concrete box varied over a smaller range than in the top compartment, in which the moisture levels changed to a greater degree (Table 4.5).

Table 4.5. The moisture content of wood mould, averaged across three measurements taken at the front left, the centre, and the back right areas of the box in both the top (above the internal shelf) and bottom (below the internal shelf) compartments of the concrete beetle box. *As the wood-mould in the top compartment had extensively decayed away by the visit on 17/09/2021, this measurement is the result of a single probe measurement rather than an average of three.

Date of measurement	**Average* moisture content of wood mould (%vol)**	
	Top compartment	**Bottom compartment**
07/05/2021	5.47	27.8
19/07/2021	20.97	28.47
17/09/2021	38.4*	31.73
Average across all measurements	21.61	29.33

4.4 - Discussion

Coleoptera found in the concrete beetle box

The diversity of Coleoptera recorded from the concrete beetle box during the present study was low, with three species being represented, of which one was saproxylic. This low diversity is likely partially due to the short time that the beetle box was in the field before sampling (Jansson, Ranius, *et al*., 2009; Carlsson *et al*., 2016). Carlsson *et al* (2016) noted that beetle box conditions became more suitable for specialist saproxylic species after four years in the field. This suggests that the number of saproxylic species in the concrete beetle box could be expected to increase with additional time in the field. The hard-wearing nature of the concrete construction material is likely to be well suited to long-term deployment, which would facilitate this.

In addition to insufficient development and colonisation time, the abundance and diversity of some groups of beetles found in beetle boxes can be negatively affected by distance from dispersal sources (Jansson, Ranius, *et al*., 2009). Although there were other deadwood features including small tree hollows on the site in which the concrete beetle box was installed, it is possible that these were not sufficient to supply the beetle boxes with a diverse saproxylic fauna. If this was the case, it is unlikely that beetles could colonise the boxes from more distant deadwood sources, as beetle species that specialise on stable tree hollow habitats have limited dispersal tendencies, with long-distance dispersal events occurring at particularly low frequencies (Nilsson & Baranowski, 1997; Ranius & Hedin, 2001). As the present study constituted observations from a single beetle box, it is difficult to identify with certainty how the colonising saproxylic beetle fauna was influenced by the surrounding landscape and the abundance of local deadwood sources. As a result, this is an area that would benefit from further research in the future.

***Carpelimus* sp**

The most abundant beetle species recorded from the concrete box was from the genus *Carpelimus*. All species of *Carpelimus* found in the UK are saprophagous and the majority specialise upon wetland habitats (Webb *et al*., 2018). This habitat preference indicates that the specimens found in this study were potential migrants from the Essex Wildlife Trust Thameside Nature Discovery Park, which is a wetland nature reserve approximately 4 miles away from the concrete beetle box location. Alternatively, they may have colonised the box from a local population in the ponds on site. It is surprising that this species was found at relatively high abundances in the concrete beetle box, which was not intended to produce wetland-equivalent conditions. Nevertheless, the presence of *Carpelimus* sp. in the beetle box suggests that the internal conditions provided a consistently high level of moisture across the time period in which sampling occurred. Consistently high moisture levels in deadwood provide more suitable habitats for some species of saproxylic Coleoptera and Diptera (Hövemeyer & Schauermann, 2003; Ulyschen, 2018; Cuff, Müller, *et al*., 2021; Lindman *et al*., 2022). This link is potentially a result of more stable temperature conditions conferred by the buffering effect of water due to its high heat capacity (Abu-Hamdeh, 2003; Davis *et al*., 2018). Because of this, the finding of *Carpelimus* sp. in this study provides evidence that beetle boxes constructed from concrete are a promising candidate for further investigation as structures mimicking tree hollow conditions for the purpose of invertebrate conservation.

Anommatus diecki

The Bothriderid species, *Anommatus diecki*, in the concrete beetle box was a notable finding, as this species has only previously been found in the UK from Cheshire and Derbyshire (Maynard, 2011; Duff, 2020). This means that the present finding from North London constitutes a considerable range expansion for *A. diecki*. It is not a strictly saproxylic species and occurs in a range of decay-related situations (UK Beetles, n.d.-j). However, the previous records of *A. diecki* from the UK have been from damp, decaying wood, which correlates well the conditions of the present observation (Maynard, 2011; Duff, 2020). As they occur in subterranean environments, *Anommatus* species have previously colonised new areas through transportation in nursery stocks (UK Beetles, n.d.-j). This is likely the reason for the presently noted range expansion, considering that the site of the present study is an actively managed wildlife garden in which regular planting activities take place.

Euplectus karstenii

The Staphylinid, *Euplectus karstenii,* was the only truly saproxylic species of Coleoptera recorded from the concrete beetle box (Schmidl & Bußler, 2004). This species has previously been recorded from real tree hollows as well as in other, previously trialled beetle boxes (Gouix *et al*. 2009; Carlsson, *et al*. 2016). Chapter 3 of the present thesis also recorded *E. karstenii* from the ground-level beetle boxes trialled in Bredon Hill. The distribution of *E. karstenii* extends from southeast to central England and into the east of Wales with 151 records of it on the NBN Atlas (n.d. -b). Like other Pselaphinae species, *E. karstenii* is predatory on mites (Alexander, 2002). This may explain why it was observed only during the second and third sampling sessions, as these were the times at which the greatest abundances of mites were recorded from the beetle box.

Other invertebrates found in the concrete beetle box

A wide range of different invertebrate groups were represented in the concrete beetle box. Previous beetle box studies have shown that higher levels of invertebrate community complexity, particularly including Diplopoda, Coleoptera larvae and Diptera larvae, promote greater rates of decomposition in wood mould substrates (Weatherbee *et* al., 2022). Invertebrate community complexity in beetle boxes is also linked to increased levels of nitrogen in wood mould (Weatherbee *et* al., 2022). As a result, the diverse invertebrate community found in the concrete beetle box during this study is likely conducive to the effective recreation of the extensively decayed nitrogen-rich wood mould in tree hollows.

The invertebrate diversity found in the concrete beetle box is similar to that which could be expected in a compost heap (Gujarathi & Pejaver, 2011), with the exception of tree-associates such as *Proteroiulus fuscus* (Blower, 1985; Webb *et al*., 2018). Compost heaps contribute to garden invertebrate biodiversity by providing specialist decay-related microhabitats (Ødegaard & Tømmerås, 2000; Smith *et al*., 2006). The results of this study show that the beetle box concept works in a similar way, with the consistent presence of decaying wood providing an additional saproxylic aspect to this microhabitat.

The most abundant woodlouse species found in the concrete box was *Haplophthalmus danicus*. The habitat preferences of *H. danicus* are largely for moist areas, similar to *Carpelimus* (Gregory, 2009). This was also the most common woodlouse species recorded from real tree hollows in Chapter 3, and it was noted that greater abundances of *H. danicus* were found in tree hollows than in beetle boxes made from either wood or plastic. It was thought that the discrepancy in *H. danicus* between tree hollows and beetle boxes may have been due to differences in moisture content. However, the moisture levels recorded from the concrete beetle box in the present study were similar to those recorded from wooden beetle boxes in Chapter 3. As a result, the reason for this difference in unclear. A possible explanation could be that the concrete box offered more consistent moisture conditions than the box types trialled in Chapter 3. Nevertheless, the invertebrates found in the concrete beetle box cannot be directly compared to those found in the study detailed in Chapter 3, as differences in box location and surrounding landscape types are likely to considerably alter the colonisation potential of the boxes by different invertebrate species. Future research that directly compares concrete beetle boxes to those made of wood and plastic would help to increase understanding of the differences and similarities between the construction materials and how these influence inhabiting invertebrate communities.

Differences in the invertebrate faunas found in the top and bottom box compartments

Preferences for the bottom box compartment were observed in invertebrate groups including Gastropoda, Diplopoda, Chilopoda, Diplura, Thysanoptera, Coleoptera adults, Coleoptera larvae, Oniscoidea and Formicidae. This may be due to preferences of these groups for the more consistent moisture levels in the bottom area of the concrete beetle box, which are further discussed in the 'Moisture content of wood mould in the concrete beetle box' section of this chapter. For example, Formicidae have been shown to become more active in substrates with higher moisture levels, likely because of lower desiccation risk under these conditions (Kaspari & Weiser, 2000).

The influence of beetle box sampling methods

The results of this study show that the use of Winkler traps in addition to hand sorting allows a considerably greater proportion of the invertebrate specimens in wood mould to be extracted, especially for the most abundant groups. Invertebrates that typically have small body sizes such as Collembola and Acari are not effectively extracted visually through hand sorting, as they can be difficult to see amongst large volumes of substrate. Hand sorting was most effective for invertebrate groups that contain larger, more conspicuous species, such as Oligochaeta, Diplopoda and Chilopoda. Hand sorting also extracted a high proportion of the Formicidae specimens found in the samples. This may be a result of the tendency of Formicidae to move quickly, making them more noticeable amongst the wood mould in the field.

Diptera larvae was the only invertebrate group that was exclusively retrieved through hand sorting, with none being found in Winkler trap samples. This may have been a result of the pale colour of the Diptera larvae found during this study making them easily discoverable amongst the dark-coloured wood mould. It is also possible that Diptera larvae were unable to pass through the mesh of the bags used in the Winkler traps, meaning that some specimens remained unextracted. This hypothesis is supported by the fact that Krell, Chung, *et al*. (2005) also did not retrieve Diptera larvae in their Winkler extraction samples, despite collecting both Coleoptera and Lepidoptera larvae using the traps. In the present study, no remaining signs of life were identified in any of the samples after the trapping period; however, it is possible that some specimens may have desiccated and died in the samples making them difficult to observe in the dry post-trapping wood mould substrate.

The results of this study contrast to previous studies into a different type of extraction trap (Tullgren funnel traps) which were found to collect lower abundances of invertebrate specimens than hand sorting (Nsengimana *et al*., 2017). It is suggested that this may be a result of the heat applied to this type of trap, as many soil invertebrates are vulnerable to desiccation and may die before they are able to leave the soil sample (Nsengimana *et al*., 2017). This is consistent with previous research that has found that Winkler extraction trapping is a preferential technique for extensive specimen extraction, in comparison to alternatives (Fisher, 1999; Kalif & Moutinho, 2000; Krell, Chung, *et al*., 2005).

Moisture content of wood mould in the concrete beetle box

The bottom compartment of the concrete beetle box (below the internal shelf) had a more stable moisture environment than the top compartment, remaining within 4% moisture volume over all sampling sessions, whilst the top compartment varied by up to 33% volume (including the final singular measurement). The more stable conditions in the lower compartment may be a result of temperature-buffering by moisture in the surrounding soil, keeping the lower box compartment cooler and minimising moisture loss through evaporation. Moisture may have also seeped through the external walls of the box, keeping the box at a more consistent moisture level to surrounding ground.

In addition, the lower compartment contained more wood-mould than the top compartment, in which wood mould volume continuously decreased during the study time-period through decay and by dropping down into the bottom compartment. The smaller volumes of wood mould in the top box compartment would have made it more susceptible to influence from surrounding temperature fluctuations. The holes in the lid may have also meant that the top compartment moisture levels were more dramatically influenced by recent rainfall, causing regular moisture fluctuations with the weather. However, the bottom compartment may also have been influenced in this way by water entering the box through the central opening, depending on the extent and direction of rain.

Study limitations

The concrete beetle box monitored in the present study constituted only a single experimental unit. While this provided an initial insight into the functioning of beetle boxes in a garden situation, urban gardens are not homogenous and can differ extensively in character and surrounding landscape. Because of this, the findings of the present study may not be widely applicable to other examples of beetle box use in gardens. Therefore, garden beetle boxes would benefit from wider replication, as discussed in the ‘Recommendations for future research’ section of this chapter.

The results of this study also constitute only preliminary investigation into the functioning of ground-level concrete beetle boxes. The invertebrate fauna is expected to develop and change over time; therefore, the present observations are a snapshot of the beginning phase of saproxylic succession within the box wood mould. The results of this study are unlikely to represent the fauna that would inhabit a beetle box that had been in situ for several years.

Summary of aims

Beetle boxes as a garden feature

Many different invertebrate groups were represented within the concrete beetle box, offering promising opportunity for them to be used as part of educational schemes such as those in schools, to teach about the invertebrates of decay-related habitats. Despite this, at the time of sampling in this study, the saproxylic component of the invertebrate fauna was small, meaning that beetle box application for education of the specific saproxylic fauna may be limited. More monitoring is needed to understand whether beetle boxes in urban areas become more representative of tree-hollow systems over time. The limited saproxylic fauna found in the beetle box during the present study also suggests that use of beetle boxes in areas that are not well connected to ancient woodland has limited conservation value for beetles. However, it is possible that the saproxylic representation will increase as the wood mould in the beetle box continues to mature. Despite the potentially limited conservation potential, the present study demonstrated the application of beetle boxes in monitoring species ranges, as the investigation of the beetle box fauna resulted in a range expansion observation for *A. diecki*.

Concrete as a construction material for beetle boxes

Concrete has shown potential as an effective material for beetle box construction. It was shown to cultivate a stable enough moisture environment to support several invertebrate species with high moisture requirements. This supports the suitability of concrete for beetle boxes, as high moisture levels are known to be beneficial for several species of saproxylic invertebrate (Hövemeyer & Schauermann, 2003; Ulyschen, 2018; Cuff, Müller, *et al*., 2021; Lindman *et al*., 2022). Due to the short timescale of the present study, the structural resilience and durability of the concrete beetle box over periods of several years could not be determined. This is an area that would benefit from monitoring in the future to further asses the applicability of concrete for more widespread use in beetle boxes.

Investigation of beetle box sampling methods

Hand sorting was able to extract a range of the larger specimens from the concrete beetle box. Therefore, hand sorting would be sufficient to show a considerable proportion of the diversity of invertebrate groups present when carried out in an educational context, for example, as a demonstration of the diversity of life found inside decay-rich habitats such as a tree hollows. However, it should be noted that hand sorting alone is likely to miss or underrepresent some invertebrate groups present in wood mould. Winkler trapping was shown to be more effective than hand sorting for the extraction of the most abundant invertebrate groups with smaller body sizes.

Recommendations for future research

To address the fluctuating nature of the invertebrate fauna in decaying wood resources, it is recommended that the invertebrates in the concrete beetle box are monitored over longer periods of time. This would allow newly colonising species to be tracked, increasing understanding of the successional processes that take place in wood mould. It is also recommended that future studies into garden beetle boxes should incorporate a greater number of experimental units in gardens of different types and in different geographical locations. Such replication would strengthen the validity of the results of the study and would allow a greater understanding of the influence of local conditions on the invertebrate fauna inhabiting beetle boxes.

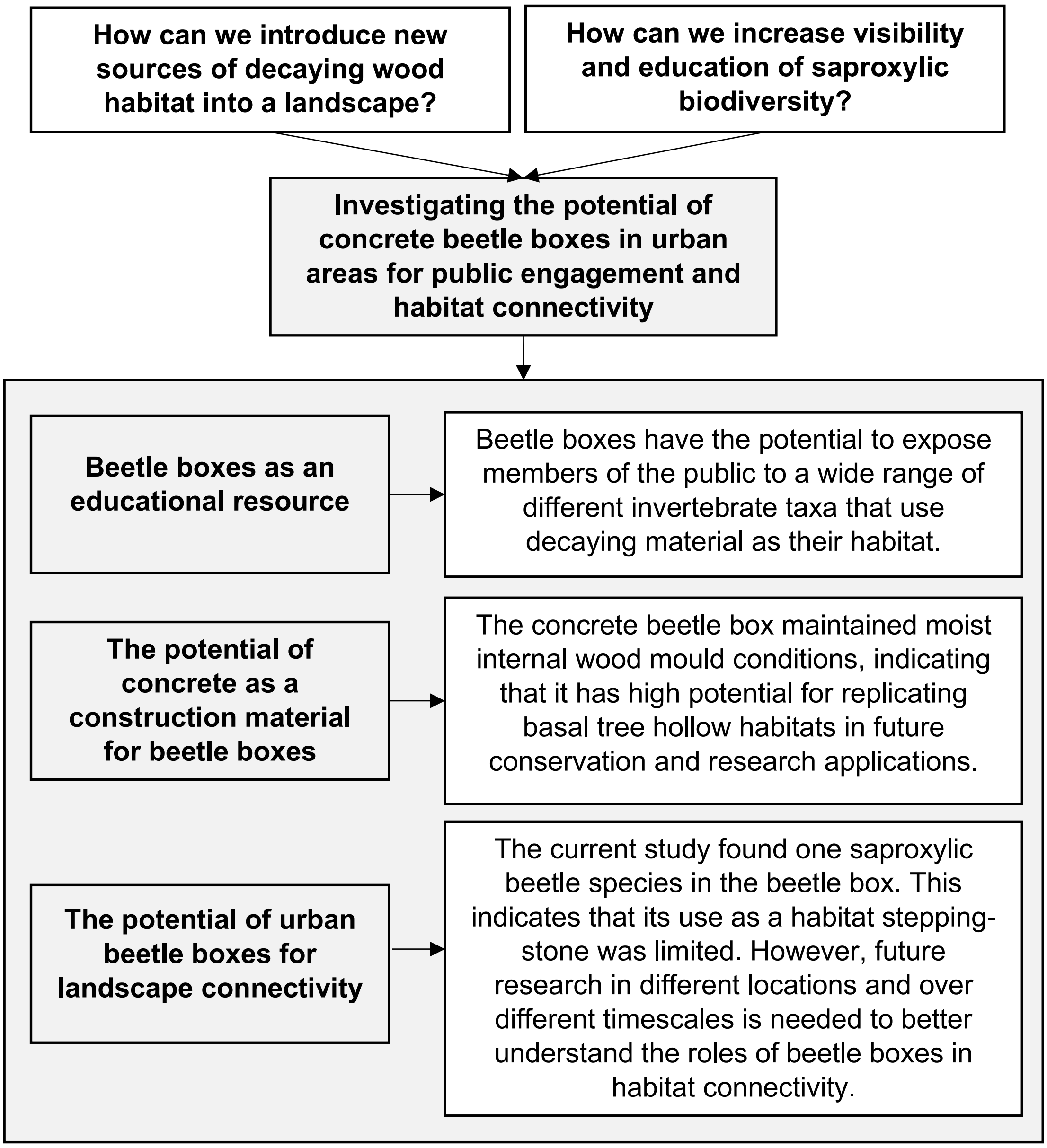


Figure 4.7. A conceptual framework outlining the key findings on the main research areas that this chapter addressed concerning the application of beetle boxes in urban areas for education and habitat connectivity.

Chapter 5 - Concluding summary

5.1 - Research findings and their implications for conservation management

Saproxylic invertebrate populations have been historically depleted through landscape development (Rackham; 1986; Buckland & Dinnin,1993). These depletions have persisted into the present due to continual reduction of habitat through intensive land management and ill-informed removal of deadwood sources for sanitisation purposes (Winter, 1993; Goodburn & Lorimer, 1998; Grove, 2002). In addition, tree age gaps indicate that deadwood habitats are likely to continue to become scarcer in landscapes of the future (Gibbons *et al*., 2008). In attempts to mitigate the effects of reduced habitat on saproxylic species, it is important that the limited resources available for their conservation are used efficiently for maximal benefit. The research of this thesis contributed valuable knowledge to aid this by investigating several interrelated areas of key importance to the conservation of saproxylic invertebrates. The results of these studies add to the emerging body of scientific evidence being used to inform conservation practices for saproxylic species. They may be used to challenge ineffective management practices, supporting progress towards a more informed, wholistic approach to woodland health maintenance. Through this, saproxylic invertebrate communities can be given the most appropriate support to maintain their biodiversity and prevent local extinctions.

Due to the threat of habitat fragmentation and population isolation, dispersal is a key area of concern in the conservation of saproxylic beetle communities (Harding & Rose, 1986; Svensson *et al*., 2011). To address this, Chapter 2 of this thesis contributed new data on the scales that are important for saproxylic species movement. This built upon previous research, such as that of Bergman *et al*. (2012), whilst providing increased relevance to UK open grown oak wooded landscapes. A key finding of Chapter 2 was that the number of habitat trees within a 250 m scale was strongly associated with the overall species richness and rare species richness of saproxylic beetles in veteran oak trees. This finding could inform the management of deadwood habitat resources in open oak woodlands. For example, it indicates that trees within a 250 m radius of high-potential veteran trees should be retained and prioritised for the application of veteranisation practices to promote future deadwood connectivity. Where existing trees are particularly sparse within a 250 m radius of a veteran tree, there is also potential for tree planting to occur to supplement deadwood stocks in the future. it is important that such planting is planned in a way that minimises the shading of existing trees and maintains the character of an open woodland (Miklín *et al*., 2018). These planting initiatives could be accompanied by the implementation of beetle boxes, as a supplementary resource to support species movement in the years before new trees show signs of deadwood habitat formation.

Furthermore, Chapter 2 provided additional evidence for the effectiveness of veteranisation practices. For example, it showed that young, small-diameter trees with saproxylic habitat features can host levels of saproxylic beetle diversity that are comparable to those of larger trees. It also found that lightning strikes are associated with several key deadwood microhabitats, such as tree hollows and areas of peeling bark, further highlighting the role that tree damage plays in shaping the formation of veteran tree characteristics. These insights could give land managers further confidence in applying veteranisation techniques to trees in wooded landscapes, demonstrating their high potential in supporting aspects of deadwood biodiversity. These findings also suggest that younger trees with fresh lightning-damage would be appropriate candidates to be prioritised for retention, as they have an increased likelihood of developing valuable saproxylic habitats as they age.

The finding of several strong associations of the richness of rare saproxylic beetle communities with habitat tree number within short distance radii in Chapter 2 supported the conclusions of previous research (e.g. Brunet & Isacsson (2009)) that rare species can have a tendency for limited dispersal. This was further supported by the observation of several rare species that were only recorded in one high-quality ancient tree, being potentially limited by a high level of isolation from other habitat trees. This highlights the need for land managers to be aware of rare species populations and to ensure that appropriate habitat resources are available, ideally within distances of 25-250 m of known hot spots, to aid movement of these species across the landscape. This would improve the resilience of rare species (Schiegg, 2000a), lowering the threat of their local extinction associated with the potential loss of a single, isolated habitat tree.

Chapter 2 also identified several links between different deadwood-associated microhabitats and particular saproxylic species. This provides evidence that the retention of a variety of different deadwood types in wooded landscapes benefit various subsets of saproxylic diversity. The fact that the wooded landscapes studied provided a sufficient range of decaying wood features to support the high numbers of saproxylic beetle species found in the traps further highlights the national importance of the chosen sites to biodiversity. This finding supports the recent changes in government legislation to confer increased protection to pasture woodlands.

These findings contribute to a body of knowledge helping to revolutionise woodland conservation, moving away from the outdated practices used in the past. They indicate that the removal of deadwood for sanitary or aesthetic reasons is likely to cause direct harm to saproxylic biodiversity at a site, with further repercussions to ecosystem services that the impacted communities contribute to. In addition, the results of Chapter 2 could play a role in the improvement of woodland planning and effective resource use. By ensuring that tree planting and deadwood creation regimes are carried out with appropriate tree spacing, funding can be used economically to allowing it to stretch further for increased conservation benefit.

This thesis further addressed habitat connectivity for saproxylic species by investigating beetle boxes, which are thought to have the potential to act as deadwood habitat stepping-stones (Jansson, Ranius, *et al*., 2009). In addition, they present an opportunity to overcome periods of depleted deadwood resource availability resulting from gaps in tree age structures (Harding & Rose, 1986). Previous research into the beetle box concept is limited, meaning that the data generated by this thesis on their benefits and limitations constitute a valuable addition to the developing knowledge around their appropriate usage.

A novel ground level design was tested in Chapter 3 in the hope that it may play a role in supporting the endangered umbrella species, *Limoniscus violaceus*, which is threatened by tree age gaps within the limited sites in which it occurs. The results of this study build upon past research (Jansson, Ranius, *et al*., 2009; Carlsson *et al*., 2016) in finding that beetle boxes can provide suitable habitat resources for tree-cavity specialist beetles. At this stage it remains unclear whether beetle boxes will play an active role in supporting populations of *L. violaceus*. However, as beetle boxes are known to be increasingly used by tree-hollow specialist beetles after longer periods of maturation time (Carlsson *et al*., 2016), future monitoring of their colonisation over time would be beneficial in fully understanding the value of beetle boxes for this species. The experimental infrastructure established during this study enables this, allowing the research of Chapter 3 to continue into the future.

Analysis of the performance of different beetle box variations allowed findings to be drawn that could inform beetle box methodologies in conservation management schemes. For example, the results of Chapter 3 showed that the addition of poultry manure to beetle box contents increased the diversity and abundance of saproxylic and deadwood-associated beetles found in the boxes over the timescale studied. As a result, the addition of manure could be recommended for future beetle box applications as a method of increasing their suitability for these groups.

Similarly, the observation of Elaterid larvae forming pupal cells in compacted sawdust around the lids of beetle boxes supports the findings of Gouix *et al*. (2012) that heterogenous consistencies of decaying wood can be beneficial for saproxylic beetle development. Therefore, the maintenance of variable textures of decaying wood should be prioritised in future beetle box trials, for example, by intentionally including compartments of compacted wood for beetle pupation.

This thesis also constitutes the first research into the impacts of using alternative construction materials for beetle boxes. Chapter 3 showed that plastic boxes supported similar levels of diversity and abundance of saproxylic and woodland associated beetles to those in wooden boxes. This suggests that plastic beetle boxes have high potential for providing tree hollow- mimicking habitats in future initiatives, offering a longer-term habitat solution than wooden boxes. It was also noted that the wood mould in the plastic beetle boxes contained significantly less moisture than the wooden design. This observation can be used to inform design alterations of plastic beetle boxes, tailoring them to future conservation applications. For example, interest was expressed into the use of beetle boxes in a recent IUCN meeting on the conservation of saproxylic hoverflies. As flies often require particularly moist tree hollow substrates (Ulyshen, 2018), it may be advised that plastic box designs are equipped with enhanced drainage features to achieve an appropriate level of water content in the wood mould for this group.

Additionally, initial steps were made into the investigation of concrete as a beetle box construction material in Chapter 3. Through this, concrete was found to have the potential to provide appropriately moist conditions for the imitation of tree hollow environments. In combination with its resilience and longevity, this finding indicated that concrete is a promising construction material for future beetle box studies.

Finally, this research investigated a potential future method of raising the public profile of saproxylic communities through the use of beetle boxes as an educational tool (Chapter 4). The examination of wood mould from a beetle box in a wildlife garden setting can allow members of the public to be exposed to a wide variety of different invertebrate groups. Such experiences can help people realise the extent of the hidden life inside decaying wood, demonstrating the need to consider these habitats in the conservation of biodiversity in their local landscapes. They may even be encouraged to add decaying wood structures like beetle boxes to their own gardens and community spaces, making a practical difference to saproxylic conservation. This potential is supported by real-world experiences, as discussion of the beetle box project at public events throughout this project raised considerable attention from conservation organisations, educational facilities, and members of the public who expressed an interest for installing beetle boxes on their land. It is therefore clear that beetle boxes have a high potential as a means to engage people and bring positive attention to saproxylic communities from a biodiversity conservation perspective.

5.2 - Recommendations for future research

Although the present research has resulted in various findings of importance to future saproxylic conservation, it is important to note that the short timescale of this work was not sufficient to study these processes to the fullest extent. This is due to the time scales associated with decaying wood maturation and the progression through ecological stages of succession in saproxylic systems (Carlsson *et al*., 2016). As a result, the most important consideration for future extensions of this research and other strands of saproxylic study, is that long-term monitoring is prioritised.

Key examples of these include:

- The long-term monitoring of the beetle boxes set up during the present study for future signs of *L. violaceus* colonisation
- Long-term studies into the application of deadwood connectivity enhancing techniques such as veteranisation and beetle boxes in open oak woodlands and their influence on species movement between isolated trees

The first suggestion would form a more rigorous investigation of the use of beetle boxes in conservation schemes for this endangered species, without the likely interference of insufficient maturation time that limit the present results. A long-term study would also offer the opportunity to thoroughly trial the longevity of the different beetle box construction materials trialled in Chapter 3, making it possible to observe the timescale of their degradation when deployed in the field for several years.

The second suggestion would provide new insights into the practical applications of novel conservation methods such as beetle boxes in supporting valuable habitats through challenges facing them, such as tree community age gaps. Investigation into combined applications of various conservation methods (such as species monitoring alongside tree veteranisation and beetle box implementation) should be prioritised in the future, as this has the potential to improve deadwood resources for saproxylic species in various contexts.

In addition to longer timescales, studies over greater spatial areas would also generate beneficial insights into the practical applications of the key concepts of this research. For example, studies into the application of beetle boxes and veteranisation processes over wider fragmented landscapes would prove valuable. The subsequent monitoring of species movement from such studies could generate a better understand of the extent to which processes need to be deployed to bring significant positive change to UK saproxylic biodiversity.

It would also be interesting to carry out wider public engagement schemes, using beetle boxes to expose non-specialists to deadwood biodiversity. This could be accompanied with a social study into the resultant impacts on public attitudes towards the value and roles of saproxylic species in woodland ecosystems.

5.3 - Concluding remarks

This research has shown that the application of novel techniques has the potential to enhance saproxylic conservation. It is hoped that the findings will be used to support evidence-based approaches to the management of wooded landscapes with a focus on deadwood habitat maintenance over space and time. This could contribute to the conservation of a threatened species group, aiding the prevention of extinctions in a time of deadwood resource scarcity.

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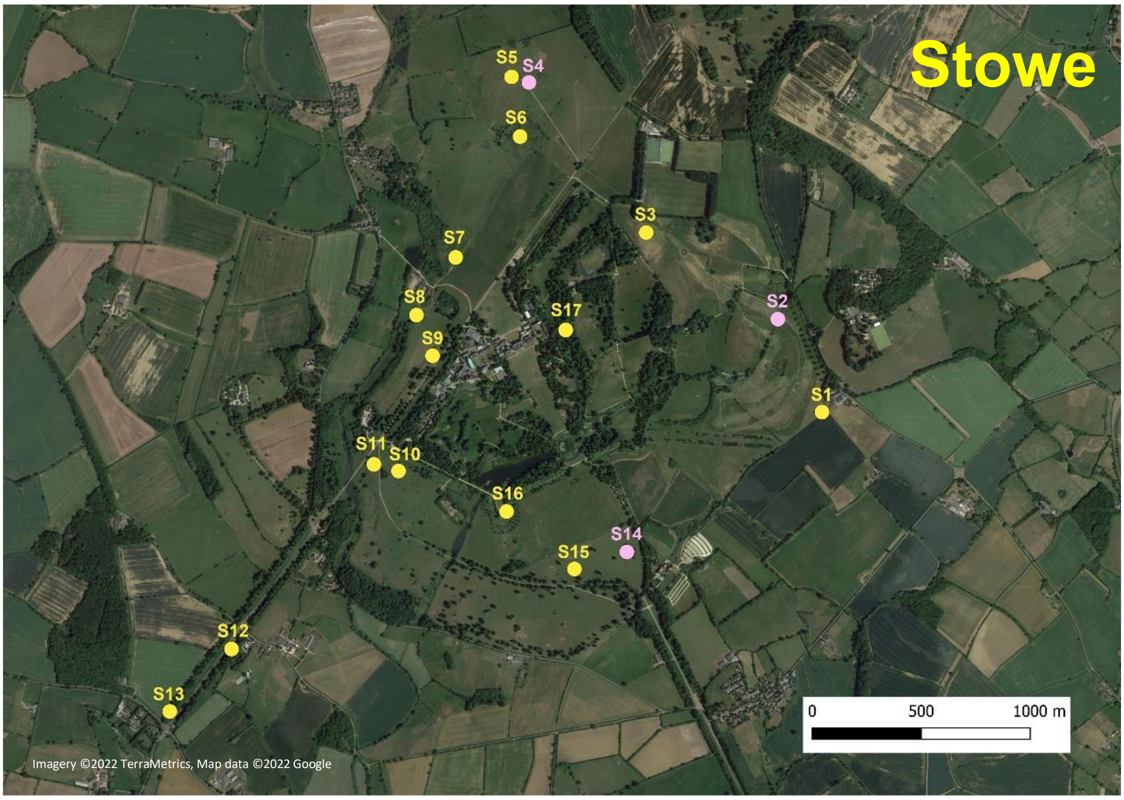
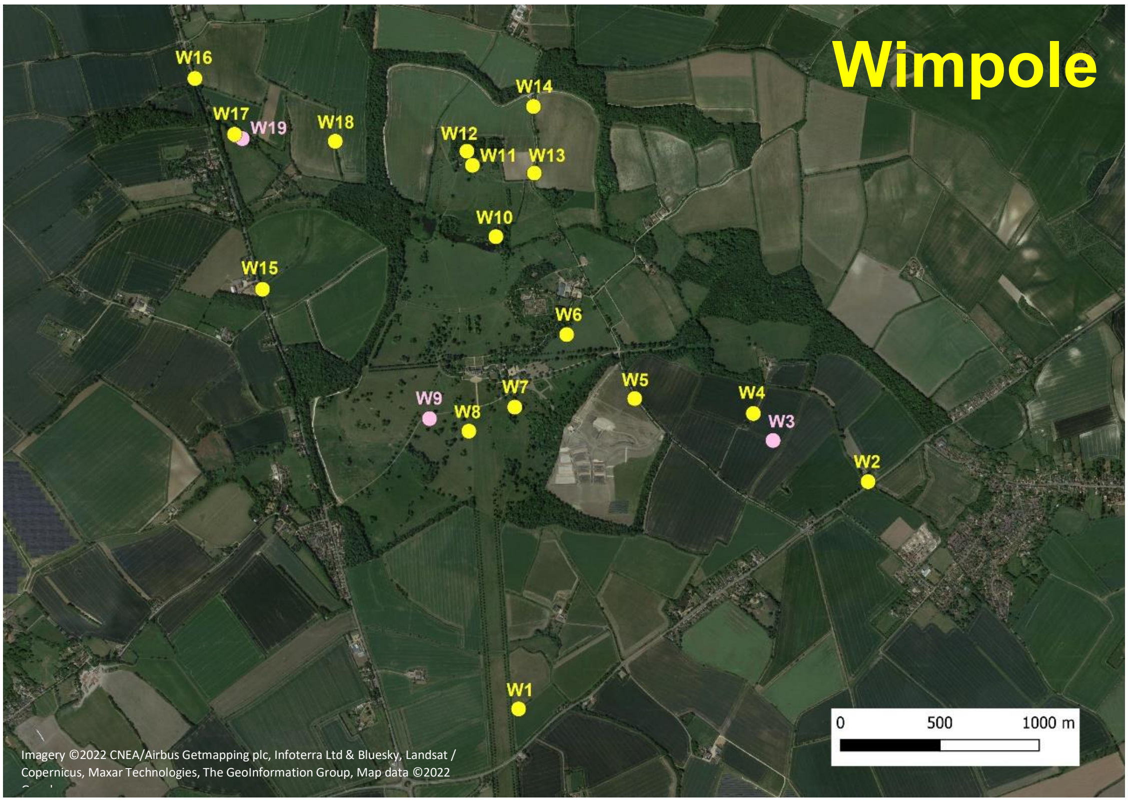
Appendix A. Maps showing the labelling codes used to identify the trapping trees in the study of Stowe and Wimpole (Chapter 2).





Appendix B. Beetle species collected from individual traps at Stowe National Trust Landscape and the surrounding arable land (Chapter 2). Codes used in the column titles correspond to the tree labels shown in Appendix 1. Columns coloured grey represent traps that were discounted from statistical analysis due to faults influencing their ability to continuously collect specimens during their periods of deployment.

Species	**S1**	**S2**	**S3**	**S4**	**S5**	**S6**	**S7**	**S8**	**S9**	**S10**	**S11**	**S12**	**S13**	**S14**	**S15**	**S16**	**S17**
Abdera biflexuosa	0	0	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0
Abdera quadrifasciata	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
Acalles misellus	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Achopera alternata	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Aeletes atomarius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Agrilus laticornis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0
Ampedus cardinalis	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ampedus quercicola	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Anaspis fasciata	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Anaspis frontalis	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Anaspis maculata	0	0	0	1	0	1	0	0	0	0	0	1	0	0	1	1	0
Anaspis regimbarti	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anisotoma humeralis	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0

Anobium inexpectatum	0	9	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0
Anobium punctatum	0	1	0	0	1	7	0	0	0	0	0	0	0	0	1	0	0
Axinotarsus marginalis	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Cerylon ferrugineum	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	2
Cis bilamellatus	0	0	0	0	0	3	0	1	4	0	2	0	0	0	2	2	0
Cis boleti	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Cis fagi	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
Cis micans	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Cis pygmaeus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Cis vestitus	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0
Cis villosulus	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0
Cryptolestes duplicatus	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Cryptophagus dentatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Cryptophagus scanicus	0	1	0	0	0	0	0	0	3	0	0	0	0	2	0	0	0
Ctesias serra	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dacne bipustulata	3	6	0	0	1	5	1	9	5	1	6	4	0	10	2	7	1
Dacne rufifrons	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
Dienerella vincenti	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Dorcatoma chrysomelina	0	0	0	0	2	0	0	0	1	2	0	0	0	0	0	0	0
Dorcatoma dresdensis	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0

Dorcatoma flavicornis	0	0	0	0	0	0	2	0	1	0	2	0	0	0	0	1	0
Dorcatoma substriata	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0
Dromius meridionalis	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Dromius quadrimaculatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Dryocoetes villosus	0	0	1	0	0	0	0	1	0	5	1	3	0	4	1	0	0
Eledona agricola	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Enicmus brevicornis	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2
Enicmus rugosus	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Enicmus testaceus	0	0	0	0	0	0	0	7	0	0	0	1	2	0	2	0	1
Ennearthron cornutum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Epuraea aestiva	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Ernoporicus fagi	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Euglenes oculatus	0	0	1	0	2	3	1	1	0	11	1	8	0	1	10	0	0
Eulagius filicornis	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0
Euophryum confine	1	1	0	0	0	3	0	10	0	0	0	1	0	0	0	0	0
Euplectus karstenii	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	1
Gnathoncus buyssoni	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0

Gnathoncus rotundatus (nanus)	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Grammoptera ruficornis	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0
Hedobia imperialis	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Hemicoelus fulvicorne	0	1	4	3	0	0	4	0	0	8	0	3	10	0	2	0	0
Hylesinus crenatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
Hylis olexai	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Kissophagus vicinus (hederae)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Lymexylon navale	0	0	0	0	0	1	0	0	0	0	0	0	0	0	3	1	0
Malthinus balteatus	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
Malthodes minimus	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Melanotus castanipes	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Melanotus villosus	1	1	0	0	0	1	0	1	0	0	0	1	1	0	0	2	0
Melasis buprestoides	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Mycetochara humeralis	0	0	1	0	0	0	0	0	0	0	0	0	0	2	6	0	0
Mycetophagus multipunctatus	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0

Mycetophagus piceus	0	3	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Mycetophagus quadripustulatus	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0
Ochina ptinoides	0	8	0	0	0	0	0	0	0	2	0	0	0	1	0	0	1
Oligella intermedia	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Orthoperus nigrescens	0	0	0	0	0	2	1	7	0	0	0	4	0	2	0	0	1
Paromalus flavicornis	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0
Platypus cylindrus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Plegaderus dissectus	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Prionychus ater	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Ptilinus pectinicornis	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Ptinella aptera	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0
Ptinella errabunda	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Salpingus planirostris	1	0	2	1	0	0	0	0	0	0	0	1	1	0	0	0	1
Salpingus ruficollis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Scolytus intricatus	0	0	0	0	13	0	0	0	0	2	0	12	0	0	0	0	0
Scydmaenus rufus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Sinodendron cylindricum	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0

Symbiotes latus	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0
Taphrorychus bicolor	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Trichonyx sulcicollis	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Triplax russica	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Trox scaber	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Xyleborus dryographus	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Xyleborus monographus	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0

Appendix C. Beetle species collected from individual traps at Wimpole National Trust Landscape and the surrounding arable land (Chapter 2). Codes used in the column titles correspond to the tree labels shown in Appendix 1. Columns coloured grey represent traps that were discounted from statistical analysis due to faults influencing their ability to continuously collect specimens during their periods of deployment.

Species	**W1**	**W2**	**W3**	**W4**	**W5**	**W6**	**W7**	**W8**	**W9**	**W10**	**W11**	**W12**	**W13**	**W14**	**W15**	**W16**	**W17**	**W18**	**W19**
Aderus populneus	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0
Agrilus laticornis	0	0	0	0	0	1	2	2	0	0	4	0	0	0	0	0	0	0	0
Anaspis fasciata	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0
Anaspis frontalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Anaspis maculata	0	0	0	0	0	0	1	0	0	0	0	0	2	2	0	0	0	1	0
Anaspis regimbarti	0	0	0	5	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Anobium inexpectatum	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anobium punctatum	0	0	0	1	2	0	0	0	0	0	1	0	0	1	0	1	0	0	0
Aulonothroscus brevicollis	35	0	0	0	3	1	0	0	0	4	1	2	0	0	0	0	0	2	1
Axinotarsus marginalis	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0
Baeocrara variolosa	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0
Cerylon ferrugineum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Cis bilamellatus	0	0	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0

Cis micans	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cis pygmaeus	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Cis vestitus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Clytus arietis	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Cryptarcha undata	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Cryptophagus dentatus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Cryptophagus labilis	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Cryptophagus ruficornis	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Cryptophagus scanicus	4	3	0	4	0	4	2	0	0	0	1	1	0	1	0	3	1	0	0
Ctesias serra	1	1	0	0	0	2	0	4	1	0	0	0	0	0	0	0	0	0	3
Dacne bipustulata	1	22	0	11	5	9	2	27	8	15	13	0	2	3	2	5	1	5	0
Dacne rufifrons	0	1	0	0	0	0	1	0	2	0	0	1	1	0	0	0	1	0	2
Diaperis boleti	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diplocoelus fagi	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Dorcatoma chrysomelina	0	1	0	6	52	4	0	0	4	26	4	13	11	0	0	0	0	0	0
Dorcatoma flavicornis	0	0	0	0	4	2	0	0	0	13	0	0	0	0	0	0	0	0	0
Dorcatoma substriata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Dromius meridionalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
Dromius quadrimaculatus	2	0	0	1	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0
Elater ferrugineus	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0

Eledona agricola	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Enicmus brevicornis	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Enicmus rugosus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	1
Enicmus testaceus	2	0	0	0	0	0	0	1	0	0	1	0	1	0	5	0	10	0	0
Ennearthron cornutum	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Euglenes oculatus	2	0	0	0	4	8	0	1	64	10	8	52	1	1	0	1	2	0	0
Euophryum confine	2	0	0	1	0	0	0	0	0	0	0	2	0	0	0	0	4	0	0
Euplectus karstenii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Grammoptera ruficornis	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hedobia imperialis	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hemicoelus canaliculatus	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Hemicoelus fulvicorne	1	2	0	0	1	10	1	1	2	0	0	0	1	2	0	0	1	0	1
Hylesinus varius	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Kissophagus vicinus	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lissodema denticolle	0	0	0	0	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Litargus connexus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0

Malthinus balteatus	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Malthinus frontalis	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Malthinus seriepunctatus	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Malthodes marginatus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Melanotus castanipes	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0
Melanotus villosus	0	2	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	1	0
Melasis buprestoides	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Mordellochroa abdominalis	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Mycetochara humeralis	0	2	0	0	0	1	1	0	0	0	1	6	0	0	0	1	4	0	0
Mycetophagus multipunctatus	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mycetophagus piceus	0	1	0	2	5	2	0	0	0	1	2	2	0	0	0	3	0	0	0
Mycetophagus populi	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mycetophagus quadripustulatus	0	0	0	2	0	0	0	1	2	0	0	0	1	0	0	0	0	0	0
Ochina ptinoides	0	10	1	2	0	0	0	0	0	0	0	1	2	0	0	0	1	0	0
Opilo mollis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Orthoperus nigrescens	5	3	0	0	0	0	0	0	0	1	1	1	2	2	8	4	1	0	6

Paromalus flavicornis	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Pediacus dermestoides	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phymatodes testaceus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plegaderus dissectus	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Prionocyphon serricornis	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Procraerus tibialis	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
Pseudocistela ceramboides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1
Ptilinus pectinicornis	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Ptinus sexpunctatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Rhizophagus bipustulatus	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Salpingus planirostris	0	1	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1
Scolytus intricatus	0	0	0	0	0	0	0	0	0	0	2	1	29	0	1	0	0	1	0
Scraptia testacea	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Sinodendron cylindricum	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Soronia grisea	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stenagostus rhombeus	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0

Stereocorynes truncorum	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Symbiotes latus	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Taphrorychus bicolor	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Tillus elongatus	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Tomoxia bucephala	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0
Triplax russica	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0
Trox scaber	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Xyleborus monographus	0	0	1	0	0	0	0	11	1	0	0	0	0	0	0	0	0	0	0

Appendix D. Tree feature data collected for trapping trees at Stowe used in statistical analysis (Chapter 2). Codes used in the column titles correspond to the tree labels shown in Appendix 1. More information on the units and categorisation methods used for each of the feature measurements can be found in Table 2.2.

Feature	**S1**	**S3**	**S5**	**S6**	**S7**	**S8**	**S9**	**S10**	**S11**	**S12**	**S13**	**S15**	**S16**	**S17**
Height (m)	8.549615	25.88889	14.30411	17.14078	15.82171	15.69208	12.17778	24.46328	25.39007	29.81236	30.52566	21.90096	24.16162	17.09418
Diameter Breast Height (DBH)(cm)	190.35	175.07	117.46	130.51	178.89	178.25	134.01	135.92	167.43	141.65	116.50	120.96	106.63	154.06
Epicormic growth base	A	P	A	A	A	A	A	A	A	A	A	A	A	P
Epicormic growth trunk	P	A	A	P	P	A	A	P	A	A	A	A	P	P
Epicormic growth crown	P	A	P	P	P	P	P	P	A	A	P	A	P	P
Bark depletion (%)	35	8	0.5	15	0	60	60	2.5	15	15	1	60	13	0
Sap runs	0	0	5	0	0	0	0	2	1	1	0	1	0	1
Split limbs	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Tears	1	6	2	2	2	1	3	1	2	6	7	3	1	1
Scars	2	1	4	1	4	2	1	3	1	0	4	0	6	3
Lightning strikes	A	A	A	P	A	P	P	A	P	A	A	A	A	A
Hollowing	1	1	1	3	1	4	3	1	1	1	1	1	1	1

Holes base	7	0	2	2	0	5	0	2	0	0	0	0	3	0
Holes trunk	4	1	3	3	1	2	10	2	2	0	0	3	1	2
Holes branches	0	3	0	0	1	1	0	0	1	3	0	0	0	0
Water pockets	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Red rot	P	P	P	P	P	P	A	P	P	P	A	P	P	A
White rot	A	P	P	P	A	P	P	A	P	P	P	P	P	P
Attached deadwood	8	56	43	40	40	25	10	18	21	18	13	70	50	18
Fallen deadwood	0	0	15	0	75	40	0	3	9	22	2	9	0	0
Fungi	P	A	P	A	A	A	P	P	A	P	P	P	A	P
Lichen (%)	7	2	1	1	2	1	1	3	4	1	1	2	2	5
Moss (%)	0	1	0	0	0	1	0	0	0	1	1	2	0	8
Ivy (%)	0	0	0	0	0	0	0	0	0	0	0	0	3	40
Mammal signs	P	P	P	P	A	A	A	P	A	A	A	P	P	P
Bird signs	A	A	A	A	A	A	A	A	P	P	A	P	A	A
Habitat context	PX	PX	PX	PX	PX	PX	PL	PL	PL	AV	AV	PL	PL	GO
Damage	A	P	P	A	A	A	A	A	P	P	A	A	A	A
Shade	0	20	0	0	0	10	5	0	0	35	40	30	20	60
Feature nearest trap	HOLLOW	BRANCH	TEAR	TEAR	TEAR	TEAR	DENUDED	BRANCH	TEAR	TEAR	TEAR	DENUDED	DENUDED	TEAR
Exposure	2	1	3	2	3	1	2	2	2	0	0	2	2	0

Appendix E. Tree feature data collected for trapping trees at Wimpole used in statistical analysis (Chapter 2). Codes used in the column titles correspond to the tree labels shown in Appendix 1. More information on the units and categorisation methods used for each of the feature measurements can be found in Table 2.2.

Feature	W1	W2	W4	W5	W6	W7	W8	W10	W11	W12	W13	W14	W15	W16
Height (m)	16.56611	19.58082	18.3791	20.05403	24.86788	20.30108	17.6874	31.555	17.50628	24.16162	14.36542	14.63277	15.82171	12.77285
Diameter Breast Height (DBH)(cm)	161.70	143.24	124.78	167.43	180.80	140.69	123.19	121.59	172.21	142.92	106.32	139.10	95.49	98.36
Epicormic growth base	A	A	A	A	A	A	A	A	A	P	A	A	A	A
Epicormic growth trunk	P	P	P	A	P	A	A	P	A	P	A	P	P	A
Epicormic growth crown	P	P	A	P	P	P	P	P	P	P	P	P	P	P
Bark depletion (%)	1	1.5	0	1	0.5	0	45	0.5	8	2	0.5	0	0	15
Sap runs	0	1	0	1	2	0	1	0	0	0	2	0	1	1
Split limbs	0	0	0	1	1	1	0	0	0	0	0	0	0	1
Tears	5	8	4	4	10	0	4	1	3	8	4	3	2	2
Scars	5	6	3	2	3	3	2	7	3	2	6	9	3	2
Lightning strikes	A	A	A	A	A	A	A	A	A	A	A	A	A	A
Hollowing	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Holes base	6	0	0	4	4	2	1	2	0	0	0	0	0	0
Holes trunk	4	3	4	0	0	0	11	2	0	1	4	1	2	3
Holes branches	2	0	4	4	2	0	0	0	4	4	1	0	0	0
Water pockets	1	1	0	0	0	2	0	0	1	0	0	0	0	0
Red rot	P	A	P	P	A	A	P	P	P	A	P	A	P	A
White rot	P	P	P	P	P	P	P	A	P	P	P	P	A	A
Attached deadwood	62	41	80	53	32	54	30	24	12	68	32	22	18	18
Fallen deadwood	3	0	0	2	74	2	0	24	14	18	0	0	0	2
Fungi	P	A	A	P	P	A	A	A	A	A	A	P	A	A
Lichen (%)	2	1	5	2	2	4	2	1	0	1	10	5	2	5
Moss (%)	0.5	0	0	0	4	2	0.5	1	8	0	5	15	0	0
Ivy (%)	0	15	60	35	0	0	0	0	0	0	0	0	3	0
Mammal signs	P	A	A	P	P	A	A	P	A	P	A	A	P	A
Bird signs	P	A	P	A	P	A	P	P	P	P	P	A	A	P
Habitat context	AR	UT	AR	AR	PL	PL	PL	PO	PL	WL	AR	AR	AR	AR
Damage	P	P	P	A	A	A	A	A	A	A	A	A	A	A
Shade	0	5	0	10	5	15	15	35	10	60	5	15	35	15
Feature nearest trap	HOLLOW	HOLLOW	HOLLOW	HOLLOW	TEAR	BRANCH	DENUDED	HOLLOW	TEAR	TEAR	BRANCH	BRANCH	TEAR	HOLLOW
Exposure	1	2	3	3	2	2	3	1	2	1	2	2	1	1