The effects of land use change on the population expansion of a poor disperser, the wood ant *Formica lugubris*

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Abstract

Habitat fragmentation and destruction is one of the most likely causes of recent biodiversity losses. Anthropogenic land use change can create highly fractured landscapes, in which patches of original habitat become isolated. Fragmentation and the associated habitat loss, can result in species range contractions, species declines and extinctions.

In the UK, areas of ancient woodland which formerly covered a large proportion of the land, are now highly fragmented and isolated due to human activities. Since the 1900's, large scale afforestation of non-native conifer plantations has occurred across the UK. Assessing the expansion of forest species into this new habitat is crucial to understand the extent to which non-native plantations support native woodland biodiversity, especially as significant colonization lags can occur when new habitat is created. This is important when considering that plantation woodland may act as corridors between ancient woodland that have acted as refuges for many UK forest species.

The hairy wood ant, *Formica lugubris*, is a forest specialist and considered to be an ecosystem engineer due to its role in shaping energy flow through woodland ecosystems. Further to this, *F. lugubris* mounds provide a crucial habitat for many myrmecophile species. In this thesis, I show how populations of *F. lugubris* are continuing to expand and colonise new areas of plantation on the North York Moors. The populations of *F. lugubris* at three different field sites were resurveyed across multiple field seasons. A combination of steady, slow, expansion and rapid expansion into new areas was seen, dependent on stand heterogeneity.

 At a unique site where detailed past forest management strategies are known, I show how row thinning could be used as a potential strategy in increasing wood ant colonisation. Using *row thinning could potentially act as corridors to connect populations which have been* isolated since the woodland was fragmented. Nest attribute and microhabitat data was collected for all nests within the row thinned area in order to see whether certain factors could predict nest survival. A predictive GLM was built and I found that nest volume was the most important predictor of nest survival in the following year. The results from this study show that populations of *F. lugubris* at the field sites are continuing to expand and suggests that row thinning may be a conservation strategy forest managers could utilise to conserve wood ants and aid their expansion. The nest data collected at the newly colonised areas could be used to inform parameters used in future dispersal models.

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Author's Declaration

I declare that this thesis is a presentation of original work and I am the sole author. This work has not previously been presented for an award at this, or any other, University. All sources are acknowledged as References.

Chapter.1 Thesis Introduction

1.0 The importance of studying the movement of populations

Understanding what governs the spatial extent of populations and how their space-use changes is important for several reasons. Beyond the intrinsic value in understanding how a species interacts with its environment to colonise new areas, it is important to understand how populations change over time in response to habitat properties and changes. The most extreme of these responses is the movement of a species when habitat is destroyed or fragmented.

1.01 Habitat fragmentation

Habitat destruction is one of the biggest threats to global biodiversity and a driver of biodiversity loss (Wilcove *et al.* 1998; Brooks *et al.* 2002; Tilman *et al.* 2014). The destruction of an area of habitat can lead to highly fragmented landscapes. Fragmented landscapes occur when only small islands of the original habitats remain. A fragmented landscape is also referred to as 'patchy'. The patches of original habitat can serve as a refuge for species that can no longer survive in the destroyed or altered habitat outside of the patch. If the patches are close enough, and the species is mobile enough, then the patches can act as stepping stones through the new landscape. However, if members of a species are not able to leave their patch, they can become isolated. The isolation of populations due to habitat fragmentation and loss is a major cause in the decline of global biodiversity (Haddad *et al.* 2017b).

The scale at which fragmentation occurs will have a different effect on different organisms. Those which are better adapted to disperse through a landscape are potentially less effected. If species have traits that lend themselves to colonisation, for instance wind pollination in plants, then they are generally less effected by the impact of isolation (Harper *et al.*, 2005; Alados *et al.*, 2010). However, slow-colonising species with short dispersal distances are more vulnerable to extinction in fragmented landscapes (Johst, Brandl and Eber, 2002). Long-range dispersal in a

dynamic landscape has a positive effect on persistence, due to long range dispersal events allowing the colonisation of newly suitable habitat (Johst, Brandl and Eber, 2002). Therefore, the effect of habitat fragmentation on a species depends on the distance between patches of suitable habitat and whether an organism can travel that distance.

Populations that become isolated suffer from a lack of new genetic material; this leads to high levels of inbreeding, which reduces the genetic diversity within a population (Wright, 1943). A lack of genetic diversity means that the population may have an increased susceptibility to pathogens, high genetic load, and less protection against environmental challenges such as droughts (Frankham, 2008; Caro and Laurenson, 2004). Isolated populations with reduced genetic variation will be less able to survive future environmental change (Aguilar *et al.* 2008; Booy, 2008; Caro and Laurenson, 2004). Fragmented landscapes that cause populations to become isolated reduce the 'health' of a population in this way. Over time the isolation of a population can lead to extinction events, resulting directly from an inbreeding depression (Frankham, 1998) or from stochastic local extinctions which cannot be repopulated due to the spatial isolation of the habitat. However, not all fragmentation leads to genetic losses, especially for plant species (Young *et al.*, 1996; Krammer *et al.*, 2008). Population size within the fragments and the ability to disperse between patches plays a large effect on extinction chances (Templeton *et al.*, 1990) To facilitate connectivity between isolated populations in order to increase genetic diversity, appropriate conservation responses are required. Understanding how individuals can move between patches and facilitating connectivity between populations is crucial to increase the chance of survival of isolated populations.

Habitat connectivity is function of the dispersal capabilities of individual species within a habitat area, taking into account the quality and spatial arrangement of the habitat (Hodgson *et al*, 2009; Olds *et al.*, 2011). Connectivity is vital for persistence and productivity (Olds *et al.*, 2011). Increased connectivity increases the resilience of ecosystems, with connected populations more able to recover from disturbances (Mumby and Hastings, 2002). Connections between habitat influence populations across a wide taxa in both terrestrial and aquatic communities (Olds *et al.*, 2011).

Fragmentation does not always lead to isolation; this is highly species dependent. Often, fragmentation and isolation are not investigated separately, or isolation is used as a measure of habitat fragmentation (Mossman and Waser, 2001; Rukke, 2000). There are also differing definitions of fragmentation: some researchers define fragmentation as 'a disruption in landscape connectivity' (With *et al.* 1997; Young and Jarvis 2001). A more common definition defines fragmentation as a process in which 'a large expanse of habitat is transformed into a number of smaller patches of smaller total area, isolated from each other by a matrix of habitats unlike the original' (Wilcove *et al*, 1986). However, the assumption that fragmentation and isolation are intrinsically connected has two weaknesses (Fahrig, 2003).

The first of these weaknesses is that habitat fragmentation is a landscape-scale process (McGarigal and Cushman, 2002; Fahrig, 2003), therefore, in studies exploring the effects of habitat fragmentation on biodiversity, the number of study sites is low. In the field the number of sites is typically two: one a landscape of continuous habitat and one with a fragmented habitat (MacNally *et al*, 2000; Fahrig, 2003). This means that other differences between the two landscapes could be responsible for any apparent effects of fragmentation (Fahrig, 2003).

The second weakness of approaching fragmentation as a process is the assumption that each of the landscapes being investigated can be in only two states; continuous or fragmented (Fahrig, 2003). When investigating the effect of fragmentation on biodiversity, this approach does not allow the study of the degree of fragmentation on the amount of biodiversity. By moving from the strictly qualitative approach to quantifying the amount of fragmentation in a landscape, a more realistic outcome can be seen. However, there is a lack of consensus in the literature about how to approach quantifying fragmentation (Fahrig, 2003). The differences in the approach to quantifying fragmentation has 'significant implications for conclusions about the effects of fragmentation on biodiversity' (Fahrig, 2003).

The use of landscape-based models, such as those used by the Range Shifter software (Bocedi *et al.* 2014), may address some of the issues found by Fahrig (2003). Using field data to build individual based models for a population, which can then be run over a simulated landscape may tackle the issue of low sample size of landscapes. The landscapes can be modified to show a range of degrees of

fragmentation. However, this approach relies heavily on the quality of life history data and knowledge of how the species' interacts with its habitat. It also only allows one species to be investigated at once, when many of the field-based landscape studies are looking at the impact of fragmentation on overall biodiversity. A combination of the two approaches may give the best overall picture.

More recently, a review of landscape-scale empirical studies by Fahrig (2017), suggested that ecological responses (such as changes in species abundance, occurrence and richness) to habitat fragmentation were in many cases statistically non-significant (70% of studies). Fahrig argues that there is little empirical evidence to support the assumption that groups of small habitat patches have lower ecological value than a non-fragmented larger patch of the same area (Fahrig, 2017). However, it is unlikely that a landscape which becomes fragmented will continue to have the same area and consist of the same type of habitat.

The concept that habitat fragmentation is a 'zombie idea' and does not negatively affect biodiversity as presumed (Fahrig, 2017) is controversial (Fletcher *et al*. 2018b). Habitat fragmentation has been shown to have large and long-term effects on biodiversity (Haddad *et al*. 2015), with the spatial configuration of habitat loss altering the effects of habitat loss in remaining habitats (Barlow *et al*. 2016; Pfeifer *et al*. 2017; Fletcher *et al*. 2018b). Studies which have found that fragmentation does not have an effect on biodiversity, are typically based on statistical models which separate fragmentation from habitat loss. When this is done, habitat loss is shown to have a larger effect on biodiversity (Fahrig, 2003; Fletcher *et al*. 2018b). However, Fletcher argues that such models are invalid as the processes of habitat loss and fragmentation are conceptually and empirically dependent, and therefore, should not be treated independently (Fletcher *et al*. 2018b). In the real world, landscapes show a high collinearity between the configuration of a habitat and the amount of habitat (Liu *et al*, 2016). There is a great deal of debate within the field of landscape ecology on whether habitat loss or fragmentation has greater importance on the conservation of biodiversity, and this has become a contentious topic (Hadley and Betts, 2016; Fletcher *et al*. 2018b).

Fragmenting a landscape increases the amount of edge habitat but reduces the amount of internal habitat. Over 70% of the world's forest is now within 1km of an

edge due to deforestation, with 20% of global forests being within 100m of an edge (Haddad *et al.* 2015). This means that the majority of forests globally are within a range where anthropogenic activities and edge effects (such as altered microclimate, presence of non-forest species) will influence and degrade the forest ecosystems (Haddad *et al.* 2015). The smaller the fragmented patches, the higher the edge to interior ratio is. This results in smaller patches having a greater reduction in key ecosystem functions than larger patches (Haddad *et al.* 2015).

There has always been a degree of fragmentation within forests, and therefore and edge and interior habitat. This is due to natural processes such as wildfires, storms and lightning creating breaks in the forest canopy. In Northern Europe, it has been found that long-term forest cover and primary forest condition does not lead to conservation value directly (Bradshaw *et al*, 2014). In the British Isles, forest degradation has been occurring since the start of Neolithic land use, with forest cover in decline for the Late Holocene period. Early in the Holocene era (12 000 BP), little forest cover existed in the British Isles due to ice cover. By 10 000 BP, the British Isles had around 70% Forest Cover. A forest cover of 80-90% in the British Isles was reached in 6000 BP before this lowered slowly to 30% in 1000BP due to anthropogenic causes (Zanon *et al.*, 2018). In England, 15% of land cover was estimated to be forest in 1086 and by 1905 this had dropped to 5.2%. This shows that for thousands of years there has been edge habitat within forests, however, due to a reduction in total forest cover, the amount of edge habitat is increasing.

In contrast to Fahrig's argument that habitat fragmentation is a 'zombie' idea and does not have a negative impact on biodiversity (Fahrig, 2017), Fletcher *et al.* argue that the effects of fragmentation on biodiversity depends on the scale at which fragmentation is measured (Fletcher *et al.* 2018a). They found that for a habitat specialist (*Chelinidea vittiger*) fragmentation resulted in a negative effect when the fragmentation was quantified at the scale of dispersal of the species, but when alternative scales were used, the effect of fragmentation on *C. vittiger* was conflicting. Habitat fragmentation thus needs to be quantified at a biologically appropriate scale for the species being studied (Fletcher *et al*, 2018a). Such scales could depend upon mating range, food or resource collecting, dispersal and ecosystem process (for instance nutrient cycling) (Lord and Norton, 1990). At finer scales of fragmentation, interactions that rely on microclimate are more likely to be

disrupted, when compared to complex ecosystems where interactions occur between many species. Specialist species are more likely to be affected by habitat fragmentation than generalist species (Lord and Norton, 1990). Understanding the different scales at which fragmentation effects species is key to conservation.

1.02 Movement of populations due to climate change

Increasingly, research has focussed on the ability of populations to move in response to climate change. Rising global temperatures are expected to lead to a shift: for populations to remain within the temperature range to which they have adapted over time, they will have to relocate poleward or to higher altitudes (Chen *et al*. 2011). By being able to predict in advance where different species will need to move to in order to survive, strategies can be put in place to ensure this movement is possible, such as wildlife corridors.

Climate change will have a larger negative effect on species living in a fragmented landscape (Travis, 2003). Habitat specialists with poor colonising ability, are least likely to be able to move through landscapes fast enough to keep pace with climate change (Travis, 2003). Species-specific dispersal information is often not incorporated in species distribution modelling, especially in studies modelling future species distributions under climate change (Jaeschke *et al*. 2012). Integrating species-specific dispersal abilities into species distribution models gives improved estimates of range changes and the connected conservation management (Jaeschke *et al*. 2012; Della Rocca and Milanesi, 2020). There is a need for studies to utilise ecologically appropriate measures of dispersal in order to target appropriate interventions for species struggling to move at the same pace as climate change makes their historic habitat unsuitable.

1.03 Movement of invasive species

A further reason to understand population movement is in the context of invasive species. Invasive species tend to be good at extending their populations through a range of landscapes, and are less affected by fragmentation. Many of the most

successful invasive species share several traits: the ability to outcompete other species for food, predator avoidance, ability to alter the environment, rapid dispersal, behavioural plasticity and fast reproduction (Weis, 2009). Due to these traits, in particular effective dispersal, invasive species are predicted to spread effectively in fragmented landscapes (With, 2004). Some of the most well known invasive species are ants, such as the Yellow Crazy Ant, *Anoplolepis gracilipes* (Drescher *et al*. 2007). By understanding how these traits interact with the landscape the invaders are able to move into, it is possible to potentially stop or slow the movement of such species.

1.04 Movement of Endangered species

Many endangered species also share common life history strategies, but these are the opposite traits to those that make invasive species successful in colonising new habitats. Many endangered species are slow reproducers, habitat specialists and poor dispersers. Examples of which include the saproxylic Beetle, *Rosalia alpina* (Drag *et al*, 2011) and the damselfly, *Coenagrion mercuriale* (Rouquette and Thompson, 2007). This means that they are more at risk than other species of isolation and resulting extinction events, due to habitat destruction and fragmentation.

Dispersal is the mechanism by which a species can become established in a new location. In many species, individuals travel away from their birth area during their juvenile phase. In plants, this can be via seed dispersal (Di Musciano *et al*. 2020). The ability of a species to disperse depends on several factors including mobility, time taken to reproduce, life cycle duration, and ability to compete for limited resources. If a species has a short dispersal distance, individuals move only a short distance away from their natal patch and will take longer to spread through an area of suitable habitat than those with a longer dispersal distance (Di Musciano *et al*. 2020). Species with a long gestation period will also take longer to disperse across a landscape. As it is often the juveniles that disperse, having a longer gestation period means that it will take longer for individuals to reach the juvenile stage than species with shorter gestation. Similar to this, if a species' has a long life cycle, with a longer

developmental stage before reaching the mobile juvenile stage and then a longer growth stage to adulthood they could be outcompeted for resources by other species who develop quicker.

When poor dispersing species are subjected to a fragmented landscape, the effect of the fragmentation on the population will be higher than the effect of the fragmentation on populations of species able to disperse across greater distances. Habitat specialists, which many endangered species are, are also affected more by habitat fragmentation as they cannot survive or disperse to other habitats (Lindsay *et al*. 2008).

1.2 Conservation methods for the improved movement of poor dispersers

1.21 Corridors

One method which could benefit poor dispersers in fragmented landscapes is the use of 'corridors'. The corridors are areas of remaining original habitat, arranged in either a continuous area or as stepping stones, connecting to another area of suitable habitat. Corridors have been effective in the movement of individuals from a range of taxa (Haddad *et al*. 2003). However, there is a mixture of opinions on the benefits of corridors (Beier and Noss, 2008; Gilbert-Norton *et al*, 2010). Corridors consisting of the original habitat have been found to be used more than corridors consisting of recreated habitat (Gilbert-Norton *et al*. 2010). The use of corridors is also species dependent with invertebrates, non-avian vertebrates, and plants moving through corridors the most (Gilbert-Norton *et al*. 2010). However, there is evidence that enlarging the patch size, as opposed to creating a corridor, has more benefit for the isolated populations residing in the fragmented landscape (Falcy and Estades, 2007). A comprehensive meta-analysis of 32 different studies testing the efficacy of corridors, across all taxa, found that it is still worthwhile to build and maintain corridors for biodiversity conservation (Resasco, 2019). Understanding how populations can colonise and move through corridors, therefore reducing their isolation, is an important consideration when reviewing the value of a corridor.

Species may not be able to keep up with climate change. For many tree species, the rate at which they can spread by seed dispersal into a new area, which is suitable in a future climate scenario, is slow. It will take a period of time before the individual trees will be mature enough to provide the woodland habitat that many other species inhabit. If forest corridors are to be utilised fully, then trees need to be planted which will be suitable for future climates. This then raises the issue of removing trees that are suited to today's climate as there is often only a finite amount of land available for areas of conservation (Millar *et al*, 2007).

1.22 Translocations

Translocations of individuals can remove the need for corridors. Translocations are the movement of living individuals of a species from one area to another (IUCN, 1987). There are three main types of translocation: introductions, reintroductions and restocking. *Introduction translocations* are where individuals of a species are moved to a novel habitat that they haven't historically inhabited. Introduction translocations can be intentional, but also commonly occur by the accidental movement of an individual by humans. *Reintroduction translocations* are where individuals of a species are translocated to an area their species has historically inhabited, but from which it is now absent. *Restocking translocations* are the movement of individuals into an area where the species is still present, in order to build up the population in an area and potentially to increase genetic diversity. To avoid unintended negative consequences, translocations must be done extremely carefully and the IUCN states that the damage caused by introductions of alien species far outweighs the benefits (IUCN, 1987).

Successful introduction translocations are less common than reintroduction and restocking translocations (IUCN, 1987). This is due to the complexity of a new habitat interacting with the translocated individuals. In both reintroduction and restocking translocations, the species has historically inhabited that location, therefore it is clearer if the habitat is still suitable, or what has changed since the species became extinct at that location, and therefore what can be modified to create a suitable habitat. In introduction translocations, the species will not have been present in that location before. It is very difficult to understand all the many

microhabitat variables and interactions between other species. In order for an introduction translocation to be reliably successful, these fine details and interactions must be taken into account.

Introduction translocations can be similar to individuals of a population who are at the geographical population edge and colonising a new habitat, or those that are re-colonising an area in which habitat change has occurred. There are more examples of individuals at the geographical edges of populations whose colonisation success can be studied, than translocations. Understanding the mechanisms underpinning the survival of the initial colonisers may inform the theory and practice of successful translocations in the future (Griffith *et al.* 1989). For species that cannot keep up with climate change whilst moving through corridors of habitat due to limited dispersal ability, translocations may be key in the survival of species (Baur, 2014).

1.3. Importance of studying the population edge at a micro level

The small-scale movement of individuals at the edge of a population's range underpin the success of a populations' range expansion. If individuals are not successful at migrating into habitat at the edge of the population, then the population will not extend its range. If the individuals that find themselves in the new habitat cannot survive, become established and reproduce, then the habitat is not a viable option for that population.

Therefore, it is critical to understand how individuals of a population interact with their microhabitat to survive and reproduce in a new habitat. Microhabitat is the small scale habitat which differs from its surrounding more extensive habitat . Microhabitat has previously been described as the environmental variables that affect the behaviour of an individual (Morris, 1987). Studying this alongside large-scale population movements give better clarity into the reasons underpinning a populations' success in a new habitat, and the ability it has to continue the movement. By understanding the microhabitat's effect on colonisation, models predicting population expansions on a larger scale are likely to be more accurate.

The survival of individuals in a new area is dictated by many factors. By measuring the survival of individuals in a newly colonised area it is possible to gain a measure of the end product of all the biotic and abiotic factors that play into an individuals' survival. For instance, competition, resource availability, ability to find a mate are all examples of factors that may affect the ability of a population to colonise new habitat. Such factors are often hard to measure for non-sessile species or for those living in fast-changing environments.

1.4 History of woodland in England

Globally, anthropogenic activities have caused a decline in forest cover (FAO 2010). In some areas, such as Europe, there is a slow process of afforestation occurring to reverse the loss of forests (FAO 2010), as loss of areas of forests has a large negative impact on the community's forests support (Aerts and Honnay 2011).

Following the industrial revolution, Britain's tree cover (total land surface area covered by trees) had dropped to around 5% in 1905 (Mason, 2007). This was due to an increase in timber usage but also in the destruction of forests for agricultural land. This led to a highly fragmented pattern of woodland across England. In response to a shortage of timber in World War One, the forestry act of 1919 was passed which led to the large-scale afforestation of timber plantations across Britain (Forestry Commission 2016). These forests typically consisted of non-native pines and firs, and were often planted in areas which had previously been woodland (Forestry Commission 2013). This increased the tree cover in Britain to a level of 13% in 2013 (Forestry Commission 2013).

Many of the plantations planted in the 1900s either surround or border patches of ancient woodland, and could act to connect previously isolated ancient woodland patches (Vanhala *et al*. 2014; Procter *et al*. 2015). If plantation forests could help facilitate the dispersal of forest specialists, previously isolated in ancient woodland fragments, then the connectivity of forest specialist populations would be greatly improved by afforestation (Procter, 2016). Further studies are required in order to understand the degree in which non-native plantation forests are improving

connectivity between ancient woodland fragments and the specialist populations inhabiting them.

There is now evidence that some forest specialist species are beginning to move into plantations and thrive, for instance; the threatened hoopoe in France (Barabaro *et al*. 2008) and the flightless cassowary in Queensland (Keenan *et al*. 1997). In the case of the ground beetle, *Holcaspis brevicula*, the species' is totally dependent on plantations as its remaining habitat (Berndt *et al*. 2008). An increase in the biodiversity inhabiting plantation forests is seen as a good thing, increased biodiversity increases the functioning of an ecosystem. The ecosystem is more stable with an increase in biodiversity as it is more resistant to collapse if one species becomes extinct (Pimentel *et al*. 1997). Others may be able to fill the role and niche of the now extinct species. However, in several cases there appear to be colonisation lags between the plantations becoming apparently suitable, mature, woodland and the woodland specialist populations moving into them (Procter 2016). Understanding the causes of this lag will help forest managers be able to create plantations that are more accessible to species that could inhabit the area and increase biodiversity.

The period of time it takes between new habitat becoming suitable and being colonised is controlled by a complex interaction between the configuration of habitat, population growth rate and individual decisions. The following persistence of that species in a new area then depends upon local and neighbourhood density (Morgan *et al*., 2019). The increased likelihood of individuals to inhabit areas close to their conspecifics also influences the ability of a population to colonise new areas (Morgan *et al*., 2019). Unpicking such complex, species specific, factors makes it difficult to improve colonisation lags using habitat management.

One example of a forest specialist which appears to be successfully colonising non-native plantations is the hairy red wood ant, *Formica lugubris* (Procter *et al*. 2015). In sites in the north of England, there is evidence of *F. lugubris* expanding their historic populations from fragments of ancient woodland into neighbouring non-native plantations (Procter *et al*. 2015). Though high proportions of conifers are not novel conditions in areas of the UK, the dominance we see of non-native plantation species and the forest management that they exist under present a changed habitat

for forest specialists (Procter *et al*., 2015) In the UK plantations have also increased the connectivity between isolated populations of both the red squirrel, *Sciurus vulgaris*, (Hale *et al*. 2001) and the wood ant, *Formica aquilonia* (Vanhala *et al*. 2014). The colonisation of the non-native plantation by the previously mentioned species suggests that for some native forest specialists non-native plantations can act as a suitable habitat.

1.5 Formica lugubris as a study system

Across Eurasian forests, the *Formica rufa* group of red wood ants are widespread and locally abundant (Stockan *et al*. 2016). Ants in the *F. rufa* group build nest mounds and inhabit forests, which they depend upon for their food sources. Wood ants have several large impacts on the forests they inhabit. They are predators, farmers and ecosystem engineers. Due to the large effect wood ants have on invertebrate community structure they can be regarded as keystone species (Hughes and Broome 2007).

1.51 Wood ant ecosystem interactions

Wood ants interact with other species around them at multi-trophic levels. The two main levels are in their mutualism with aphids and their predation of invertebrates (Robinson *et al*. 2016). Both of these interactions have a large effect on the communities of invertebrates present in tree crowns, when wood ants are present. Wood ants tend or farm aphids, from which they gain honeydew as a food source (Rosengren and Sundström 1991).

Wood ants reduce the abundance of aphids they do not tend (Robinson *et al*. 2016), but increase the abundance of aphid species that are ant tended (Puntilla *et al*. 2004). The ant-tended aphids are protected by wood ants, but also used as prey if other prey items are not present (Billick *et al*. 2007). The wood ants may prey on aphids which are less beneficial in the production of honeydew. Such aphids may be injured, dead or producing poor quality honeydew (Sakata 1994).

One way in which the wood ants form a mutualistic relationship with the aphids they tend is the removal of other predators (Liere and Perfect 2008). Other predators, which tend to be invertebrates, form a large part of the wood ants' prey (Puntilla *et al.* 2004). By protecting the aphids, the wood ants secure a source of carbohydrate which they gain from honeydew (Mooney and Mandella 2010), which can constitute to between 62- 94% of the foraged biomass consumed by wood ants (Wellenstein 1952; Rosengren and Sundström 1991). The presence of wood ants in the tree crown reduces the invertebrate species richness, due to their predation of other invertebrates (Warrington and Whittaker 1985). When wood ants are present, herbivory of trees is reduced on branches with ant-tended aphids due to the wood ants reducing the presence of herbivorous invertebrates (Styrsky and Eubanks 2007).

There are many conflicting opinions on whether the presence of wood ants in plantations are economically beneficial. On the one hand, as previously mentioned, they reduce herbivorous pests which can reduce tree productivity (Ito and Higashi 1990). However, they also increase the abundance of aphids within the tree crowns, which remove sap from the trees which could reduce tree growth. With the increase in invasive pest species, wood ants may become more important in plantation forests as biological control agents (Robinson *et al.* 2016, Nielsen *et al.*, 2018), with an increased economic benefit to creating suitable habitats for them. For instance, in apple plantations, wood ants have been used to reduce the numbers of harmful winter moth larvae, which reduce apple production (Offenberg *et al.*, 2019). Areas of plantation woodland with high wood ant presence has been found to reduce the distribution and abundance of a range of carabid species, therefore reducing biodiversity (Hawes *et al.*, 2002).

1.52 The role of wood ants in nutrient cycling

Wood ants also play an important role in nutrient cycling (Frouz *et al*, 2016). The construction of wood ant nests using organic materials which then decompose, enriching the surrounding environment with nutrients. The honeydew foraged by wood ants is brought to the nest, with an average of 13-16kg of honeydew dry mass is transported annually (Frouz *et al.* 1997). Additionally to this, around 25kg of prey

dry mass will also be transported into a nest annually (Frouz *et al.* 1997). Nests are long-lasting structures with some nests being present for over a century (Frouz *et al*, 2016). Over the lifetime of a nest, one wood ant nest alone can be responsible for the movement of large quantities of foraged nutrients.

Wood ant nests consist of an above-ground dome, and underground galleries. The dome can typically have a volume of between 0.3 and $1.0m^3$, with the underground galleries having approximately the same volume as it's dome (Frouz *et al.* 2016). The galleries are created by digging and excavating soil from deep layers which can be heavy in minerals. This soil is then deposited on the nest surface around the nest margins (Nkem *et al*, 2000). The wood ants also deposit decomposing plant remains and ant metabolism products at the nest margin which enriches the margins in minerals. The gallery digging also mixes soil layers ensuring that there is no vertical gradient in nutrients in the soil.

Several microclimatic factors found around wood ant nests increase the speed in which organic matter can decompose. With a wood ant nest, the raised internal nest temperature, increased moisture content, and aeration all increase the rate of the decomposition of organic matter (Frouz *et al*, 2016; Paul and Clark 1996; Brady and Weil, 2002). Their effects on microbial communities also extend beyond the nest into the surrounding soil (Wardle *et al.,* 2011). Therefore, wood ants have a large effect on the ecosystem they inhabit in their role as ecosystem engineers.

1.53 Myrmecophile species

Further to the above stated roles wood ants fill, their large nest mounds provide a habitat for many myrmecophilous species who also reside within the nest. In wood ants that form large colonies, there is a greater diversity of ecological niches which will last longer in a large, established colony (Hölldobler and Wilson 1990). Over 100 different species that are myrmecophiles of wood ants have been identified so far (Robinson *et al.* 2016). Some wood ant myrmecophiles, such as the shining guest ant (*Formicoxenus nitidulus*) are endangered and are only found in wood ant nests (Robinson *et al.* 2016). Therefore, conserving wood ants will also conserve the habitat these specialist myrmecophiles require to survive.

1.54 Wood ants in Great Britain

In Great Britain, there are three species of wood ant from the *F. rufa* group: *Formica rufa, Formica lugubris and Formica aquilonia* (Stockan *et al.* 2016). Each of these species has a slightly different preferred habitat. In Southern England and Wales, *F. rufa* occurs, nesting in areas with less dense canopy cover. *Formica lugubris* is found in England, Scotland and Ireland, and the species crosses ranges with *F. rufa* and *F. aquilonia. Formica aquilonia* is found at higher altitudes and in more dense canopy covers than *F. rufa* or *F. lugubris*. In the UK *F. aquilonia* has only been reported in Scotland (BWARS, 2001).

1.55 The study species, *Formica lugubris*

Our chosen study species was *F. lugubris*. Like other members of the *F. rufa* group, it is an obligate forest dweller. Although dispersal by winged queens and social parasitism occurs in some parts of its range, in the UK, *F. lugubris* disperses and forms new nests by the process of budding (Hughes, 2006). Specifically, workers from an existing nest build a new nest and once the nest is large enough, the workers move queens and brood into the new nest. As the nests are within the same colony, resources may be shared between the nests (Ellis *et al.* 2014). This means that newly formed nests can be used to reach new food sources: the resources foraged into the new nest can then be passed to other nests within the colony (Ellis and Robinson, 2014). This means that within the UK, *F. lugubris* is a short range disperser. Therefore, *F. lugubris* in the UK is an ideal candidate to assess the effects of changes in landscape on its colonisation ability.

If a nest is considered equivalent to an individual in a population, then budding could be viewed as the reproductive event, in which a new reproductive unit is produced in the new nest. The formation of the new nest could be considered the juvenile stage, in which movement away from the original 'parent' nest occurs. The movement of the brood and queens to the new nest makes the new nest a reproductive unit. This is a crude analogy, but could be utilised to create models for wood ant population movements, using the nest as the individual. A thorough literature search at the time

of writing found no studies which had previously used the nest as an individual in this way.

Wood ant mounds tend to be large and easily identifiable. Though the size of mounds can vary, the thatch of forest debris that forms the mound is highly identifiable. The nest mounds are also sessile, with movement of a nest mound only occurring in response to the original site becoming less ideal (i.e. due to increased density of the tree canopy above resulting in a lowered nest temperature). This movement is on a very small scale, with the nest usually moving less than a meter, often due to a change in shape with more thatch been added to the parts of the nest in the more favourable conditions leaving thatch in less favourable conditions to degrade (Holgate, pers. obs. 2018). The sessile, long-lasting, easily identifiable nests, create a good system in which to study population movements.

1.56 *Formica lugubris* at the study sites

On the North York Moors, the predominant wood ant species is *F. lugubris*. There are several large populations of *F. lugubris* in the forests which span the southern edge of the National Park. These populations have now been monitored for several years, and historic records of wood ant presence exist from when the Forestry Commission plantations were established. Population surveys of six populations on the North York Moors have been carried out over multiple years, shown in figure 1 (Procter, 2016).

Most of the woodland on the North York Moors consists of plantation forests, planted after 1920 (Rylance, 2018). Many of the plantations were planted on areas which had previously been native woodland until the industrial revolution. This means that many of these plantations surround small pockets of remaining ancient woodland, which have been used as refugia by forest specialists. If plantations could be utilised to increase connectivity between remaining ancient woodland fragments, then the health of forest specialist populations which have been previously isolated could be improved due to increased gene flow.
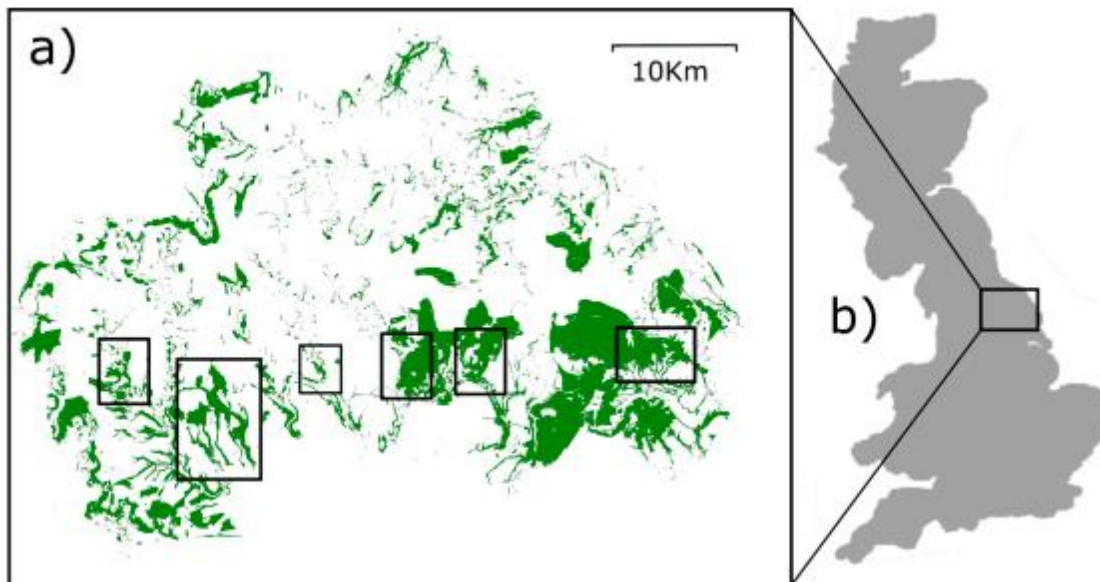
Figure 1.1: Figure taken from Procter (2016), showing the location of field sites containing F. lugubris populations on the North York Moors. Green polygons show current forest cover, black rectangles show the location of F. lugubris populations (Procter, 2016)

1.57 Background information on the North York Moors field sites

At the study sites, a previous study by Procter (2016), surveyed the populations of *F. lugubris* across five plantation forests on the North York Moors. In this study three were selected in which population expansion of *F. lugubris* was still possible where the forests were not saturated with *F. lugubris*. This meant further research on the expansion of *F. lugubris* could occur. Past work by Procter (2016) gives high confidence that no further *F. lugubris* populations were present in the areas studied that could lead to colonies entering from other adjacent fragments.

At these sites, Procter found that *F. lugubris* had colonised the non-native plantations from pockets of surviving ancient woodland (Procter *et al.* 2015). A colonisation lag occurred between the plantation forests becoming mature and capable of supporting the *F. lugubris* population and the colonisation of the plantations by *F. lugubris.* The severity of the lag means that *F. lugubris* at the sites had expanded under 800m in 160 years of forest expansion. Softwoods such as pine, fir, spruce, and ash, which the field sites primarily contain, reach maturity at around 40 years (Forestry England). Procter also identified that several of the

populations of *F. lugubris* across the field sites showed genetic isolation. The different populations were in some cases highly unrelated (Procter, 2016). The potential for the plantation forests to increase connectivity between isolated *F. lugubris* would mean that genetically isolated populations could be connected again, increasing the health of the overall population of *F. lugubris* on the North York Moors. At the site, winged males have been seen outside of the nests (Holgate pers. Obs. 2018), and there is no literature to suggest that males would not be able to disperse to other colonies if they were close enough. At the sites used in this study, individuals from genetically isolated colonies showed very little aggression to each other (Procter, 2016) which could potentially stop successful mating events.

Many of the plantation forests on the North York Moors now follow a minimal management forestry routine, such as Broxa and East Moor Wood (Rylance, 2018) (Fig. 2.1). Little commercial logging still occurs, and managers have tried to increase the biodiversity of the forests by planting native species within the plantations. The plantations are often bordered or surround pockets of ancient woodland consisting of oak, ash, birch, and rowan, with an understory or hazel and hawthorn (North York Moors National Park).

In contrast, Cropton Forest (Fig. 2.1) has large amounts of commercial logging occurring, with many different forestry techniques being used across the site. Areas have been clear felled, row thinned, under minimal management and replanted. At Cropton, the differences in management can occur between tree stands, creating a plantation with high temporal variation in forest structure between stands. This provides an excellent opportunity to investigate how these different forest management strategies affect the expansion of *F. lugubris.*

1.6 This study

The aim of the research in this thesis was to investigate whether the populations of *F. lugubris* at established field sites on the North York Moors were still expanding their populations into the non-native plantation forests from the ancient woodland they previously occupied. If expansion was occurring, we aimed to measure the rate of expansion and how this was shaped by site-specific features, such as difference

in forest structure and management, as well as microhabitat. By undertaking the further field work carried out in this study on these *F. lugubris* populations, it may be possible to identify potential barriers to their continued population growth through the plantations. If these barriers are identifiable, forest management practices could be utilised in order to increase the chances of population growth and the speed at which it could occur.

In one area of Cropton Forest, an area of the field site had been row thinned in 2015/16. This practice involves removing rows of trees from a forest stand. Prior to the row thinning, the forest stand was too dense for *F. lugubris* to establish nests within the stand, and previous surveys corroborate this with no *F. lugubris* nests being found within the forest stand prior to the 2017 survey (Procter *et al.* 2015). We will investigate how this management practice has affected the population expansion of *F. lugubris* at this part of the site, and compare the rate of expansion in the newly colonised row thinned area to other areas of expansion at Cropton Forest. By measuring microhabitat and nest attribute data for the nests in the newly colonised area, we will also investigate what influences the survival of nests in newly colonised areas. This study represents a unique opportunity to observe the response of a population of habitat specialists to a change in habitat, and the population's survival across multiple field seasons in a newly colonised area.

Chapter 2; Expansion of Formica lugubris populations in plantation woodland on the North York Moors.

2.0 Introduction

Climate change and anthropogenic habitat degradation cause global change in many species' abundances and distributions (Warren *et al*, 2001). While climate change and anthropogenic change are regarded as having a negative impact on biodiversity, they can also create new habitat into which species may expand their range. When species expand into new areas there are difficulties such as colonisation lags (Procter *et al,* 2015: Ellis and Coppins, 2007), increased local extinctions (Mott, 2010) and reduced reproductive fitness (Mott, 2010). It is important to understand how species will expand into new habitats in order that conservation practices can be shaped to assist species spread where appropriate.

Increased habitat connectivity is key in the conservation of species in both empirical studies (van Langevelde, 2008: Bailey, 2007: Damschen *et al,* 2006) and theoretical models (Hodgson *et al*, 2009). A loss of connectivity within a landscape can obstruct the dispersal of species residing within it, dispersal that can be vital for the viability of these species (Pascual-Hortal and Saura, 2007). Understanding what constitutes effective connectivity in areas where land use change or habitat degradation has occurred is crucial if restoration attempts are to be successful.

Anthropogenic habitats can be used to increase connectivity within a landscape. An example of increased connectivity is the introduction of coastal defences systems increasing connectivity between rocky seashore habitats by removing isolating barriers (Moschella *et al*, 2005). When artificial ditches were used to connect streams, biodiversity was higher in streams connected via these ditches than non-connected streams (Simon and Travis, 2010). Gravel pits increase the waterbird species richness when the gravel pit location increases connectivity to natural or artificial wetlands (Santoul *et al*, 2010). Understanding how anthropogenic habitats

within a landscape affect species movement is important when considering the impact the addition of such habitats has at the landscape level

Many ecosystems are in some way dynamic and therefore understanding how species move through dynamic landscapes is important. For instance, forest fires and logging both cause ongoing change in forests (Moretti *et al,* 2004: Mönkkönen *et al,* 2014); trawling and storms can cause dynamism in coral reefs. Both anthropogenic and natural factors are involved in ecosystem dynamism and understanding how species' cope with this is important. Global changes, such as climate change and land use change to feed a growing global population all increase the impact humans have on the dynamism of landscapes.

Sixty-five percent of the world's terrestrial taxa are supported by forests (Lindenmayer *et al.* 2006: World Commission on Forests and Sustainable Development, 1999). Forests support the highest species diversity for birds, invertebrates, and microbes (Lindenmayer *et al,* 2006). Many forests have some form of disturbance, be it natural (i.e. forest fires) or anthropogenic (i.e. logging). Understanding how disturbance affects the species residing in forests is crucial to conserving forest biodiversity.

A large proportion of the UK land cover previously consisted of ancient woodland; however,
active deforestation reduced forest land cover to 5% in 1905 (Mason, 2007). Following this, a large afforestation effort led to forest land cover rising to 13% in 2013 (Quine, Bailey and Watts, 2013). Much of the planting in this afforestation effort was of large non-native plantations (Rylance, 2018: Procter *et al,* 2015). These plantations were often planted around the remaining ancient woodland fragments which acted as refugia for native woodland species. Over time, native species have begun to inhabit the surrounding plantations, however, a colonisation lag can elapse between the new plantations becoming suitable habitat and species moving into them (Procter *et al,* 2015).

Plantation forests may act to improve connectivity between ancient woodland fragments, and it is important to understand how populations of habitat specialist species with differing dispersal abilities may expand through these plantations.

Plantation forests are not static landscapes, instead they are landscapes with both spatial and temporal dynamism (Schmiegelow and Monkkonen, 2002: Angelstam 1998). Stands within a plantation may be highly heterogeneous in species composition with respect to each other. The management of each stand may operate on different time scales and in different ways (i.e. selective thinning versus clear felling) and therefore the forest is dynamic at the landscape scale. Understanding how this landscape dynamism interacts with the connectivity between populations in ancient woodland fragments may be key to the conservation of woodland specialist species.

One such woodland habitat specialist is the hairy wood ant, *Formica lugubris. Formica lugubris* has a dramatic impact on the forests where it is found. It creates large and long-lasting nests which influence nutrient cycling, invasive species control and food web structure within the forest ecosystem (Frouz *et al,* 2016). A colony can inhabit several of these nests, and is therefore termed polydomous (Ellis and Robinson, 2014). A result of this polydomous nesting structure is that new nests are formed by budding. *Formica lugubris* is thus considered to be a poor disperser due to the short distances of up to 200m over which budding can occur (Rosengren & Pamilo, 1983). *Formica lugubris* can also be considered to be a habitat specialist as the species requires both tree aphids for food, and insolation for growth, and thus can survive only on woodland edges (Stockan and Robinson, 2016). Due to the large mounds of forest material which *F. lugubris* build as nests, identifying the area inhabited by a population is relatively easy due to the conspicuous nature of such structures. This means *F. lugubris* is an ideal candidate to study how dynamic landscapes may affect slow moving habitat specialists.

Study sites were chosen on the North York Moors (North England) based on the existence of detailed past population information on *F. lugubris,* providing a baseline for this study. At these sites, *F. lugubris* populations have expanded their populations from ancient woodland fragments into the neighbouring plantation woodland (Procter *et al,* 2015). The past survey data from 2011 and 2013, combined with detailed forest management plans from the Forestry Commission allow for a unique site in which to further study the population expansion of *F. lugubris* and how forest management may affect the movement of a poor disperser.

2.01 Aims of this study

1. Assess whether populations of *F. lugubris* on the North York Moors are continuing the expansion observed 2011-2013 (Procter 2016)

2. Identify any management strategies associated with increased expansion of *F. lugubris* populations

Hypothesis 1: population expansion

- **Hypothesis:** The population margin of *F. lugubris* at the field sites has moved further into the plantation woodland

Rationale: The pattern would continue the expansion pattern observed in previous years (Procter, 2016)

Hypothesis 2: effect of management

- **Hypothesis:** Forest thinning increases the presence and abundance of *F. lugubris* within a forest stand relative to areas with no active management

Rationale: Forest thinning increases the amount of edge habitat for edge specialists, therefore increasing the presence or abundance of *F. lugubris* within a forest stand.

2.1 Methods

2.11 Study Sites

Formica lugubris is found in upland wooded areas throughout Northern Europe. In Great Britain, it inhabits woodland in Scotland, Northern England, and Wales. Previous work at sites on the North York Moors found population expansion of *F. lugubris* from ancient woodland fragments into the neighbouring plantation forests (Fig. 1) (Procter *et al,* 2015).

Systematic surveys of *F. lugubris* populations across the North York Moors were undertaken in 2011 (Procter, 2016). The surveys focussed on 5 sites, of which 3 were chosen for further investigation in this study; the other 2 small sites showing no previous population expansion due to lack of suitable habitat in which to expand (Fig 2.1). *Formica lugubris* populations have expanded from ancient woodland fragments into the surrounding plantation forest at the 3 larger sites; Broxa, Cropton, and East

Moor Wood (Procter *et al,* 2015). These 3 sites are all plantation forests; however, there is variation between them in the age and species composition of the forest stands and differing management strategies in place, shown in Table 1.

The ancient woodland on the North York Moors the populations of *F. lugubris* have spread from historically consisted of scots pine, oak, hazel and alder trees 10 000 years ago (North York Moors National Park). The ancient woodland that remains now consists of oak, ash, birch, and rowan, with an understory or hazel and hawthorn (North York Moors National Park).

	Broxa (Rylance, 2018)	Cropton (pers. obs.)	East Moor Wood (pers. obs.)
Forest Management practices at population margins	Minimum intervention	Variable: minimum intervention, clear felling, row thinning, selective thinning	Minimum intervention
Year Planted (majority)	1940-1950	estimated 1950	1950-1960
Ancient Woodland	25%	Estimated 8%*	Estimated 10%*
Main species groups	Larch and Pine	Scots Pine, Norwegian Spruce and Larch (Pers. Obs.)	Larch and Scots Pine (Pers. Obs.)

*Estimated from Forestry
Commission Maps

Table 2.1: Comparison of the 3 Forests. More detailed information is available for Broxa due to a recent review (Rylance, 2018)

Not mapped due to lack of past expansion at margins

East Moor Wood
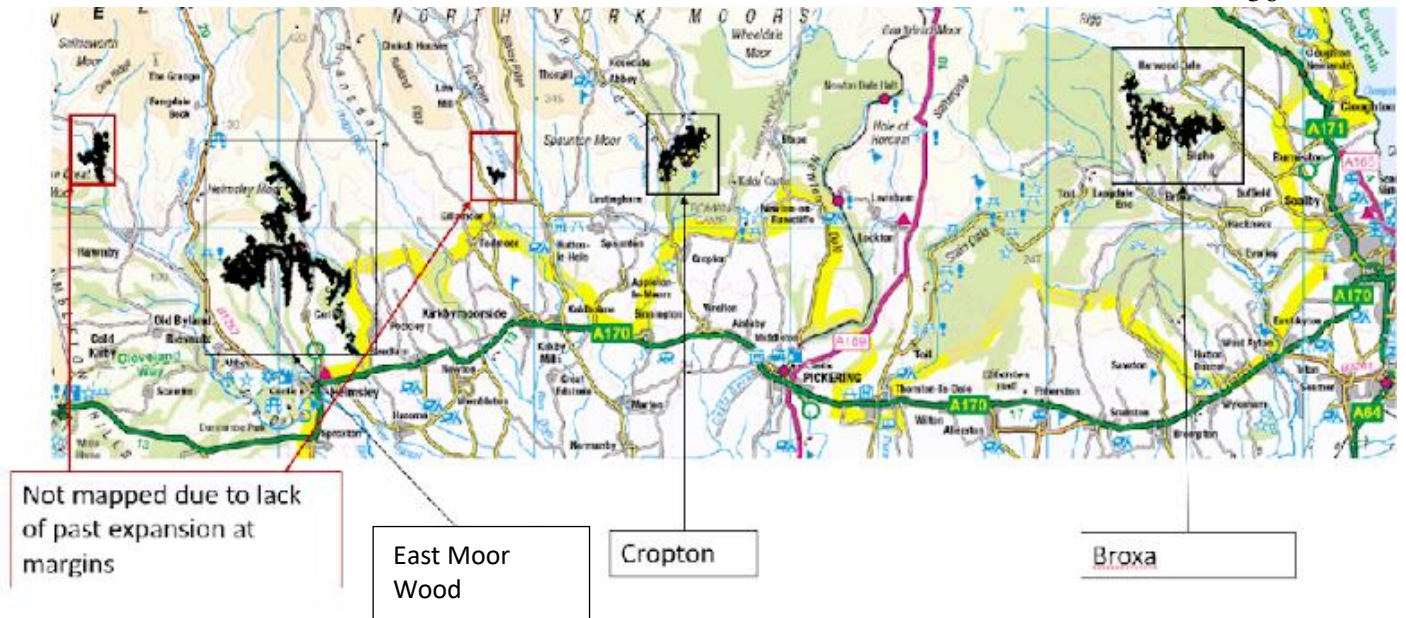
Cropton

Broxa

Figure 2.1 The locations of sites with past F. lugubris *population surveys. Black dots indicate nest presence in 2011 (as surveyed by Procter (2016)*

2.12 Population margin surveys at Broxa, Cropton and East Moor Wood sites

To investigate if the population expansion of *F. lugubris* seen between 2011 and 2013 had continued and whether any forest management strategies occurring since 2013 could have had an effect on the *F. lugubris* populations, the population margins were resurveyed in 2018. The locations with evidence of population expansion as shown in Duncan Procter's surveys in 2011 and 2013 were returned to and transects were used to find the current population margin (Procter, 2016).

Most *F. lugubris* nests occur within 10m of an edge of the plantation (Procter 2016). Edges, in this case, are described as tracks or rides in the forestry which cause a break in the canopy. Transects were spaced at 5m along the forest edge and extended 10m into the plantation forestry (Procter *et al*, 2015). Surveying began behind the population front recorded by Procter to demonstrate that the nests recorded in 2013 were still present and had not moved, meaning any 'new' nests past this point were previously unrecorded. Surveys were undertaken in June-Sept 2018 at Broxa, Cropton and East Moor Wood. Nest locations were recorded using a handheld GPS. The distance which the population front had moved was estimated by how far the nests recorded in 2018 were from the nests from previous surveys. This was calculated using the Measure tool in ArcMAP.

The population margins of Cropton and Broxa were resurveyed in June-September 2019 in order to gain an annual rate of expansion. Little expansion was seen at East Moor Wood from 2013 to 2018, so this site was not resampled in 2019.

2.3 Results

2.31 Overview

Expansion was evident at all three sites between the 2013 population margin survey and the 2018 survey, but the sites differed in the extent and context of expansion. At Broxa steady, slow expansion was seen. At East Moor Wood, very minor expansion occured. The site at Cropton showed both steady, slow expansion spreading along rides and paths but also the dramatic impact of management resulting in fast unexpected expansion through the forest stands.

2.32 Steady expansion: Broxa (Hypothesis 1)

We found that at the Broxa site, slow and steady expansion had occurred along habitat edges (Figure 2.2). We found 44 newly-recorded nests at the population margin highlighted in the zoomed in box in Figure 2.2, along rides and paths. In the original survey of the whole population at Broxa, 1264 nests were found (Procter, 2016). In the following 2013 survey of the population margins, 25 new nests were recorded (Procter, 2016). As only the population margins were resurveyed, some nests from within the population may have become abandoned during this time. The enlarged box (A) in fig 2.2 shows the population expanding into Langdale Forest, the population margin has moved by 54m over 5 years, i.e. averaging 10.8m per year. Due to forestry operations, an area labelled 'B' in figure 2.2 could not be surveyed in 2018, therefore the expansion recorded in 2018 may not be fully comprehensive. All expansion at Broxa appeared along pre-existing edges and rides into the neighbouring Langdale Forest, as would be expected of a species that disperses by local budding.

Population expansion into Langdale Forest appears to be occurring in at least two directions. Between 2018 and 2019, the northern population margin (Fig 2.3) had

moved a further 21m in a North West direction through a previously clear-felled area, since the 2018 survey. The area in figure 2.3 is the same as shown in box A of figure 2.1. More nests were found in this area in 2019 than in previous surveys (Fig 2.3). In the southern section of the population moving into Langdale Forest (Fig 2.3), newly recorded nests were recorded in the 2019 survey along a ride (expansion of 47m in 1 year) (Fig 2.3).
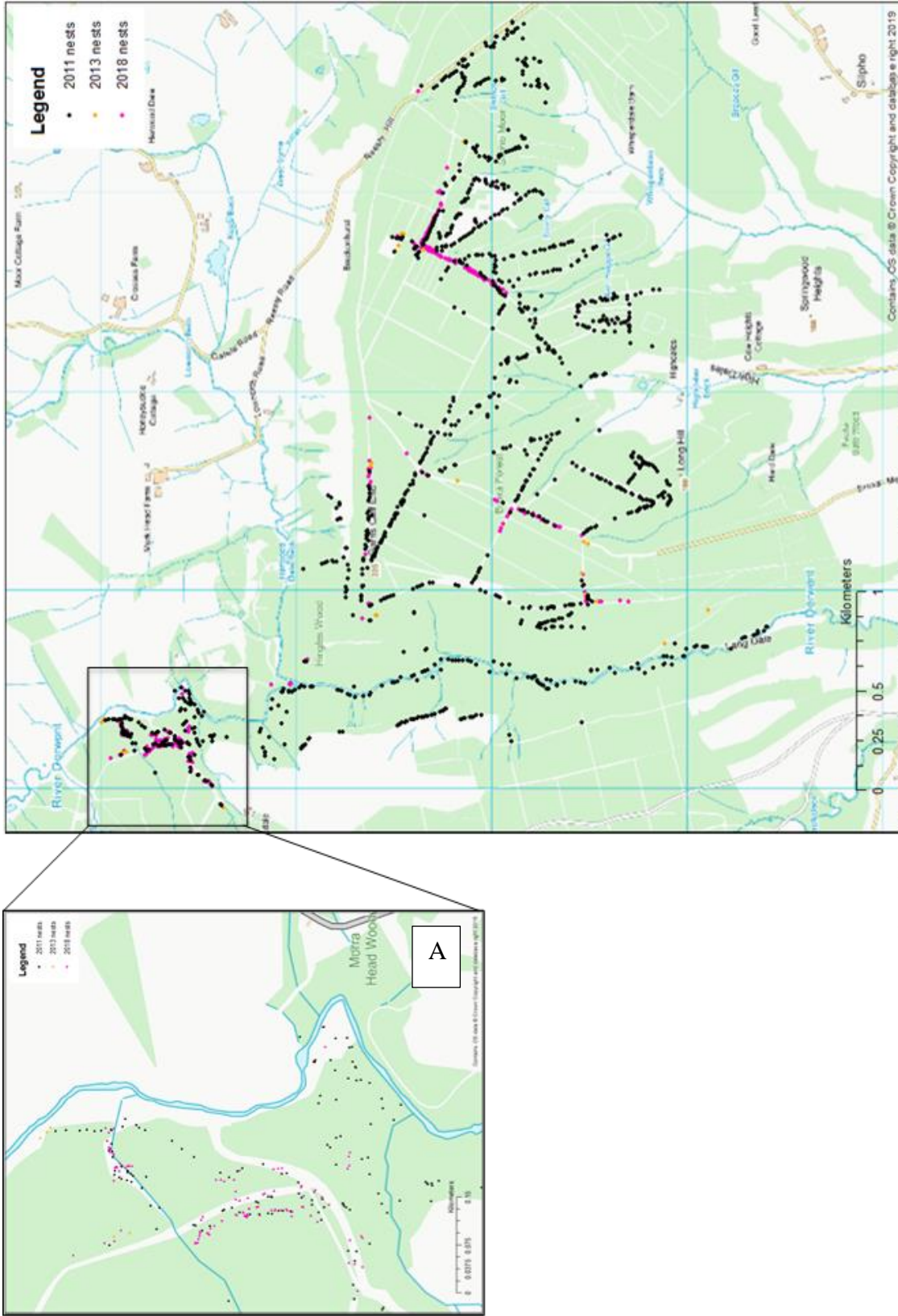
Figure 2.2 Broxa site. A large historic population, with the area of interest shown in area A. This area shows steady, slow expansion into neighbouring Langdale Forest. The rectangle, labelled 'B' shows an area which was not possible to map, due to logging.
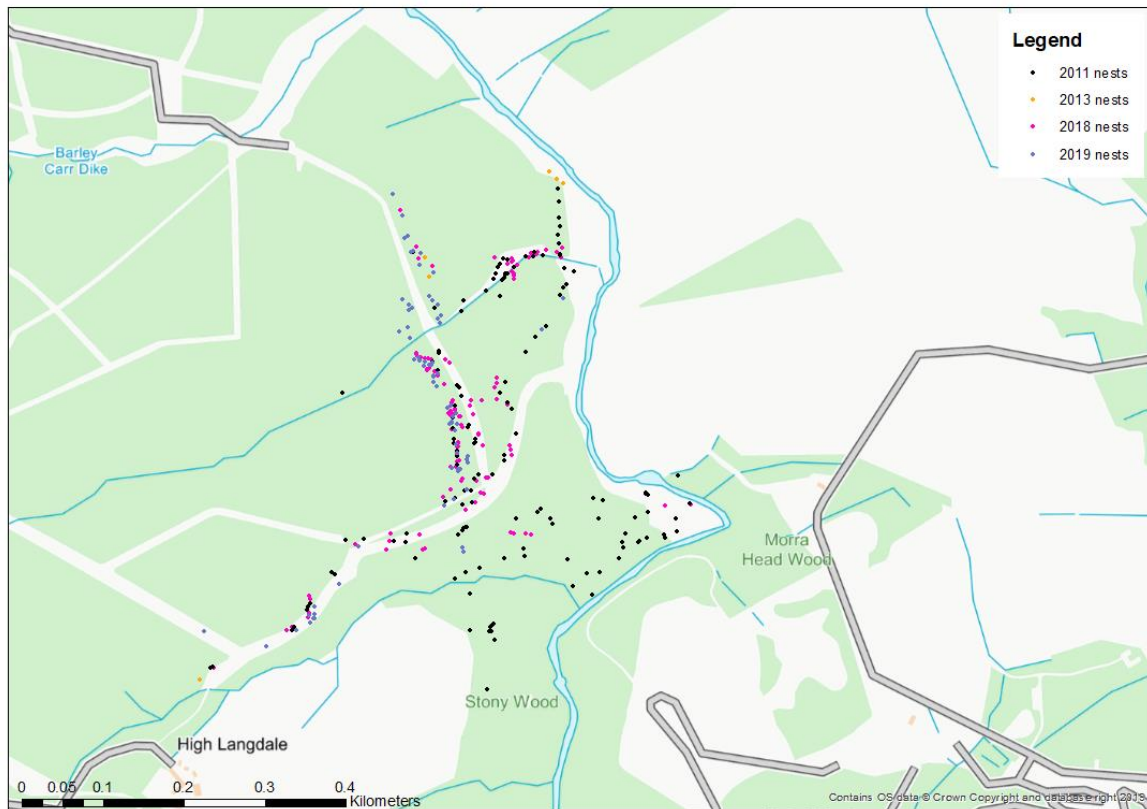
Figure 2.3 Broxa in 2019 (previously shown in Fig 2.2 as Area A for 2018 data)

2.33 Population at saturation: East Moor Wood (Hypothesis 1)

At East Moor Wood, we found very little expansion, indicative of a habitat approaching saturation due to limited suitable unoccupied habitat left for the ants to expand into. The lack of suitable habitat is not entirely obvious in figure 2.4 due to the map not reflecting the current forest layout. Many of the apparent rides and paths shown in Figure 2.4 no longer exist or are heavily overgrown with no break left in the canopy. Unfortunately, no maps showing this appear available at the time of writing. In the 2018 survey, 8 new nests were found at the population margins (average of 1.6 new nests per year); in the 2013 survey 9 new nests were found at the margins (Average of 4.5 new nests per year). Due to the site saturation, the population margins were therefore not resurveyed in 2019.
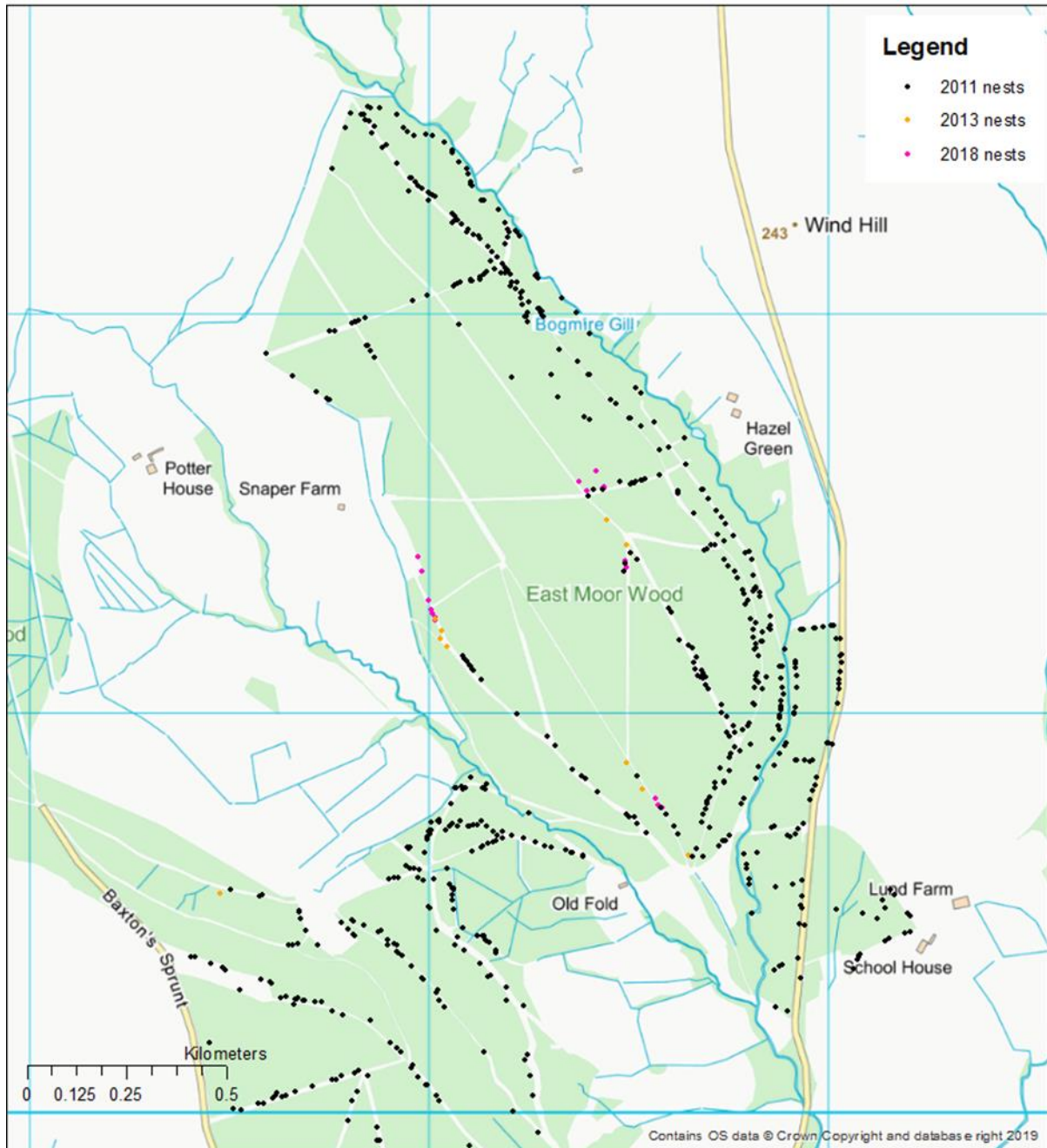
Figure 2.4 East Moor Wood (Helmsley) site. Some expansion seen on rides

2.34 Impact of forest management: Cropton (Hypotheses 1 and 2)

Slow and steady expansion was also seen at Cropton along the rides shown in areas A, B and C of Figure 2.5, where 57 nests were recorded at the population margins, in keeping with the expansion seen 2011-2013 (Procter 2016). At these areas there was little active management and stands had been left to mature.

At the Cropton site, row thinning of the stands had occurred along the population margin in area C of Figure 2.5. In 2018 237 nests were recorded that had formed

since the 2013 survey. Of these, 138 were within the now-thinned forest stand (i.e. not on an edge). An additional 28 abandoned nests (with no *F. lugubris* appearing to reside within them) were also recorded within the stands. The population margin was increased by a maximum of: 150m eastwards in area a, 46m north eastwards in area b, and 209m south eastwards in area C.

Slow, steady expansion along rides was seen again in 2019, shown in Areas B and C of Fig 2.6. The expansion margin had moved by 108m south-westward and 173m south eastward in Area C. No further expansion was seen in Area A of Fig 2.6. Three new nests were recorded on the population margin in Area C which had previously seen rapid population expansion in 2018. This rapid expansion can be inferred from there being no nests present in Procter's earlier surveys, and the forest previously being inhospitable to *F. lugubris* until the row thinning in 2016/17. However, these nests were along the margin and so did not move the population margin. Area C is covered in more detail in Chapter 3.

Rapid expansion within the stand was seen in a newly thinned (across 2017-2018) area of Cropton shown in Area B of Fig 2.6 in 2019. 80 new nests (not present in 2018) were recorded within the stands.
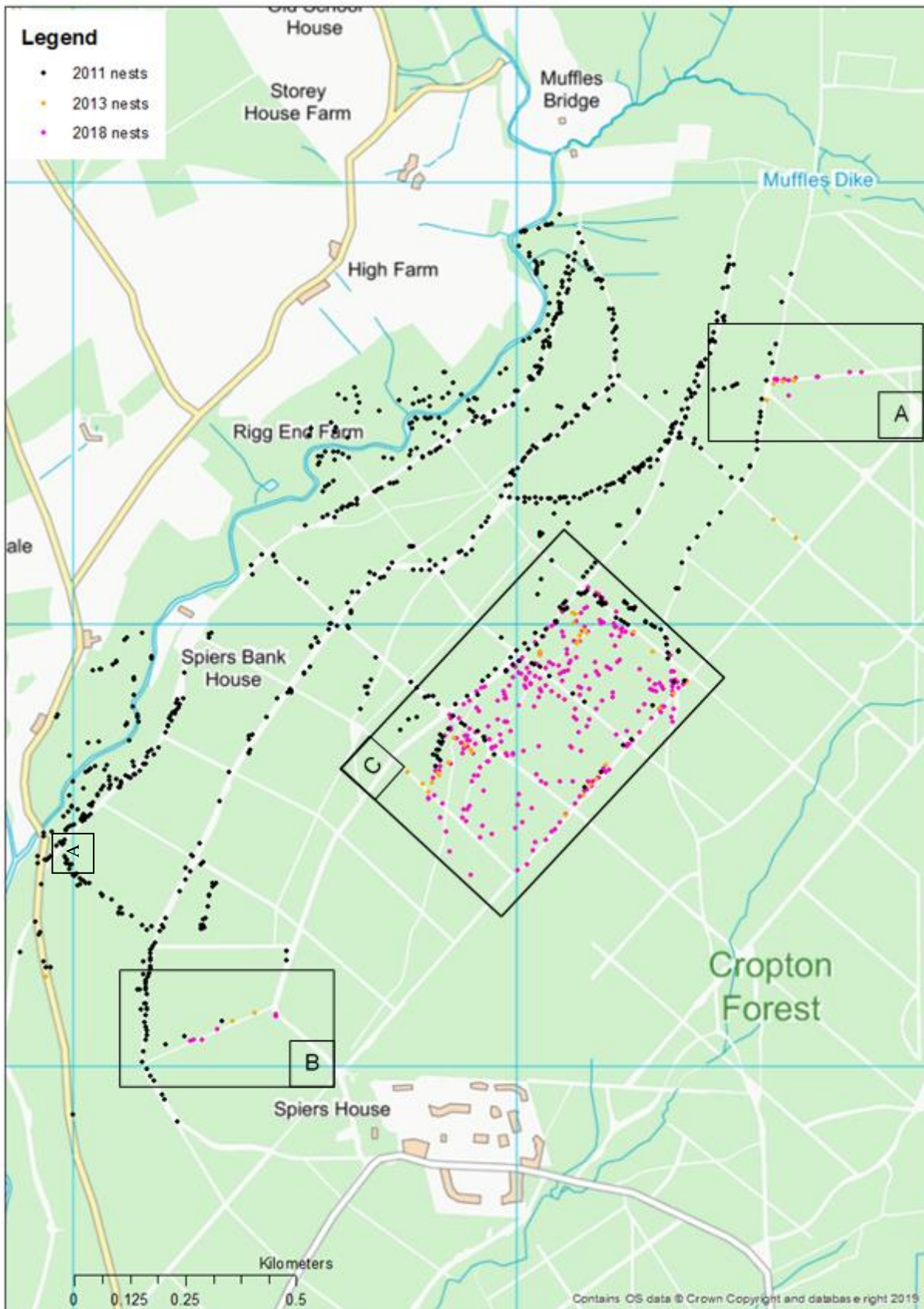
Figure 2.5 Cropton site, black dots represent nests from the 2011 population survey, orange dots: resurveyed 2013 margins (Procter, 2016), pink dots: resurveyed margins in 2018. Areas A and B show slow, steady expansion. Area C shows fast expansion due to row thinning.
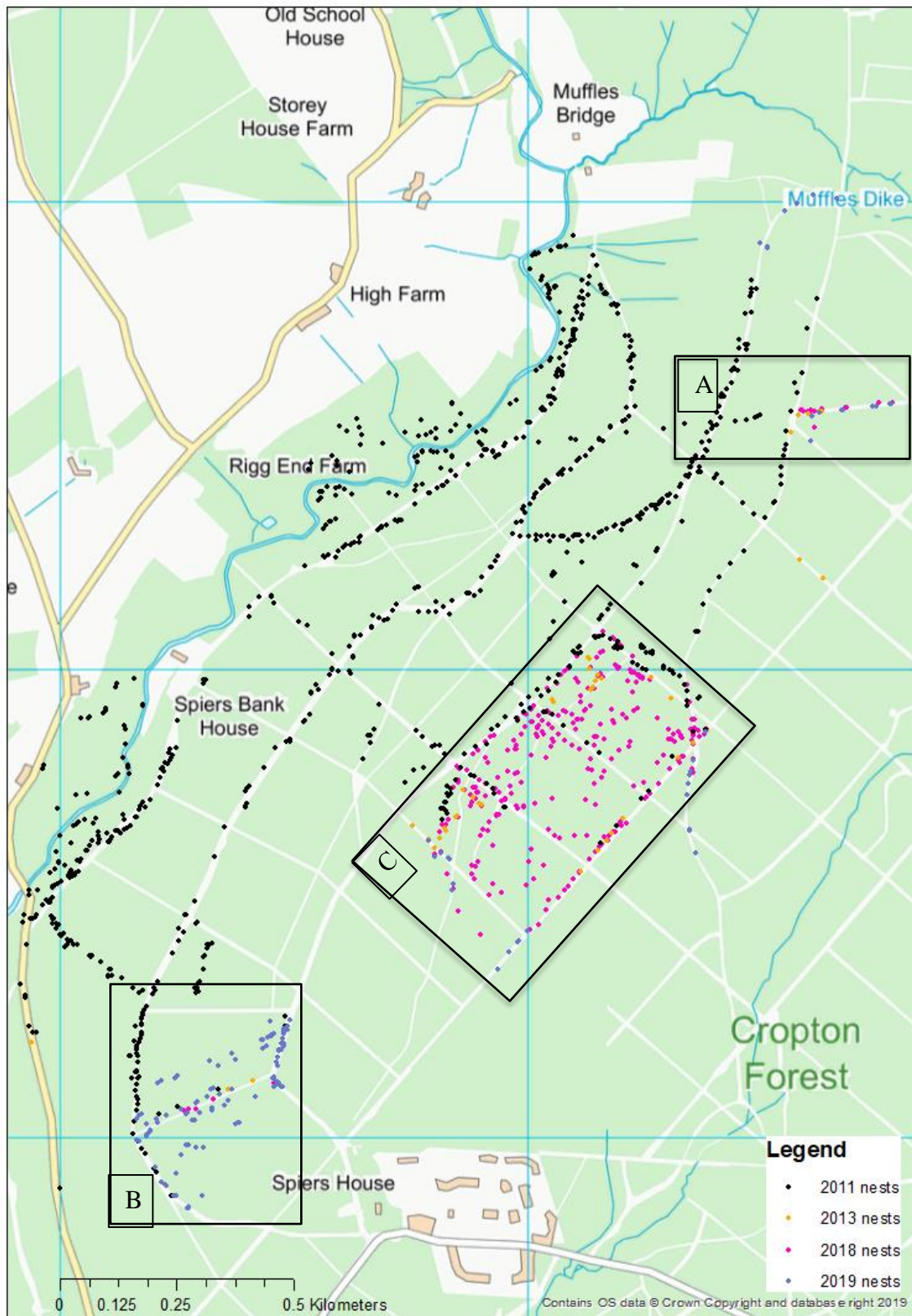
Figure 2.6 Cropton site showing the 2019 survey. Areas B and C show rapid expansion due to forest management

2.4 Discussion

This study shows a range of population expansion scenarios: rapid expansion into newly-suitable habitat, limited expansion in a site with little unoccupied suitable habitat, and steady, slow expansion in stable environments.

At both Broxa and Cropton steady, slow expansion was evident when comparing the 2018 and 2019 surveys with the previous surveys undertaken by Procter in 2011 and 2013 (Procter, 2016). The expansion occurred along the path edges and rides, shown in Figures 2.5 and 2.3. Expansion into these areas was expected as the path edges and forest rides represent areas of pre-existing edge habitat which is preferred by *F. lugubris* (Maeder *et al*, 2016). This is the type of expansion observed at these sites previously and is thought to be how the *F. lugubris* populations expanded from the areas of nearby ancient woodland fragments into the newer plantation forests (Procter *et al,* 2015). We were able to use data over 8 years to calculate average expansion rates where edges are available; these will be valuable for predicting spread in other wood ant populations.

At Cropton in 2018, new *F. lugubris* nests were found within the forest stands, indicating rapid expansion into areas previously without ants (Figure 2.5, area C). Expansion into the interior of stands was unexpected, as previously Procter *et al.* reported 78.5% of nests being within 10m of forest edges (Procter *et al*, 2015). The large number of apparently new nests is unlikely to be accounted for by sampling error in the 2013 survey, as the survey effort was found to be 96% accurate (Procter *et al* 2015). Instead, the area in which these nests have occurred appears to have been made suitable habitat by a forest management thinning process which has decreased the canopy cover within what were previously dense larch and pine stands.

A similar instance of rapid expansion of the *F. lugubris* population into a newly suitable area (thinned in 2017-2018) was found when Cropton was surveyed in 2019 (fig. 2.6 area b). In previous surveys no evidence of *F. lugubris* nests were found in this location. Given that the two different areas where rapid expansion of the *F. lugubris* has occurred area areas where recent row thinning has been carried out

adjacent to an existing F. lugubris population suggests, that this is a forest management practice which favours the movement of *F. lugubris* populations.

The process of non-selective row thinning, seen at Cropton, is currently out of favour with forest managers as it is thought to have a negative impact on biodiversity. Selective thinning, in which specific trees within a stand are thinned, is now the norm (Rylance, 2018). Heterogeneity across forest stands may be more important for increasing plantation forest biodiversity than thinning practices (Muir *et al.* 2002). The presence of hardwood trees and shrubs can increase biodiversity within forest stands (Muir *et al.* 2002). The non-selective thinning at the Cropton site removes and reduces the understory and presence of shrubs so other species, such as Bilberry, will be negatively impacted.

Thinning alters the habitat within the forest stands and will affect habitat specialist species differently. Thinning increases edge habitat, so it is expected that it would be beneficial to other edge specialists as well as *Formica lugubris* for example; common voles (Schlinkert *et al,* 2016). Myrmecophiles which reside within or around wood ant nests would also benefit from thinning due to the increased number of *F. lugubris* nests, and therefore increased suitable habitat. Over 100 different wood ant myrmecophile species have been identified, with many more species considered as associates of wood ants (Robinson *et al*, 2016). However, the removal of the canopy by row thinning may reduce the humidity and affect the temperature of the understory, as well as reducing the amount of non-edge habitat. Therefore, row thinning will have a negative impact on the biodiversity of non-edge specialists such as woodland interior birds, for example the nuthatch (Bailey, 2007: van Langevelde, 2008).

In contrast to this, it is suggested that forest plantations that are left to mature to 'old-growth' (categorised by a high proportion of old, large trees, with multiple age classes and high volumes of fallen deadwood), have large benefits to species such as hole-nesting birds, mammals such as the red squirrel, bryophytes, lichens, and fungi (Humphrey, 2005). However, old growth takes 80-100 years to develop and is difficult to balance with the production of timber (Humphrey, 2005), given that spruce plantation can reach maturity (when felling occurs) at 40 years (Forestry England).

Thinning also increases the disturbance to the interior of the stands. For managed boreal forests, a beneficial strategy for maintaining biodiversity of all forest species is to diversify management strategies (which act as disturbance regimes), as management combinations are highly taxon-specific (Mönkkönen *et al,* 2014). Management which reduces canopy cover by either harvesting or by planting shade intolerant tree species benefits ant community structure (Grevé *et al.*, 2018). By integrating forest stands with more open and warm conditions and diversity is increased (Grevé *et al.*, 2018).

The newly-created edge habitat is likely to only be available for a short time. As the neighbouring trees to those removed continue to grow, and underbrush develops, the canopy cover will likely increase, and as such this 'edge' will be lost. The interior of the stand may become unsuitable for *F. lugubris* nests to survive within the stand, unless they have achieved a very large size (Chen and Robinson, 2014). The survival rate of *F. lugubris* nests within newly thinned stands is under investigation as part of this project (See Chapter 3).

Though the newly-created edge habitat may only be ephemeral, it could act as a stepping-stone to more stable suitable habitat. Dense forest stands have a low permeability to edge specialists. Thinning may enable *F. lugubris* to spread to previously inaccessible rides or edge habitat. If this is the case, then the thinning management practice could be utilised to increase the movement of *F. lugubris* through a landscape. Stepping-stone habitats are crucial in allowing species to spread over long distances, acting as a corridor, and without stepping stones the distance a species can travel across a landscape is greatly reduced (Saura *et al*, 2013). In wetlands, a form of dynamic landscape, the presence of temporary stepping-stones reduced the isolation of populations of poor dispersing species (Ruiz *et al.* 2014), and therefore the ephemeral nature of this landscape is important to the success of poor dispersing species residing within it. Artificial stepping-stones can also increase the movement of species in marine habitats; for example, offshore power structures have created new habitats for intertidal marine organisms with pelagic larval forms (Adams *et al.* 2013). Further research is needed to understand how introducing anthropogenic novel habitats into a landscape will affect species distributions, including invasive species and 'climate migrants' (Adams *et al.* 2013).

The process of thinning, and other forest management techniques such as clear felling, create a dynamic landscape system within the forest (Wintle *et al,* 2005). Each stand may have different turnover rates of habitat and not all stands may be suitable habitat. The dynamism may in fact be beneficial for *F. lugubris* as the thinning can create ephemeral stepping stones through the forest (Matlack and Monde, 2004). However, as thinning is only temporary, so are the stepping stones provided, and the stand interior will likely return to being inhospitable. Here, the low average rate of population spread in stable habitats mean that this species potentially benefits particularly highly from short-term interventions that accelerate that spread. More research is needed to examine the relationship between landscape turnover and how this interacts with different species' dispersal capabilities and life histories (Matlack and Monde 2004: Wimberly 2006).

Can row thinning be applied elsewhere? If row thinning is a way in which *F. lugubris* populations can reach areas of suitable habitat which are inaccessible to them due to an area of dense forest, then row thinning could be a good management practise at Broxa. The Broxa population has expanded, in a slow and steady way, from Broxa into Langdale Forest (Fig 2.2 and 2.3), which Procter *et al* (2015) showed large areas of which to be suitable for *F. lugubris*. No *F. lugubris* is known to inhabit other areas of Langdale Forest, nor the connected Dalby forest. However, Procter *et al.* (2015) showed via habitat modelling that there are areas of Langdale Forest which are not as favourable for *F. lugubris* as others and may form impassable areas in their current state. If these areas identified by Procter *et al* could be made more accessible by row thinning, then it is possible that the *F. lugubris* population could spread beyond them into suitable habitat in Langdale Forest.

Currently the areas in which *F. lugubris* populations are expanding into at Broxa are under minimum intervention plans (Table 2.1) (Rylance, 2018), in which very little anthropogenic interference will occur. The continuing expansion into neighbouring Langdale Forest may slow because there is a lack of suitable habitat ahead of the current population margin. From our findings, a forest management strategy such as the row thinning at Cropton, could potentially be used to increase the potential suitable habitat for *F. lugubris* in the forests connected to Broxa.

Conclusions

Our results confirm that *F. lugubris* can be viewed as a 'poor disperser', spreading just a few metres each year, even when suitable habitat is available. However, when in a heterogenous ephemeral habitat with beneficial habitat *F. lugubris* was able to disperse rapidly into the area. From the results of our study, we conclude that the practice of row thinning is beneficial to the short-term population expansion of *F. lugubris* and may be responsible for large population expansions through a landscape. Our study shows how certain anthropogenic disturbance regimes can increase the population expansion of poor dispersing habitat specialists in a natural environment. Modelling work which could utilise this data in the future would allow us to investigate how different rates of disturbance may affect the movement of a habitat specialist. We hope this will have impacts for the conservation of such species.

Chapter 3; Can nest attributes and microhabitat predict the survival of *Formica lugubris* (hairy wood ant) nests in a newly colonised area?

3.0 Introduction

3.01 Survival in a new habitat

Understanding what governs species survival when moving into a new suitable area is essential because human activities require species to make these moves more rapidly and extensively than ever before. As climate change progresses, it is accepted that many species will have to shift their ranges to higher altitudes or polewards (Parmesan and Yohe, 2003; Hickling *et al.* 2006; Chen *et al.* 2009). The most severe driver of biodiversity change has been identified as land-use change (Sala *et al.* 2000). Land-use change results in habitat loss and fragmentation, both of which can drive the movement of populations into new areas. Therefore, understanding the factors governing the ability of a species to survive in their new habitat is crucial.

3.02 Initial habitat colonisation

The initial colonisation of new habitat is risky. Individuals may be moving into an already established habitat, and potentially competing for resources with already established species (Levine *et al.* 2004), resulting in very high mortality rates in newly colonised areas. Becoming established is difficult, as new individuals must either outcompete already established species for resources or be able to reproduce at a rapid rate.

To successfully colonise a new area, individuals must first arrive at it, which may involve dispersing across unsuitable habitat. Species differ in their dispersal abilities, which can explain the variety in species diversity and community structure in

different landscapes, especially patchy habitats (Logue *et al.* 2011). For more information on how habitat layout affects successful dispersal please see Chapter 2. Species that are especially good at colonising new habitat often have high fecundity, long-range dispersal capabilities, fast life-history strategies and are able to fill a broad ecological niche. Many species that display such traits are invasive due to their ability to quickly colonise an area.

In contrast to this, many species that do not display such traits are poor dispersers, and understanding the dispersal of poor dispersers into a new area is especially important. Endangered species are often poor dispersers, due to their slow reaction to habitat change. Habitat destruction which leaves a fragmented landscape of suitable habitat poses a serious threat for poor dispersers. Poor dispersers often have multi-staged life histories and short dispersal distances. A species' dispersal ability will determine the outcome of a colonisation event. For more detail on poor dispersers please see chapter 1. If a species' can rapidly move into a new habitat and outcompete established species, then it is more likely to become established.

3.03 Why are life stages important?

Different life history stages have different mortality rates. In colonisation events, the survival and length of the juvenile phase is especially important. Mortality rates in juveniles tend to be high due to lower body size, rendering juveniles more vulnerable to competition and predation. Many poor dispersers produce fewer offspring and take longer to mature to a reproductive state. This means the survival of poor dispersers' juvenile stage is especially important.

The length of time taken for an individual to mature from a juvenile to an adult also affects the chances of a successful colonisation event. Species which have a short juvenile phase have a better colonisation ability (Rejmanek and Richardson, 1996). A short juvenile phase results in fast population growth. Many invasive species have high fecundity paired with fast maturation providing consistent reproduction (Sakai *et al.*, 2001). This fast growth and 'reproduction' can also be applied to the nests of eusocial invasive species such as the invasive argentine ant (Suarez *et al.*, 2008) who are quick to build new nests which reach 'maturity', or a point where individuals can leave the nest and set up a new nest. Argentine Ants can reach maturity within 2

months of being hatched, when a queen reaches maturity, she can leave the nest to form a new nest (Drees and Summerlin, 2011) . When considering eusocial insects, and using the nest as the individual the phase of the nest reaching maturity could be considered the 'juvenile phase'.

3.04 Why measure survival?

Survival of a population is a combination of the likelihood of individuals surviving the juvenile phase to be able to reproduce themselves and eventual reproductive success. In this study, we are measuring initial survival rather than reproductive rates as survival is the product of successful reproduction in a newly colonised area, and a necessary precursor to future reproduction. Here we look at the survival of individual nests within a population as a way of investigating the factors affecting population survival at a individual level.

3.05 Microhabitat and individual attributes

Many factors contribute to an individual's chances of survival: genetics, intra- and interspecific competition, predation, foraging success and many other factors may play a role here we will focus on the microhabitat an individual resides in, and certain individual attributes.

Microhabitat

The microhabitat surrounding an individual is especially important to survival, especially for sessile organisms. Microhabitat can be quite different from the overall habitat an individual is in, with microrefugia existing (Lenoir *et al.* 2017). This is especially prevalent in forest ecosystems, where the conditions below different areas of the canopy are highly heterogeneous often depending on shading (Lenoir *et al.* 2017). The collection of data on the effects of microhabitat on survival is important when considering habitat suitability models: without incorporating microhabitat, models underestimate the probability of local species persistence due to the presence of microrefugia (Lenoir *et al.* 2017).

By measuring the microhabitat around an individual, especially a sessile organism, we can observe the relationship between small scale variation and survival. Sessile organisms cannot leave their microhabitat if it is not suitable, so we would predict microhabitat to have a large impact on survival.

Individual attributes

Measuring the attributes of individuals allows us to control for variation in such attributes (i.e. size, social connectedness, etc) whilst examining the effect of microhabitat on survival. Individual attributes can also capture some of the historic conditions of an individual, both in terms of the quality of an individual and the environment the individual has been exposed to. Individuals of a high quality could be better foragers, and if they have resided in a stable environment, with plentiful resources, they are likely to be larger than lower quality individuals in areas with lower resources. Individual attributes can provide information on the conditions of the individual and environment in the previous year. Body size is potentially the most important attribute due to its effects on most physiological and morphological traits (Atkinson, 1994; Blankenhorn and Demont, 2004).

There may be threshold levels of certain attributes an individual must reach to survive. For instance, the size of *F. lugubris* nests has been found to have a threshold size for the survival of that nest. If a nest does not reach a certain size, then thermoregulation cannot be maintained, and a sufficient nest temperature cannot be reached (Frouz and Finer, 2007; Brandt, 1980). By collecting nest attribute data we hope to be able to add to the evidence for threshold levels of attributes.

3.06 Study species

At our study site (Cropton Forest) we used the wood ant, *Formica lugubris*, as our study species. *Formica lugubris* is a poor dispersing edge habitat specialist. For more detailed information on the importance of *F. lugubris,* and the benefits of using wood ants as a study species please see chapter 1.

Wood ants present a good system in which to study the survival of poor dispersers as the life-history of a wood ant nest is somewhat similar to many other poor dispersers. In this study we consider the wood ant nest as the reproductive individual unit, rather than the individual ants. Though individual ants are mobile, the nests are sessile and display similar characteristics to many poor dispersers.

Formica lugubris colonies can be regarded as a superorganism, with the colony being a biological analogue for the body of an individual (Chen and Robinson, 2013; Clémencet and Doums, 2007; Lanan *et al.* 2011). All the organisms within a superorganism form a cooperative unit to reproduce their genes (Seeley, 1989). This means that for organisms such as polydomous *F. lugubris* there are two levels of organisation; the superorganism and the individual ant (Chen and Robinson, 2013). In this study, we use nests to refer to the reproductive individual unit, who by budding, form new nests. Survival does not necessarily lead to death of the ants within a nest as they are often absorbed into other established nests within the colony. Instead, survival in our study refers to the success or failure to establish a new reproductively active unit.

A wood ant nest must reach a certain volume and maturity before it can be reproductively active by the process of budding. The delay in a new nest being formed and the nest being able to produce new nests is comparable to the juvenile phase many poor dispersers have. The survival of these juvenile nests is important as they are the nests that will be in new areas of habitat (having budded from established nests). For the successful colonisation of an area, these new 'juvenile' nests must survive, become established, and bud. As this population does not have successful mating flights (Maeder *et al*, 2016) the only way for these wood ants to colonise an area is through budding.

3.07 Cropton study area

The study site was located at Cropton Forest, in three forest stands which had undergone row thinning in the winter of 2016/17. The row thinning created newly available edge habitat extending into forest stands which were previously unsuitable habitat and thus provided a unique opportunity to observe how wood ant nests survive in a recently colonised area. From past surveys (Procter *et al*, 2015), the

former population margins of the *F. lugubris* population at the site are known, and no nests had been located within the study site stands in 2012 and 2013. As the site is managed by Forestry England, detailed past, present and future forest management plans are available. The combination of past surveys and management practices gives a unique area in which to study the survival of *F. lugubris* nests in a newly colonised area.

3.08 Field vs. laboratory approach

It is necessary to carry out this research in a field environment rather than in a laboratory setting. A nest's microhabitat and attributes form a complex mix of potential predictors. A laboratory setting would be better suited if only one potential predictor was being investigated in detail. However, as survival is an end product of many interacting issues, such as predation, foraging success, genetics, climatic factors and more, the laboratory setting would not capture this. Additionally to this, nests are part of socially connected colonies, and to re-create the social interactions between nests in the laboratory would be difficult. Therefore, a field-based approach is necessary.

3.1 Study aims

In this study, we aim to identify microhabitat variables and nest attributes that can predict the survival of a nest in newly colonised areas by addressing the following hypotheses:

Hypothesis1: The microhabitat of the nest predicts nest survival in newly colonised areas
Rationale: The microhabitat, such as canopy cover and food availability around a nest affects the nest's chance of survival into the following year.

Hypothesis 2: Nest attributes in the previous year predict nest survival in newly colonised areas
Rationale: Nest attributes such as size and social connectedness to other nests affect the survival of the nest into the following year. Nests which are larger

(therefore able to maintain heat over winter and consist of more ants) with more connections (and therefore resource sharing) are more likely to survive.

By testing these hypotheses, we aim to inform predictions of the survival of a wood ant nest in a newly colonised area, and identify any threshold levels at which survival becomes possible. The life history data and microhabitat data collected here will provide data for parameterisation of future models that could predict the spread of *F. lugubris* and other poor dispersers, for whom collecting life history data is more difficult.

3.2 Methods

3.21 Natural history

The wood ant, *Formica lugubris,* is an edge specialist found in upland wooded areas throughout Northern Europe. In Great Britain, the species inhabits woodland in Scotland, Northern England, and Wales. Previous work at sites on the North York Moors found population expansion of *F. lugubris* from ancient woodland fragments into the neighbouring plantation forests (Procter *et al,* 2015). At the study site, the species is both polydomous and polygynous with multiple nests within a colony. *Formica lugubris* builds nest mounds made of forest debris to create thatch, which are easily identifiable when surveying (Risch *et al.* 2016).

3.22 Field site

The study site used for this work was situated in the west of Cropton Forest on the North York Moors. Cropton Forest consists mainly of non-native conifers and was first planted in the 1950s. There is high heterogeneity in tree species, age class, and management between plantation stands. The study site consisted of 3 stands measuring 200 by 300 metres that had undergone non-selective row thinning between 2016 and 2017, resulting in disruption of the forest stands' interior. Previous field surveys of *Formica lugubris* by Procter recorded *F. lugubris* nests present at the edges of the stands. No nests had been found within the forest stands apart from along a natural edge where a ditch is situated (Procter, 2016).

3.23 Fieldwork Methods

To understand if there were identifiable microhabitat drivers of nest survival in newly expanded areas, microhabitat variables and nest attributes were recorded at nests in 2018 and again in 2019 at the study site.

In the 2018 surveys, the microhabitat variables were recorded for all nests in the study stands. Nests were found using transects, spaced 10m apart, running through the forest stands. This is an effective method of locating all wood ant nests at this site (Procter *et al*, 2015). In 2019, all of the 2018 transects were revisited and microhabitat variables were recorded for a subset of nests. Some nests were still inhabited, while others had been abandoned, but were still clearly recognisable as former nests. To ensure microhabitat variables were recorded for an equal number of abandoned and inhabited nests whenever an abandoned nest was recorded its microhabitat variables were recorded and the next inhabited nest along the transect also had its microhabitat variables recorded.

At each nest where microhabitat variables were recorded, the nest location was marked on a handheld GPS. In 2018, a flag with a nest identification number was also placed in the ground beside the nest to assist with the identification of the nest in future surveys. Nest volume was recorded by taking measurements of nest height, width (at the widest point of the nest), and length of the nest (90º to the width measurement) with a metre rule. The nest volume was then calculated by using half the volume of an ellipsoid (Chen and Robinson, 2013; Ellis *et al*, 2014). Nest surface temperature was taken with a handheld temperature scanner (Mini RayTemp Thermometer ± 0.1ºC), at three different places on the nest surface and the mean calculated. Foraging trails and social trails from the nest were counted. Foraging trails were identified by the presence of foragers returning to the nest with food, or the trail going up a tree (Ellis *et al*, 2014). Social trails were identified by those leading to another nest (Ellis *et al*, 2014). Foraging trail presence can depend on weather conditions, the surface temperature of the ground underneath the foraging trails 1m away from the nest was measured with a handheld temperature gun. The strength of the social trail, as a measure of 'social connectedness' with other nests, was measured using an established method (Ellis *et al*. 2014) involving identifying a point 2m along the trail from the nest, and measuring distance along the trail from

that point until 10 *F. lugubris* were encountered (ingoing and outgoing ants were counted). This took place away from the nest so the ants were more likely to be on the trail and not spilling over from the surface of the nest (Ellis *et al.* 2014). Canopy cover above the nest was photographed using a smartphone (Apple iPhone 6) with a fisheye lens attached (Bianchi *et al.* 2017). The photographs were then analysed to calculate percentage canopy cover using the '%Cover' mobile application (Miganelli, 2017). Slope aspect was taken using a compass at each nest. Temperature across the day was recorded at the North York Moors weather station (North York Moors Weather, 2019).

In 2018 the closest five trees to the focal nest were identified to genus, and their diameter at breast height was measured. This was to give an indication of the food sources available to the nest. As the forest stands were very homogenous in tree species and age, this variable had no potential explanatory power at the nest level. It was not recorded in 2019, and not used in the predictive model.

If time and cost had permitted, humidity and air temperature under the canopy would have been additional microhabitat measures to be collected. However, due to the public nature of the Cropton site, leaving equipment such as data loggers in place was not appropriate. Humidity under the canopy can vary compared to the overall humidity of an area, and thinning has a large impact on humidity. Collection of air temperature at the site of the nests through the study would have been beneficial as the temperature readings of the nests do not reflect this as nests both absorb heat and give out heat. Air temperature at the nest sites, due to being below the canopy, can be very different to the temperature provided by weather stations.

3.24 Analysis methods

Data exploration was carried out following the protocol described in Zuur, Ieno & Elphick (2010). All analyses were performed using R statistical software (R version 3.6.3; R Core Team 2020). To check for clustering of predictor variables in the 2018 and 2019 survey data, a PCA was done. Clustering was checked using 'hclust' and 'dist' functions (R Core Team 2020). The PCA was carried out using 'prcomp' (R Core Team 2020). To check whether closer nests had more similar canopy cover,

and that effects of canopy cover weren't due to spatial autocorrelation, spatial autocorrelation between canopy cover and distance between the abandoned and inhabited nests surveyed as pairs in 2019 was plotted and correlated using Spearman's correlation coefficient through the 'cor.test' function (R Core Team 2020). Where possible, variables were checked for correlations between 2018 and 2019. Correlations of the number of social trails and social trail strength between 2018 and 2019 were not included as if the nest was abandoned in 2019 the values for these variables will be 0.

The location of large, inhabited nests (those whose nest volume in 2018 was in the upper quartile) were checked to see if the nests could have plausibly been missed in a previous survey. Two nests which were along a ditch with a canopy break predating the row thinning were removed from the data set on these grounds. The two nests removed from the analysis were also close to nests found in the 2013 survey and within the area of GPS error.

Of the microhabitat data collected (canopy cover, identification of nearest 5 trees, and diameter at breast height of the nearest trees) only canopy cover was included in the model due to stand homogeneity meaning trees in the stand were all of the same species and age class.

A preliminary GLM (generalized linear model) was used to see if there were any variables in 2019 which predicted the nest state between the abandoned and inhabited nests. This was to see if any of the variables were different between the abandoned and inhabited nests as changes in the surroundings of the nest could of occurred since the previous 2018 survey. The GLM was undertaken with a binomial error structure and a logit link. The dependent variable was nest state (abandoned or inhabited) in 2019. The predictors used in the full model were; 2019 nest volume, 2019 distance to nearest nest, social trail strength in 2019, number of social trails in 2019 and canopy cover in 2019 (Table 3.1). As nests found abandoned in this survey would have no social connections a further GLM was carried out to see if there were predictors of nest survival from the 2018 nest attributes.

The initial preliminary GLM included all predictor variables and all possible pairwise interaction terms. Model selection was then undertaken using a two-stage backward

deletion method, based on Crawley (2007) using the R function 'glm' in the 'stats' package (R Core Team 2020), At each step of the GLM, the least significant interaction term in the model was removed, as long as the removal did not reduce the model fit. When removing terms led to a model in which all predictors had a significant effect, no further terms were removed.

Table 3.1 variables used in the preliminary GLM

Variable	Further information
Nest Volume	2019 nest volume
Distance to nearest nest	2019 survey
Canopy Cover	2019 survey
Number of Social Trails	2019 survey
Social Trail Strength	2019 survey
Nest State (dependent variable)	2019 survey

The AIC of the minimal model GLM was calculated to check for the best fit of the simplified model and any nested models within this using the 'stepAIC' in the MASS package (Venables and Ripley, 2002). The model with the lowest AIC was selected. The data were checked for outliers using the influencePlot and outlierTest functions in the R package "car" (Fox and Weisburg, 2019). Plots of the residuals vs fitted, QQ plot, scale-location, and residuals vs leverage were also used. A check for outliers was carried out.

The GLM was evaluated for fit and an ANOVA was done to check for a significant difference between the final model and the base model containing all variables and interactions. Model assumptions were checked by plotting Pearson's residuals versus fitted values. Each covariate in the model was also plotted against Pearson's residuals. Model overfitting was then checked by calculating the R^2 value. The residual deviance of the model (G^2) was calculated to assess the goodness of fit of GLMs, and the theta value calculated to check for overdispersion following methodology outlined by Burnham and Anderson (2002) and Marthew (2019).

To test whether there were any identifiable nest attributes or microhabitat (canopy cover) in 2018 could be used to predict the survival of a nest in 2019 a further GLM analysis was undertaken with a binomial error structure and logit link function. The dependent variable was 2019 nest state (abandoned or inhabited). The predictors in the full model were from the 2018 survey; nest volume, distance to nearest nest, social trail strength, number of social trails and canopy cover (table 3.2). All other stages of GLM analysis as previously described were followed.

Table 3.2 variables used in the predictive GLM

Variable	Further information
Nest Volume	2018 nest volume
Distance to nearest nest	2018 survey
Canopy Cover	2018 survey
Number of Social Trails	2018 survey

Social Trail Strength	2018 survey
Nest State (dependent variable)	2019 survey

Results

In 2018, 215 nests were recorded in the study area. In 2019, 102 of these nests were resampled in the area which showed the most expansion, 51 nests which had become abandoned since the 2018 survey were recorded, and 51 nests that were still inhabited. 102 nests were selected as only 51 abandoned nests were located in the survey area and an even number of abandoned and inhabited nests were required.

The PCA showed no evidence of clustering in the 2019 and 2018 predictor variables. After checking predictor variables for collinearity using a significant correlation as the cut-off value for collinearity, nest surface temperature was removed as it correlated with canopy cover in 2018 (R^2= -0.26, df= 67, p= 0.03) and weakly in 2019 (R^2= -0.19, df= 68, p= 0.11). No spatial autocorrelation was found between canopy cover and distance to nests within the abandoned and inhabited nest pairs sampled in 2019. Spatial autocorrelation was carried out by plotting canopy cover against distance to nearest nest. The number of foraging trails in 2019 was removed as this variable would have no bearing on why the nests would have been abandoned. Aspect was also removed in both GLM's due to the study area being on one slope and therefore the aspect differed little between nests. Correlations of variables included in the GLM are included in table 3.3.

Table 3.3 Correlations of variables included in the GLMs

Variables tested	Abandoned Nests	Inhabited Nests

Canopy cover 2018 and 2019	R= 0.65, p=4.17 e-06, n=51	R=0.66, p= 5.52 e-06, n=51
Distance to nearest nest 2018 and 2019	R= 0.41, p=0.01, n=51	R= 0.49. p= 0.003, n=51
Canopy Cover and Log Nest volume 2018	R= -0.06, p=0.70, n=51	R=0.26, p= 0.11, n= 51
Canopy Cover and Log Nest volume 2019	R= -0.0001, p= -0.999, n= 51	R= 0.0995, p= 0.49, n=51

Preliminary GLM

The preliminary GLM aimed to identify any nest attributes or variables in 2019 which could predict the 2019 nest state (abandoned or inhabited). The minimal model indicated that nest volume (2019) and Canopy Cover (2019) predicted 2019 nest state (Table 3.4). One outlier was identified, however, as this referred to a large nest and was biologically significant its removal could not be justified.

The residual deviance of the GLM was calculated to be $G^2 = 72.99$, p= 0.29. As this p-value is >0.05 we assume the model fitted well. The R^2 of the model = 0.36. A statistic of over dispersion was calculated (theta= 1.09) and the data was found to be slightly overdispersed, but not enough to cast doubts on fit results as theta was between 1 and 2. A weak interaction was seen between Nest Volume and Canopy Cover; however, the effect was not large enough to be included in the all predictors significant model shown here. A plot of the model residuals against fitted values showed a good fit (Figure 3.1).

Table 3.4 GLM output of the minimal model for the preliminary GLM. Nest volume in 2019 and Canopy Cover 2019 were the only predictors of nest state

Variable	Estimate	Standard Error	Z value	Probability
Intercept	9.21171	3.50077	2.631	0.00850

Nest volume (2019)	2.30016	0.81229	2.832	0.00463
Canopy Cover (2019)	-0.12530	0.04394	-2.852	0.00435
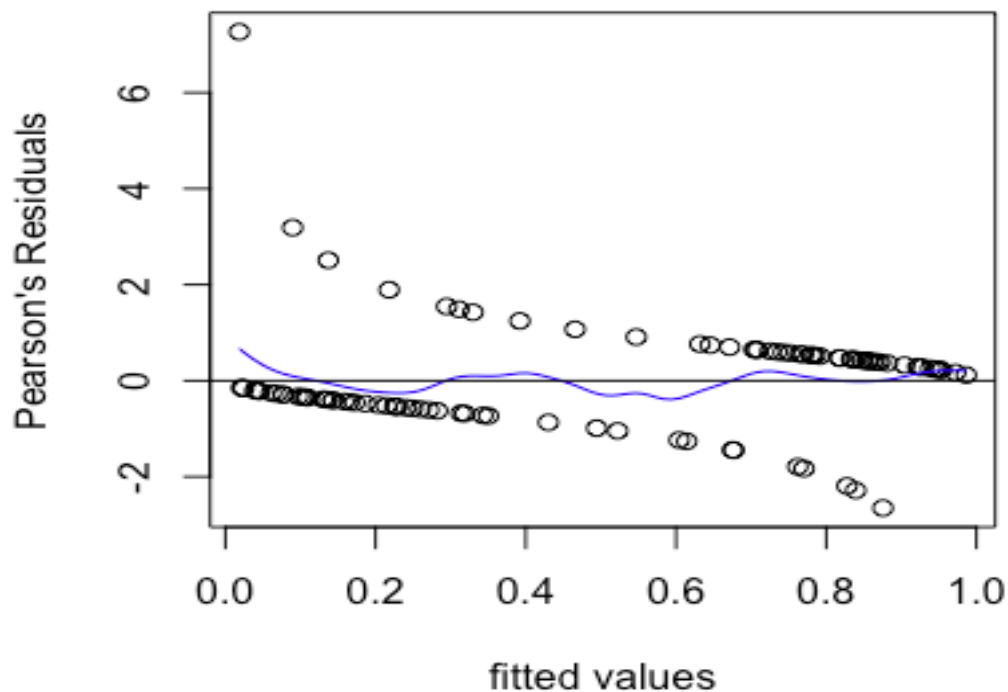
Figure 3.1 Pearson residuals vs model fit for the preliminary GLM to show model fit. The closer the blue line to the 0 line, the better the model fit

Predictive GLM

For the predictive model, using 2018 nest attributes to predict nest state in 2019, the minimal model consisted of 2018 nest volume only. Outliers were tested and no data points were removed. Although one large nest was identified as an outlier, there was no biological reason to remove the nest from the model. The dataset originally had 70 degrees of freedom, this fit has 2, leaving 68 residual. The model was found to have an $R^2 = 0.10$, with the residual deviance (G^2) of 87.1, p=0.06. As p>0.05 the fit of the model is adequate, shown by figure 3.2. GLM output shown in table 3.4. The data was found to be slightly over dispersed (theta= 1.28) but not enough to cause

doubt on the model fit (theta <2). Figure 3.3 shows how survival between years increases with nest volume. The model shows that larger nests are more likely to survive between the two surveys. Figure 3.4 shows the difference in nest volume between survived and abandoned nests. From the data collected in this study it is impossible to estimate nest growth or shrinkage as abandoned nests become smaller due to the thatch of the nest degrading, however the effects of individual nest volume changes over time would be an interesting further study.

Table 3.5 results of the predictive GLM predicting 2019 nest state from 2018 nest volume

Variable	Estimate	Standard Error	Z value	Probability
Intercept	-0.5645	0.3001	-1.881	0.0599 .
Nest volume (2018)	1.9762	0.8056	2.453	0.0142 *
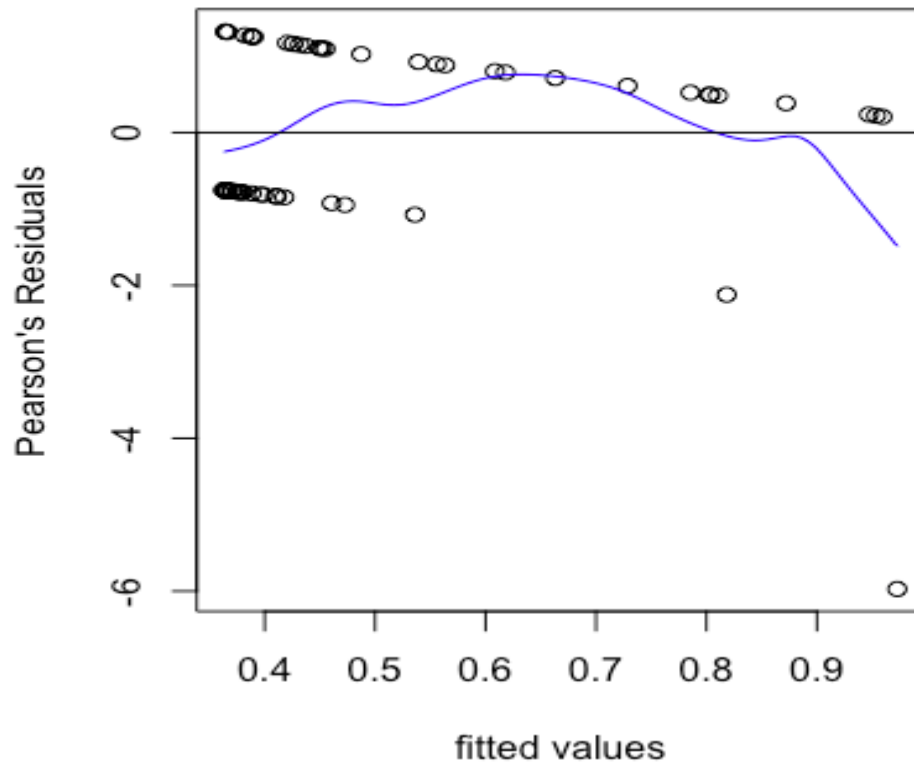
Figure 3.2 Fitted predictive GLM values against residuals.
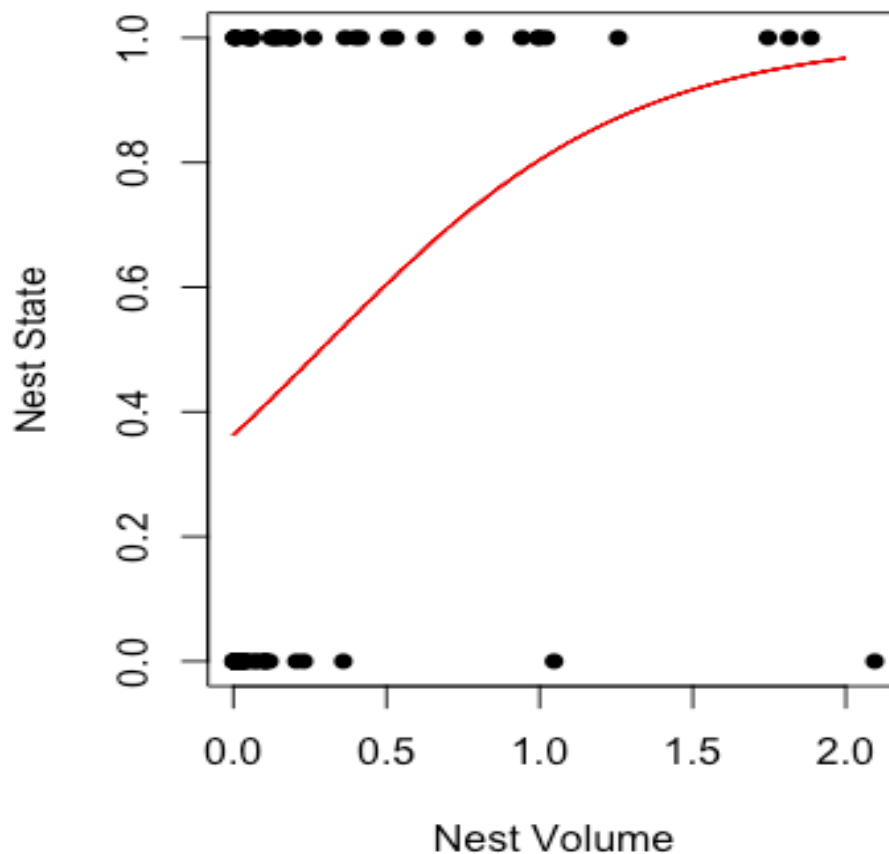
Figure 2.3 Binomial plot for predictive GLM. Nest Volume predicts Nest State (1= inhabited, 0= abandoned). Total N for abandoned nests is 51, total N for inhabited nests is 51.

Both canopy cover and number of social trails were weakly correlated with the nest survival in the following year (Fig. 3.5 and 3.6), however, their effect was not large enough to be included in the minimal model GLM. To check whether the canopy cover effect was due to a change in canopy between 2018 and 2019, a paired t-test was undertaken. No difference in canopy cover between 2018 and 2019 was found.
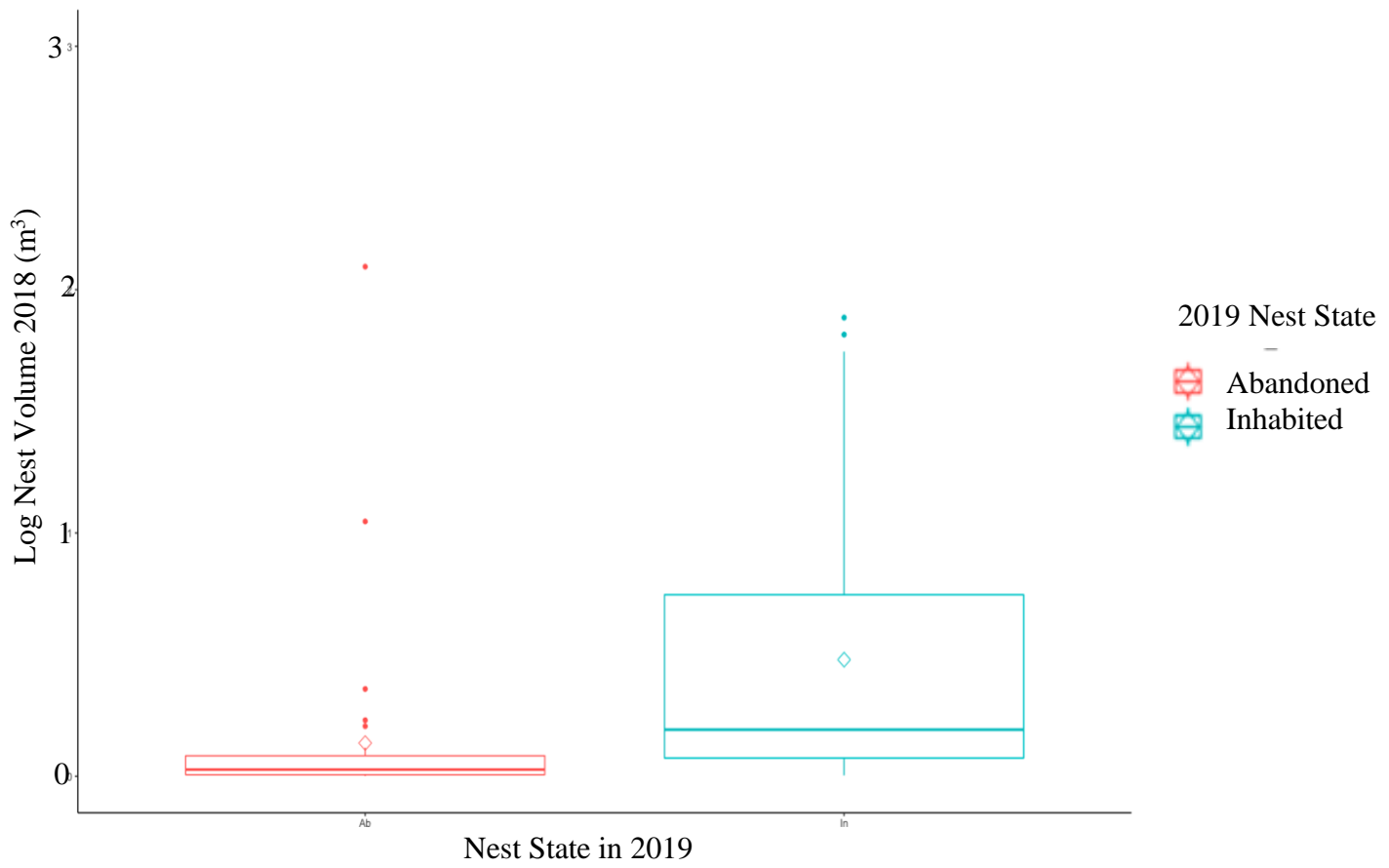
Figure3.4 Nest Volume in 2018 of abandoned and inhabited 2019 nests
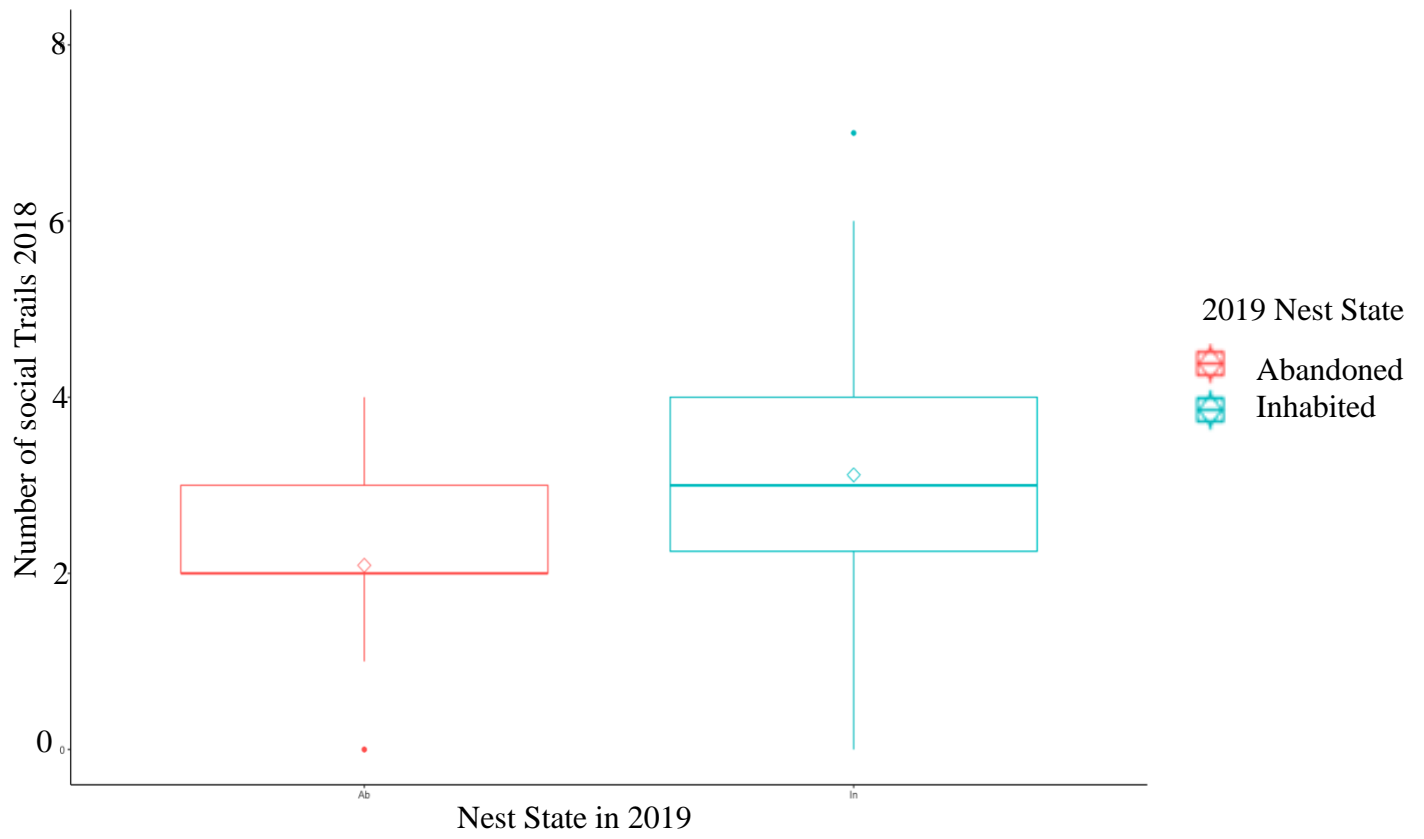
Figure 3.5 Number of social trails a nest had in 2018 of abandoned and inhabited 2019 nests
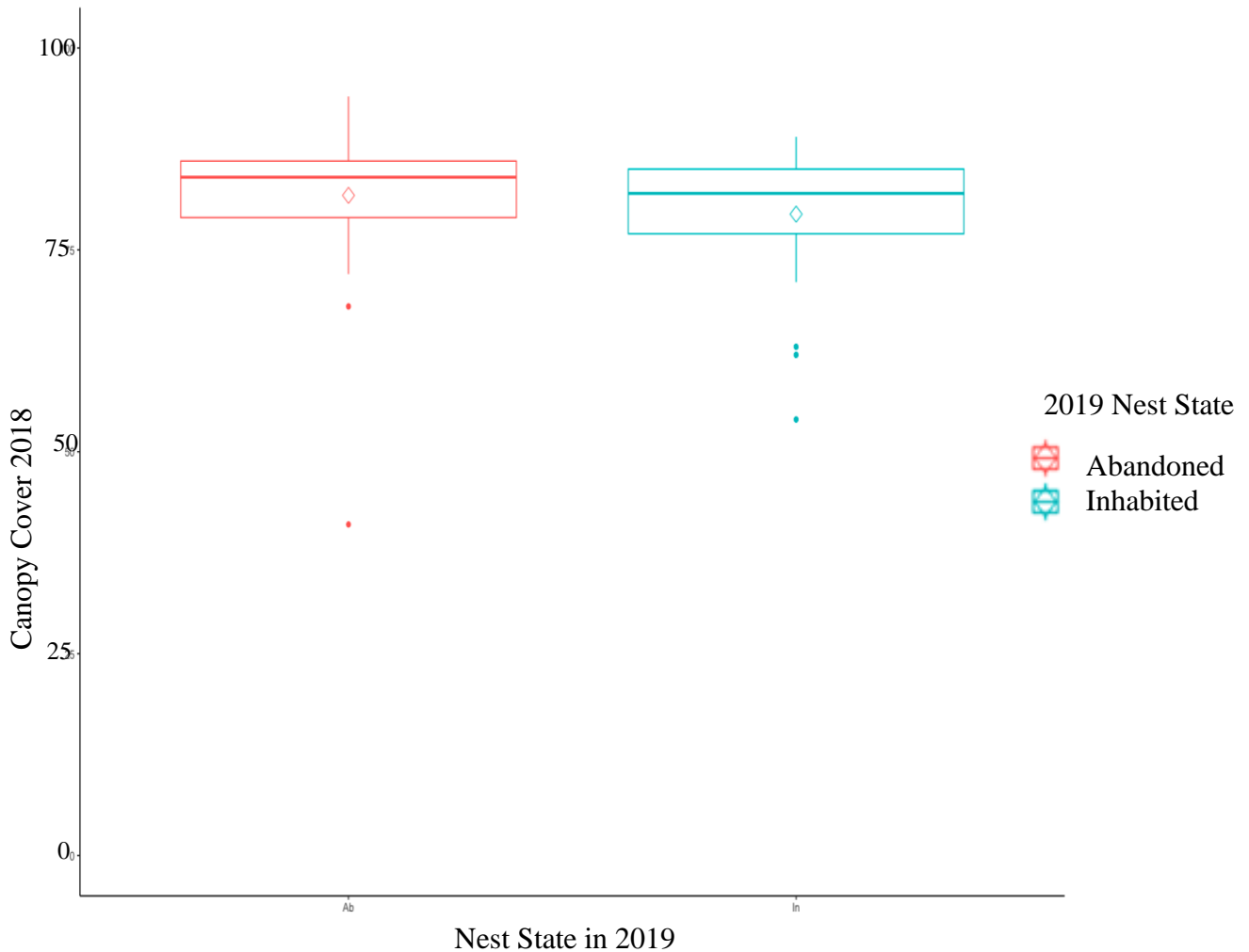
Figure 3.6 Canopy Cover above a nest in 2018 of abandoned and inhabited 2019 nests

4.0 Discussion

Our results show that *F. lugubris* nest volume and the canopy cover above a nest were the most important factors in predicting the occupancy state of a nest, with nests more likely to be occupied if nests were larger and less shaded. We also found that the previous year's nest volume predicts nest survival in the following year: larger nests were more likely to survive. Survival was positively related to lower canopy cover and higher social trail strength in the previous year; however, these were weak effects and not statistically significant.

There are several different reasons why nest volume may affect the survival of a nest. Wood ants use their nest mounds for thermoregulation: the temperature inside

a wood ant nest is often higher than the surrounding air temperature (Lenoir *et al.* 2001). Canopy cover and temperature are negatively correlated (Rodriguez-Garcia *et al.* 2001: Huang *et al.* 2014). Increased canopy cover results in increased shading below the canopy, and therefore cooler temperatures. Smaller nests require direct sunlight to be able to reach and maintain a working inner nest temperature. In contrast, larger nests can reach a sufficient inner nest temperature due to worker clustering behaviour, metabolism and heat produced by microbes (Rosengrun *et al.* 1987; Frouz, 2000; Coenen-Stass *et al.* 1980). Larger nests are found in more shady areas, and nest size increases with increasing canopy cover (Chen and Robinson, 2014). This suggests that for nests in shadier areas, there is a threshold size at which sufficient thermoregulation becomes possible. The higher range of nest volume for inhabited nests compared to abandoned nests in our data could be due to there being more inhabited nests that survived because they are in shadier areas and due to the shading, are larger. Increased nest size in shaded areas due to thermoregulation could explain the positive correlation we see between nest volume and canopy cover. Canopy cover and nest volume were both predictors in the preliminary GLM, however, we were not able to detect an effect of canopy cover in the predictive GLM. The positive correlation between nest volume and canopy cover suggests that a weak effect is present. However, due to the correlation between the variables we could not identify the effect.

Larger organisms (or nests) have a smaller surface area to volume ratio than smaller ones, so larger organisms are less likely to be badly affected by desiccation. Size-related resilience to desiccation has been observed in many different systems (Couvillon and Dornhous, 2010). *Formica lugubris* nests in less shaded areas tend to be smaller than those in shaded areas and are exposed to more changeable temperature conditions (Chen and Robinson, 2014). In our results we found that average nest temperature was negatively correlated with canopy cover, confirming that shadier nests were at cooler temperatures and therefore less likely to dry out. Therefore, desiccation, due to a combination of smaller nest size and lower canopy cover, could be a potential factor behind nest abandonment.

One hypothesis for why larger nests are more likely to survive than smaller nests is that larger nests can store more resources to survive winter. Wood ant nests in the UK go into a period of hibernation over winter during which they do not forage

(Maeder *et al.* 2016); therefore, to survive this period the nest must contain all the necessary resources. As nest volume is a proxy for the number of ants in a nest (Chen and Robinson, 2013), larger nests have more workers to collect and store these resources. This could be a further reason for the increased ability of larger nests to survive across winter.

A related issue is the ability of a nest's occupants to access a sufficient foraging range, which is critical for the survival of a nest. Most wood ant diet comes from the farming of aphids to produce honeydew (Domisch *et al* 2016). Honeydew can provide 62- 94% of the food brought into a nest (Wellenstein, 1952; Rosengrun and Sundsröm, 1991). As the aphids wood ants farm reside in trees and on other forest plants, a wood ant nest needs to be large enough to hold enough foragers to be able to maintain enough aphid farms, with ample foragers to transport the honeydew back to the nest. At the study site, food availability is unlikely to be a limiting survival factor as food sources (conifer trees) are abundant. We found no relationship between survival and the presence of foraging trails; however, these data were not high quality due to foraging trail presence being weather dependent.

In many populations, *F. lugubris* colonies display territoriality over foraging areas (Domisch *et al,* 2016). Larger nests or colonies are able to defend a larger foraging range as they have more foragers. This can result in a larger nest having a higher chance of survival due to an increased foraging range. Larger individuals holding larger foraging areas are seen in many species, often due to the increased metabolic needs of a larger body compared to a smaller one (Keeley, 2000). Changes in foraging range are often a result of fluctuations in food resources. When food sources are limited, foraging ranges are larger, as a larger area is needed to find sufficient resources. Smaller foraging ranges are found where food is plentiful as individuals do not need to cover a large area to gain enough food. However, as the food availability at the field site was abundant and highly homogenous through the forest stands, access to a sufficient foraging range is unlikely to impact survival of nests in this case.

Nest size could potentially change the level of predation to which a nest is subject. Larger nests could be targeted more as they are more obvious and a more bountiful resource; conversely smaller nests could be more vulnerable to predation as they

have fewer workers available for defence. Nest size is a proxy for the number of ants in a nest (Chen and Robinson, 2013); therefore a smaller nest could be more at risk of being abandoned if a portion of the workforce is predated. Wood ants have few predators, with woodpeckers being the most significant (Johansson and Gibb, 2016). The diet of black woodpecker (*Dryocopus martius)* can consist mainly of wood ants (Otto, 2005). *Dryocopus martius* may eat over-wintering wood ants, thus causing the nest to be more vulnerable to poor weather (Otto, 2005). Wild boar (*Sus scrofa)* and deer are attracted to wood ant nests by the warmth and potential for finding beetle grubs and can cause nest disturbances by wallowing in wood ant nests (Zakharov and Zakharov, 2010). Brown bears (*Ursus arctos arctos)* predate wood ants, and can cause extensive nest damage as they excavate the nests for both food and to use as warm day beds (Elgmork and Unander, 1998). Most of these species, including black woodpeckers, are not found in the UK; the native woodpecker species are smaller and their predation affects wood ants less. At the study site, there was very little evidence of predation or nest disturbance. There was some evidence of woodpecker (*Picus viridis*) presence in waste pellets found nearby to nests; however, little damage to the nests was observed. Cropton Forest does not have a wild boar population, and though there was evidence of damage to nests by deer in other areas of Cropton Forest, none was found at the study area. There are no wild bears in the UK currently. In this case, we believe the effect of predation on nest survival is minimal.

Polydomy can also play a role in the survival of small nests. In established polydomous *F. lugubris* populations, a higher level of nest abandonment is found in the first 2 years, with larger nests less likely to be abandoned (Burns *et al.* 2020). When thinking in terms of a polydomous colony composed of multiple connected nests, this makes sense because abandoning a small nest is less costly than abandoning a larger nest (Gibb and Hochuli, 2003). By being polydomous, the cost of nest abandonment is decreased as ants can retreat into larger, well-established nests within the colony. It is also possible for a colony to re-occupy an abandoned nest in future years (a follow-up survey will investigate this in the future), further reducing the costs of abandonment, because at least some of the previous investment can be recouped later. In *F. lugubris* and other polydomous wood ants, smaller nests could also be at a higher risk of abandonment due to their queens having relatively shorter life spans (Sorvari and Hakkarainen, 2007). At Cropton, the

social connections of a nest did not predict nest survival; however, there was a weak positive relationship (Fig. 3.5) so it remains possible that social connection does play a role in the survival of nests, though we did not find strong evidence of it in this study.

Formica lugubris displays seasonal patterns of nest abandonment but on a much smaller and more local scale than *Formica yessensis* and its relative *Formica truncorum* (Elias *et al.* 2005), where a colony has overwintering nests in forest and migrates to summer nests in rocky areas (Rosengren *et al.* 1985; Elias *et al.* 2005). In contrast to this, in the UK *F. lugubris* colonies may abandon smaller nests in less ideal spots and the ants from these are absorbed back into other nests in the colony. These small abandoned nests are often re-occupied in following summer years (Higashi 1976). In this study, it was possible to conduct only one site survey a year, which may mean some of the abandonment of small nests and re-occupation has been missed; follow-up studies in future years may shed more light on this aspect

At the study site, the forest is heavily managed and presents a highly homogeneous habitat of mainly non-native plantation forest. Therefore, the relationships we see here between the nest micro-habitat and survival may not hold in other, more natural, woodland where *F. lugubris* resides. However, at a field site at the Longshaw Estate in the Peak District, Burns *et al.* also found that larger nests were more likely to survive than smaller nests (Burns *et al*, 2020). In this study multiple surveys were conducted each year, and the site comprises of much more heterogeneous woodland than at Cropton. In a previous study at Longshaw, Chen and Robinson found that, with a larger range of canopy cover than present at Cropton, canopy cover did affect *F. lugubris* nest volume (Chen and Robinson, 2014). This adds further evidence that canopy cover has some interaction with nest volume in the survival of nests, which we were unable to detect in our study.

The plantation would directly affect the outcomes of this study in a number of ways. For instance, the disturbance regime of the Cropton woodland is far higher than in a non-plantation woodland under natural disturbances. This could act to fast forward effects such as the colonisation of newly formed edges. Plantation woodland also impacts the density of the canopy cover within the forest stands. Coniferous plantation, such as that at Cropton, has minimal understory within the stand due to

the closed canopy. This in turn changes the food supply for *F. lugubris* as invertebrate biodiversity is reduced due to less niches. Predator abundance between plantation and non-plantation woodland remains similar for *F. lugubris* as it is regarded as an apex predator with woodpeckers being the main predator. The potential for nest disturbances in less intensely managed plantations could be higher. As deer and other mammals occasionally use the heat of the nests to warm themselves. In a forest with a more open stand structure, such occurrences could happen more frequently due to it being easier for the nests to be reached.

Though previous work carried out at Cropton had mapped the wood ant population expansion in 2011 to 2013 (Procter *et al,* 2015), there was a gap in surveying between 2013 and 2018 when this study started. We know the study site was row thinned during the winter 2016-2017 (Forestry Commission, pers. comms, 2018). Before this, the stand interior would be inhospitable for *F. lugubris* because these stands consist of densely planted spruce with a lack of edge habitat. Previous *F. lugubris* surveys have found 78.5% of nests within 10m of an edge or path (Procter, *et al*, 2015). Therefore, we can be confident that the population of *F. lugubris* had not spread into the study area before 2016/17. In the surveys carried out by Procter *et al.* the only nests found in the study area were along natural edges (a ditch runs through the stands) and clearings (Procter *et al*, 2015). Repeatability tests showed that the Procter surveys had a high confidence that all nests present were recorded (96%). This means we can be confident in the location of nests before the row thinning, and that the 5-year gap in surveying has little effect on the data collected here, due to the previous lack of suitable habitat.

The life history and survival data collected in this study is important for several reasons. The first of these is the potential for forest management plans which could increase the amount of suitable habitat for wood ants. In areas of forest which have been identified as suitable wood ant habitat (such as in Procter *et al.* 2015), and where wood ants are present nearby, strip cutting could be utilised to help create temporary corridors along which wood ants could spread. As habitat fragmentation by humans is becoming more common, understanding how to provide permeable corridors to reconnect habitat patches and allow dispersal is crucial for conservation. By understanding more of the life-history of *F. lugubris*, we are better informed of how long ephemeral habitat (such as the edges created by row thinning) needs to be

available to wood ants for them to be able to access more suitable stable habitat patches.

In addition to the general conservation benefits of assisting the spread of a woodland specialist, forest managers may be inclined to encourage the presence of wood ants within forests as they play several roles within the forest ecosystem. Please see chapter 1 for more detailed information on this.

Many red wood ants are currently listed as 'near threatened species' on the IUCN red list, including *F. lugubris*, with habitat loss being a major threat (Sorvari, 2016). Habitat loss affects wood ants in different ways. As the main part of their diet comes from farming aphids for honeydew in the tree canopies, a large scale loss of canopy (such as clear felling or forest fire) will have a dramatic effect on a nest's ability to access enough food. Clear felling has a dramatic impact on worker survival due to lack of food (Sorvari *et al.* 2011), but here we show that smaller-scale felling can actually be beneficial in promoting spread of wood ants. Understanding how different forest management practices interact with wood ant life histories and their ability to survive is key to the continued success of wood ants in managed forests.

When considering a wood ant nest as a reproductive unit, wood ants share many life-history traits with other poor dispersing species. Nests could be considered to have a juvenile phase, like many mammals, where they are developing and not able to reproduce. Wood ant nests may reach a certain size to hold brood and to form new nests by budding. This is similar to many other animals which have a juvenile stage, such as chicks in birds, insects with a larval stage, and many mammals. Not all life-stages will have the same dispersal capabilities, and understanding the likelihood of survival and dispersal for the different stages is key to understanding whether they will survive. Collecting such life-stage data is difficult, especially for poor dispersers. The collection of wood ant life history data may help us understand poor dispersing species abilities to react to habitat change better.

Wood ants could represent an ideal system to study poor dispersing, multi-staged organisms' reactions to change. They are considerably cheaper to study than many other systems due to the species being native and relatively easily accessible, and there are fewer ethical constraints on studying invertebrates than other organisms.

As nests are static and do not move through the landscape (in comparison to an animal such as a deer), their life-histories and micro-habitat are relatively easy to study. Wood ants could be utilised more to gain insights into the survival and life-histories of poor dispersers, a topic which is becoming more and more critical as habitat destruction and climate change continue.

An additional year's survival data on the nests is being collected this year (2020) by a PhD student in Dr Robinson's lab to see if the trends seen between 2018 and 2019 continue. The additional field season will allow us to see if the rate of survival increases once nests become established. We also hope to identify any threshold nest volume a nest must reach to survive. Having two years of survival data and nest volume measurements will allow more confidence in the findings. We will also be able to observe whether nest volume continues to be the most important factor for survival after the nest's first year. From this, we intend to publish a paper describing this case study of dispersal into new habitat and establishment of an expanded population.

Further research in this area could utilise the life-history and survival data collected here to build a model to predict the future spread of *F. lugubris* through this site. The microhabitat data collected could be combined with LiDAR data to create a fine-scale landscape on which a predictive model of expansion could be run. If further empirical data were collected, using the same methodology as used here in different types of forestry, then a more general model of wood ant expansion in plantation forests could also be created, which would be valuable to inform forest managers of how different felling plans could impact on wood ant populations.

Chapter 4; Discussion

4.1 Overview

In this thesis, I have shown that *Formica lugubris* populations on the North York Moors are continuing to spread through plantation forests. In Chapter 2, I show the location and extent of two focal *F. lugubris* populations and how they have continued to spread through the forests, beyond the bounds of previously recorded expansion Procter *et al* (2015). I have identified potential areas in which the continued spread may be challenged by current forest management practices. In other areas of the field sites I have identified potential forest management strategies which would increase the permeability of forest stands to *F. lugubris*, namely row thinning. This was shown by the increased colonisation and spread of *F. lugubris* in areas of row thinning compared to areas of Broxa and East Moor Wood which are under a practice of minimal intervention. Row thinning could be utilised to increase the rate of spread of *F. lugubris* through a forest stand. In Chapter 3 I was able to observe the survival of *F. lugubris* nests in newly colonised areas at the population margins and investigate which nest attributes predict nest survival. The research carried out in this thesis builds on previous studies by Procter (2016), in which *F. lugubris* populations were found to be inhabiting plantations forests at the field sites, having spread from nearby ancient woodland refugia. By collecting further survey data at the population margins and focussing on a unique site where the impact of forest management on *F. lugubris* colonisation could be investigated at a microhabitat scale, I was able to provide detailed information on why *F. lugubris* is able to spread and survive in some areas of plantation and not in others.

4.2 Species reaction to changing landscapes

The microhabitat factors predicting the survival of *Formica lugubris* nests has been studied previously in established populations (Chen and Robinson, 2014). Chen and Robinson found that canopy cover had the greatest impact on nest survival. In chapter 3 of this thesis, we have added to this work by investigating microhabitat and nest attribute factors around nests in a newly colonised area. Though our predictive model did not find canopy cover as an important predictor of nest survival, canopy

cover was correlated with nest volume. Nest volume was our predictor of nest survival, so some effect of canopy cover is likely. This finding was different to previous work by Chen and Robinson who found no significant relationship between nest volume and canopy cover, however, they did observe a positive correlation between nest size and canopy cover (Chen and Robinson, 2014).

Chen and Robinson also found that nests tended to be larger in shadier areas. We had some evidence of this at Cropton, however, many of the abandoned nests could have been unsuccessful satellite nests that had been reabsorbed into more established nests. The increased number of small, abandoned, satellite nests would be expected in an area of new colonisation as nests are most likely to be abandoned in the first two years of formation (Burns *et al*. 2020). The field site used by Chen and Robinson (Longshaw Estate, Peak District, UK) holds a long-established *F. lugubris* population and is a less heavily managed site than Cropton Forest, so less of these smaller satellite nests may have been in the Chen and Robinson study site compared to the newly colonised area in our study.

The discrepancy between this study's finding and Chen and Robinson's could be due to the increased habitat disturbances at Cropton. The Longshaw Estate has much less canopy cover disturbing events compared to Cropton. The higher rate of canopy cover changes at Cropton between the 2018 and 2019 surveys (as the freshly cut row thinned areas started to grow back) could be a reason why we did not find canopy cover to be as an important predictor.

This study adds evidence to Chen and Robinson's findings that canopy cover and nest temperature are key factors in the survival of *F. lugubris* nests in different forest types. However, Chen and Robinson also found that larger nests occurred in more shadier areas. Shadier areas require a denser canopy cover which in turn, reduces thermal radiation to the nest. This would suggest that, at their study site, the most successful nests were in areas of increased canopy cover. However, this may be due to *F. lugubris* population at the Longshaw site consisting of long established polydomous nests. There may be higher amounts of resource sharing between such nests than those in the newly colonised area of Cropton.

4.3 Poor dispersers in fragmented habitats

Understanding how species react to changing landscapes is an important consideration when predicting the fate of a population. With factors such as anthropogenic habitat destruction and climate change, many populations will need to react to changes in their landscapes in the future (Chen *et al.* 2011). The work in this thesis adds an understanding of how poor dispersers at population margins may survive in new areas. The study species and site provided a unique opportunity in which to do this, due to detailed knowledge of the forest management plans and past population surveys by Procter (2016). The combination of these two sources gave a unique opportunity to monitor the survival of nests in an area which we knew was previously unpopulated in the previous year, along with any differences in forest management strategies, such as row thinning.

By utilizing the past survey data at the sites, and carrying out further field seasons, it was possible to investigate the different patterns of expansion across the different sites. By taking microhabitat variables and investigating previous and present forest management strategies at the different forests, it was possible to infer why the different forests had differing patterns of expansion.

The plantation forest at Cropton behaves as a fragmented landscape due to each stand being managed in a different way, with some management strategies leading to uninhabitable forest for *F. lugubris* creating a matrix habitat (Forestry Commission Pers. Comms. 2018). Large areas of the forest are uninhabitable to *F. lugubris* due to a lack of edge. This creates an effectively fragmented landscape for *F. lugubris.* The work carried out in this thesis adds to the wider understanding of how poor dispersers survive in fragmented landscapes. In this work we found that slow and steady expansion occurred in areas of suitable habitat (i.e. edge); however, as edge habitat became less available or saturated, then population and range expansion slowed or in some cases stopped.

A benefit of using *F. lugubris* in this study was that the microhabitat around a nest is relatively easy to measure for factors such as shading, potential food sources, and surface temperature, as the nest is sessile. Using the nest as a proxy for the reproducing unit also allows a comparison to species with complex, multi-staged, life

histories. Nests go through three stages of development; new, juvenile and mature. It is only when a nest is mature, that it can produce 'offspring' (new nests by budding). This means that studying the expansion of a population of *F. lugubris* nests could be a proxy for multi-life staged organisms. This gave an opportunity to study a poor disperser who displays similar dispersal traits to large mammals and to also measure the microclimate and habitat around the 'individual'.

Alternatives to row thinning

Alternatives to row thinning could be methods which also reduce the canopy cover, and therefore raise the temperature of the forest stand. A reduction in canopy cover increases overall species richness across different ant species in the temperate zone (Grevè *et al.*, 2018). The increased ground temperature due to a reduced canopy accelerates the development of brood and therefore colony growth (Kipyatkov and Lopatine 2015). Therefore, a wide range of forest management strategies which reduce canopy cover are beneficial to *F. lugubris* (Grevè *et al.*, 2018). Other methods of reducing canopy cover could include even-aged management systems which contain more developmental stages so not all canopy is closed (Schall *et al.* 2018), chosing species of tree which form less dense canopy cover such as pine and oak (Grevè *et al.*, 2018), and avoiding single tree harvesting as the gaps created are closed rapidly by the surrounding trees (Juchheim *et al.*, 2017). Therefore, it is not just row thinning which could be used to improve *F. lugubris* colonisation.

Low grazing levels can also have a negative impact on wood ants as the lack of grazing can cause habitat succession within the woodland to shade nests. However, overgrazing can lead to a lack of tree regeneration, and therefore food sources for wood ants (Cairngorms National Park Authority, 2021). When row thinning or clear felling, if the remaining edges are scalloped a greater area of suitable edge habitat can be created, therefore increasing the suitable *F. lugubris* habitat (Cairngorm National Park Authority, 2021).

4.4 Further data collection

In 2020, the population in the newly colonised area was re-surveyed. Although these data are beyond the scope of this thesis, future analysis of these survey data will give further insight into current expansion rates through this new habitat, and

whether the expansion is at a constant rate. The additional 2020 survey data will also allow a survival rate to be calculated for the area of new colonisation at the Cropton site, as multiple years' nest survival will be available.

4.5 The importance of survival data

Survival is a particularly important property to gain insight into, because it is the cumulative end result of many variables. Nest survival in this case, is the result of a successful budding event, and critical nest mass reached to survive the winter (if the nest has survived to be counted in multiple surveys). Presumably for the nest to survive, the colony must have adequate food resources and the nest site must be favourable (Ellis *et al.*, 2017).

The interaction of biotic and abiotic factors on survival has been observed across different taxa. Microhabitat has been shown to have a large impact on the survival of the European Woodwasp due to tree placement (Garnas *et al.*, 2020). The interaction between temperature and population density of tadpoles determines survival rates (Govindarajulu and Anholt, 2006). Mean daily temperature and access to sheltered microclimates for overwintering significantly impacts *Drosophila suzukii* with males and females survival rates affected to different levels (Stockton *et al.*, 2019). By measuring survival, we see the end result of countless different biotic and abiotic interactions. Survival of a nest also indicates a beneficial microhabitat surrounding the wood ant nest if the nest has remained occupied.

Measuring survival at a population margin is crucial to understanding how a population will colonise a new area. To successfully establish in a new area, individuals must survive to maturity, allowing reproduction. If survival of individuals is reduced at the margins of the population, then it may indicate that the potential movement of the population into the new habitat will be slow or unsustainable. This in turn may indicate where land management is required in order to help a species colonise the new habitat. The row-thinned area at Cropton inadvertently showed how a management strategy can help make a new area more accessible to an edge-specialist population.

4.6 General comments

Limitations

The study area in chapter 3, where rapid expansion had occurred, was a recently row thinned area. It would be interesting to see if the same patterns of expansion in response to increased edge habitat due to thinning occurred for other edge specialists. Due to the scale of the thinned tracts (approximately 5m wide) we argue that this is the creation of edge habitat due to a full break in the canopy, rather than thinned habitat. There are some examples of the impact of increased edge on forest specialist butterflies being beneficial, but it can also have a negative effect if increased edge reduces the abundance of host and nectar plants for certain species (Van Halder *et al.* 2011). Overall, Van Halder's study found that increasing edge habitat increased the abundance and diversity of butterfly assemblages with few cases of interior specialists such as the critically endangered *Coenonympha oedippus*. Therefore, management strategies such as row thinning may benefit several edge specialists, but could be at the detriment of forest interior species. By increasing the edge within a forest stand, the amount of dense forest is reduced, therefore lowering the habitat suited to forest interior specialists. This raises the interesting question of which species' habitats should be conserved or prioritised?

The process of deciding which species to prioritise for conservation is a complex and controversial topic. Species that are endangered in one context can even be viewed as invasive elsewhere. One example of this is *Bombus subterraneus*, which was declared locally extinct in the UK in 2000 by the IUCN (Gammans and Allen 2014). However, in New Zealand the species is regarded as an invasive species after being released into the country around 120 years ago (Lye *et al.* 2010). In the UK, a reintroduction programme of *B. subterraneus* has occurred since 2009 (Brown *et al*, 2017). The argument whether globally rare species or locally rare species should be prioritised often has conflicting views, depending on the scale of focus for the conservationists involved.

Effects of thinning on biodiversity

The row thinning seen at Cropton Forest depicts a potentially ideal strategy to help conserve *F. lugubris.* However, with the creation of additional edge habitat, there is a loss of interior habitat. This benefits species which thrive in the increased opening in the stands, however, for those specialists who reside in the forest interiors, this represents a loss of habitat. At Cropton Forest, there is low biodiversity due to the dense tree planting. This results in little understory growth and few niches, and so the loss of interior habitat is unlikely to reduce biodiversity greatly. However, in other plantation forests or more natural woodlands, increasing the edge habitat may have a larger impact on biodiversity. Examples of forest interior specialists being negatively impacted by increasing edge habitat exist across taxa. For instance, the Bobolink in North America (Fletcher Jr, 2005), a range of small mammals in Brazil's Atlantic Forest (Stevens and Husband, 1998), amphibians and reptiles in Madagascan forests, and dung beetles in Bolivia (Spector and Ayzamer, 2006) have all been negatively affected by an increase in edge habitat. Therefore, if forest managers were to choose a method such as row thinning to increase the connectivity of wood ants, the effects on other species present at the site would need to be carefully considered.

Forest thinning has been found to have a neutral or positive effect on diversity and abundance across all taxa. The intensity and type of thinning drives the size of the response (Verschuyl *et al.*, 2010). Though the obvious effect of thinning is to reduce canopy, it can lead to a more complex understory (Garman, 2001). This increased understory can then have negative impacts on species which favour the more open canopy as they are shaded (Cairngorm National Park Authority, 2020). A review by Verschuyl *et al.* (2010) found that forest thinning leads to a positive response by birds across species, and leads to increased abundance and diversity (Hayes *et al.*, 1997, Kalies *et al.*, 2010). Due to the increased amount of understory and variation within the forest structure, more niches exist for bird species (Hayes *et al.*, 1997; Sullivan *et al.*, 2002; Carey, 2003; Verschuyl *et al.*, 2010).

In small mammals, thinning has a positive response (Zwolak, 2009), and creates opportunities for open-habitat and generalist species due to the increased light and understory shrubs. Species such as the deer mice, jumping mice and most vole species have been seen to increase in abundance due to the increased foraging

opportunities and cover (Wilson and Carey, 2005; Suzuki and Hayes, 2003; Homyack *et al.*, 2005). However, this increase may be short lived due to the canopy reclosing (Suzuki and Hayes, 2003). The increase in flying insects within thinned forests means that bats favour thinned forests (Loeb and Waldrop, 2008). Little is known about the effects of thinning on large mammals though (Suszuki and Hayes, 2003; Verschuyl *et al.*, 2010)

Heavy thinning can have a negative impact on species who favour closed canopy conditions (Lehmkuhl *et al.*, 2002). Northern flying squirrels and American Red Squirrels both show low abundances in heavily thinned forests, but high abundance in moderately thinned forests (Ransome *et al.*, 2004). Therefore, the amount and rate of thinning can play an important role in species abundances.

The effect of thinning on reptile species is less obvious, as reptiles require solar radiation and thermal cover within their habitat (Kiester, 1971). Clear cutting gives large areas of solar radiation but may not provide thermal cover over night. Thinning may provide a more balanced habitat with areas of solar radiation but retaining a degree of thermal cover (Todd and Andrews, 2008).

Amphibians appear to be highly affected by stand disturbance created when thinning, even in less severe thinning scenarios (Semlitsch *et al.*, 2009). This is due to processes such as soil compaction and stream sedimentation. It is suggested though that as thinning creates less overall habitat disturbance than clear felling, it may be a better management strategy for amphibians (Petranka *et al.*, 1993). Thinning may retain the biophysical characteristics required for moisture sensitive amphibians (Ford *et al.*, 2000; Verschuyl *et al.*, 2010).

Invertebrates show a mixed response to thinning depending on their life history characteristics (Verschuyl *et al.*, 2010). Many arthropods show a significantly positive response to thinning, due to increased vegetation for herbivores, therefore increased prey for predators and increased resources for detrivores (Verschuyl *et al.*, 2010). However, some invertebrate species are affected minimally (Schowalet *et al.*, 2003; Apigian *et al.*, 2006) or negatively (Niemela *et al.*, 1993).

At a landscape level, a mosaic of stands with different age-classes of trees within managed forests may be the best way to promote overall biodiversity (Schall *et al.*, 2017). Across taxa, even aged forest's management systems provide greater biodiversity than uneven aged stands due to increased variation in microclimate and structural attributes (Schall *et al.*, 2017). Creating a mosaic of different aged stands would perhaps avoid the situation of deciding on what species habitat to conserve, as it would create diversity within the available habitat. However, there could still be the issue of connectivity between different suitable stands within the mosaic.

Ephemeral habitat

When considering how representative plantation woodland could be of non-plantation woodland, it is important to consider the stability of the habitat over time. Plantations tend to be highly homogenous in biodiversity (Kerr, 1999), with few tree species, and little understory due to the dense planting of trees. However, plantations tend to be an ephemeral habitat, which often changes dramatically due to events such as logging, thinning and other management strategies. In contrast to this, non-plantation woodland is more heterogeneous in biodiversity than even-aged plantation but tends to be more stable over time (Humphrey *et al.* 2001).

While not subject to large-scale dramatic changes, unmanaged natural forests tend to be more dynamic at the small scale, compared to managed forests, such as plantations. As trees are of differing ages, localised tree death by natural causes (storms, lightening, disease and age) will cause temporary gaps in canopy cover. It is probable that wood ants would utilise these as if they were edge habitats. This habitat would only last a short time before the canopy cover above the nest became more dense as other trees competed for space, after which the habitat would likely revert to being inhospitable to wood ants.

Increasing the edge in plantation forest is only a temporary measure, and though it may act as a corridor to further suitable habitat, the row thinned area will not remain as suitable habitat, as the canopy cover will increase to cover the new edges. I would expect that row thinning only has a long term benefit of increasing the population size of a species when it connects to other, more long term, suitable habitats.

When considering other wood ant species, such as *Formica rufa* or *Formica aquilonia* (both found elsewhere in the UK), changing the amount of edge within forest stands would potentially have differing effects (Stockan *et al.* 2016). *Formica rufa* would potentially find this a favourable change, as *F. rufa* prefers a less shaded habitat and does not build mounds within dense woodland (Eichhorn, 1963; Mabelis, 1991; Risch *et al.* 2016). *Formica aquilonia* could be negatively affected by row thinning, as *F. aquilonia* builds mounds within areas of more dense canopy cover than *F. lugubris* (Punttila and Kilpeläinen, 2009; Travan, 1998). Increasing the edge within a forest stand would decrease the canopy cover, and thus make the habitat less suitable for *Formica aquilonia*.

When considering wood ants outside of the UK, then similar patterns of expansion may be expected in those species that disperse by budding. However, certain populations of *F. lugubris* in Switzerland and Finland found new nests by either budding or social parasitism (Ellis, 2016). Depending on the success of the more risky long-range social parasitism option, then the patterns of expansion in this study, where some areas of the forest seem impassable due to lack of edge habitat may prove less of a barrier. At the Broxa site, a previous habitat suitability map showed large areas of suitable habitat in a region of forest currently inaccessible to the wood ants due to a small section of dense forest halting their process. Barriers such as this may not affect populations where nest founding by social parasitism occurs. However, this does depend on the host species being also able to spread through the landscape successfully.

Formica lugubris can form new nests in two different ways; the polygynous strategy of budding or the monogynous strategy of social parasitism. In England, there is only evidence of *F. lugubris* nest formation by budding. The expansion shown in this study is relevant to wood ants who colonise an area through budding. Elsewhere, *F. lugubris* and other members of the *F. rufa* group can colonise by temporary social parasitism, which results in more long range dispersal events (Risch *et al.* 2016). The patterns of expansion seen in this study would likely be less representative of such populations.

The difference in dispersal strategies appears to depend on whether the population of wood ants is polygynous or monogynous. Monogynous populations have higher numbers of dispersers which are capable of quickly dispersing over large distances via social parasitism. Polygynous populations tend to spread by budding, which results in a slower dispersal through a landscape. However, due to budding, wood ants that disperse by this method tend to reach high densities and dominate the landscape they are in (Risch *et al.* 2016). Polygynous populations of wood ants tend to be found in older, well established woodlands (Seppä *et al.* 1995; Puntilla 1996; Vepsäläinen *et al.* 2000). It has been suggested that budding could represent a dispersal strategy that emerges as populations become mature and dominant within the habitat, whereas monogynous populations are more common in smaller, isolated, forest patches (Risch *et al.* 2016).

By looking at the possible dispersal distances involved in budding versus social parasitism, it could be expected that populations able to spread by social parasitism are less affected by fragmentation due to the longer dispersal distances. However, social parasitism depends on the success of the mating flights of individual gynes (Maeder 2006) and the presence of a suitable host colony, such as the *Serviformica* genus (Maeder *et al.* 2016). This may lead to a small number of long distance dispersal events, rather than the many smaller dispersal events used in the less risky budding strategy. Therefore, the patterns of expansion seen in this study may not be relevant to populations of wood ants who can form new nests using social parasitism.

A further consequence of dispersal by budding, is the reliance on potential new habitat having to connect with the habitat the population currently occupies (Risch *et al.* 2016). At the sites used in this study, dispersal into the plantation had occurred by budding from fragments of ancient woodlands that held mature populations of *F. lugubris.* Both Procter (2016) and Sudd (1977) observed the movement of *F. lugubris* into plantation forests from ancient or undisturbed woodland at the field sites. Being limited in dispersal ability in such a way means that habitat fragmentation will have a large impact on populations who solely rely on budding to disperse and colonise. Another large plantation woodland on the North York Moors, Dalby Forest, has no adjacent ancient woodland fragments hosting wood ants, and so despite containing suitable habitat, will never be colonised through the process of budding.

The benefit of the increased heterogeneity in forest structure seen at Cropton fits with the findings of Greve *et al.* who found that in temperate forests, the abundance, species richness and functional diversity of ant communities increased under forest management (Grevé *et al.* 2018). Similarly, to our findings at Cropton, Grevé indicated that this was due to reduced canopy cover and structural complexity resulting in warmer stand-scale conditions. Our study supports the findings that increasing plantation stand heterogeneity can be beneficial in the conservation of ant species.

In other taxa of forest specialists, the effect of fragmentation on the spatial configuration of habitat patches seems to have a large effect. The impact of landscape heterogeneity on a larger scale has a larger effect on poor dispersers, such as Carabid beetles, than better dispersers such as bird and spider assemblages (Barbaro *et al.* 2004). Dispersal ability between patches across areas of unsuitable habitat appears to be the most important factor when investigating whether a population can access fragmented patches of habitat.

4.6 Questions remaining and future research

Potential use of LiDAR in population surveys

One thought for future research projects in this area would be the use of satellite imagery, more specifically LiDAR, to survey nest locations over a large area remotely. For much of the UK, LiDAR data is available to $0.25m^2$ resolution (Environment Agency, 2017). At this resolution, nests could potentially show up. Different LiDAR settings could be used to give detailed information about the canopy cover and forest structure around nests, thus giving information on shading and food sources. LiDAR has been used successfully in creating high resolution habitat suitability maps for both Red Tree Voles (Johnston and Moskal, 2017) and for the red squirrel (Flaherty *et al*, 2014) both of which are forest habitat specialists. However, in plantations such as at Cropton, the use of LiDAR to identify wood ant nests would not be possible due to the large number of tree stumps left from logging operations which are similar shapes and sizes to nest mounds. A further caveat with

this design may also be the inability to detect whether a nest is inhabited or abandoned if they are of similar shapes. LiDAR may provide a good low man-power option in unmanaged forests, where large scale population surveys are required, but where field surveys are not possible.

Future predictive models that could be utilised

If a large scale surveying strategy such as LiDAR could be used effectively, this could be paired with a population modelling program to predict future areas of population expansion. A programme such as RangeShifter, which runs individual based models through a landscape to predict potential areas of expansion (Bocedi *et al*, 2014). This could mean that large scale wood ant population predictions could be made using remotely sensed data. When considering the expansion of the *F. lugubris* population, we assumed the nest as a reproducible unit, rather than the ant colony residing within it. This was due to *F. lugubris* colonies being polydomous and polygynous. Reproduction occurs by budding, which means if the production of new nests were modelled, comparisons in reproduction between clonal fungi and plants with *F. lugubris* could be relevant due to the similarities in dispersal method. Using the nest as the individual in an individual based model of expansion could be a way of predicting the spread of *F. lugubris* through a landscape. A literature search yielded no studies which have attempted this at the time of writing.

The landscapes used in the predictive models could contain different forest management plans, and the potential impact of these plans on wood ant populations could be predicted. The outcomes of these models could then be used to inform forest management plans in the future.

In order to build effective predictive models, detailed life history and microhabitat data is required (Lembrechts *et al*. 2018). The surveys undertaken in this thesis have added to several life history variables have been calculated for which little data existed on before (i.e. survival rate in a newly colonised area). Without surveys to collect such data, reliable predictive models are impossible. If predictive models of

expansion could be made utilising the life history data collected in this thesis, these could inform forest managers of likely future expansions. This in turn could inform the impact of possible forest management strategies on *F. lugubris* populations within the field sites.

As previously discussed, *F. lugubris* shares many traits with a wide range of species, especially poor dispersers. This could mean that *F. lugubris* could be used as a bioindicator for successful connectivity. If *F. lugubris* was seen to colonise a plantation, it would suggest that the plantation has a level of connectivity that is beneficial to poor dispersers. Although this is a generalisation, and dispersal capability is highly species dependent (see Chapter 1), it is a hypothesis that is worth exploring.

Figure 4.1 shows how all the above mentioned future areas could be incorporated into answering the broader question of 'how does a dynamic landscape affect the movement of habitat specialists'. Figure 4.1 shows how the research undertaken in this study sits within this larger ecological question.

Question
- How does forest management affect *F. lugubris* population expansion? (Dynamic landscape)
- How does forest management affect *F. lugubris* population expansion? (Static landscape)
- Can LiDAR be used to create better informed micro-habitat models for expansion? (Compared to a SEM informed SDM)
- How do dynamic landscapes effect the rate of population expansion for different life history strategies?

Labels/arrows: Highlights need for this · Creates landscape for... · Case study based predictive model · Compare the outputs · Data driven case study · Theory vs. Reality · Outputs give theory for... · Defines scope of potential effects of dynamic landscapes

Question 1 — How does forest management affect *F. lugubris* population expansion? (Dynamic landscape)

Outputs:
- Predictive model of *F. lugubris* on the NYM including changing future landscapes
- Identify key forest management practices which affect the expansion temporally
- Identify barriers to expansion which may appear over time
- How does the changing mosaic of landscape patches affect expansion and connectivity?

Gap filled for overall question:
Real world example of how poor dispersing forest specialists' expansion capabilities are effected by dynamic landscapes
How the management of plantations can improve expansion
This theory could be utilised in corridors for climate induced range shifts

Literature gaps:
Unique case study in which a past data set exists so the predicted trajectory of range expansion can be tested against current data

Big Picture:
Use of a real life dynamic landscape with an actual species in an individual based model which can be verified with current data
Show the need for dynamic landscapes in expansion models using landscapes which are temporally heterogeneous
How differing forest management or landscape decisions effect expansion of poor dispersing forest specialists

Question 2 — How does forest management affect *F. lugubris* population expansion? (Static landscape)

Outputs:
- Predictive model of *F. lugubris* on the NYM based on past data
- Identify key forest management practices which affect the expansion
- Identify barriers to expansion

Gap filled for overall question:
Identify current forest structures which benefit *F. lugubris* spread most
Identify which management strategies benefit wood ant population expansion
This theory could be utilised in corridors for climate induced range shifts

Literature gaps:
Unique case study in which a past data set exists so the predicted trajectory of range expansion can be tested against current data
Opportunity to use LiDAR data to create a very fine scale microhabitat suitability model in which the individual based model can be run through

Big Picture:
Show the need for dynamic landscapes in expansion models in landscapes which are temporally heterogeneous

Question 3 — Can LiDAR be used to create better informed micro-habitat models for expansion? (Compared to a SEM informed SDM)

Outputs:
- Fine resolution model representing the landscape on a more ant appropriate scale
- Able to incorporate micro habitat effects
- Combines the DP SEM with LiDAR

Gap filled for overall question:
Ability to create a landscape at an appropriate scale for *F. lugubris*
More detailed micro-habitat information

Literature gaps:
Calls for use of LiDAR to create landscapes which incorporate the microhabitat the study species lives in

Big Picture:
Does incorporating LiDAR improve accuracy of habitat specialist range expansion models?

Question 4 — How do dynamic landscapes effect the rate of population expansion for different life history strategies?

Outputs:
- Difference in expansion rates under different habitat persistence, habitat availability, mean dispersal and emigration probabilities

Gap filled for overall question:
Identify important factors in dynamic landscapes which effect the rate of species expansion depending on life history strategy

Literature gaps:
Individual based modelling approach to dynamic landscapes
How differing life histories interact with differing temporal mosaics

Big Picture:
How a temporally changing landscape affects expansion
Potential threshold levels of landscape stochasticity at which greater connectivity exists (currently seen in graph theory papers)

Central box: How does a dynamic landscape affect the movement of habitat specialists?

Acronyms used:
SEM- spatial elevation model
SDM- species distribution model
DP SEM- Duncan Proctor's (2016) spatial elevation model
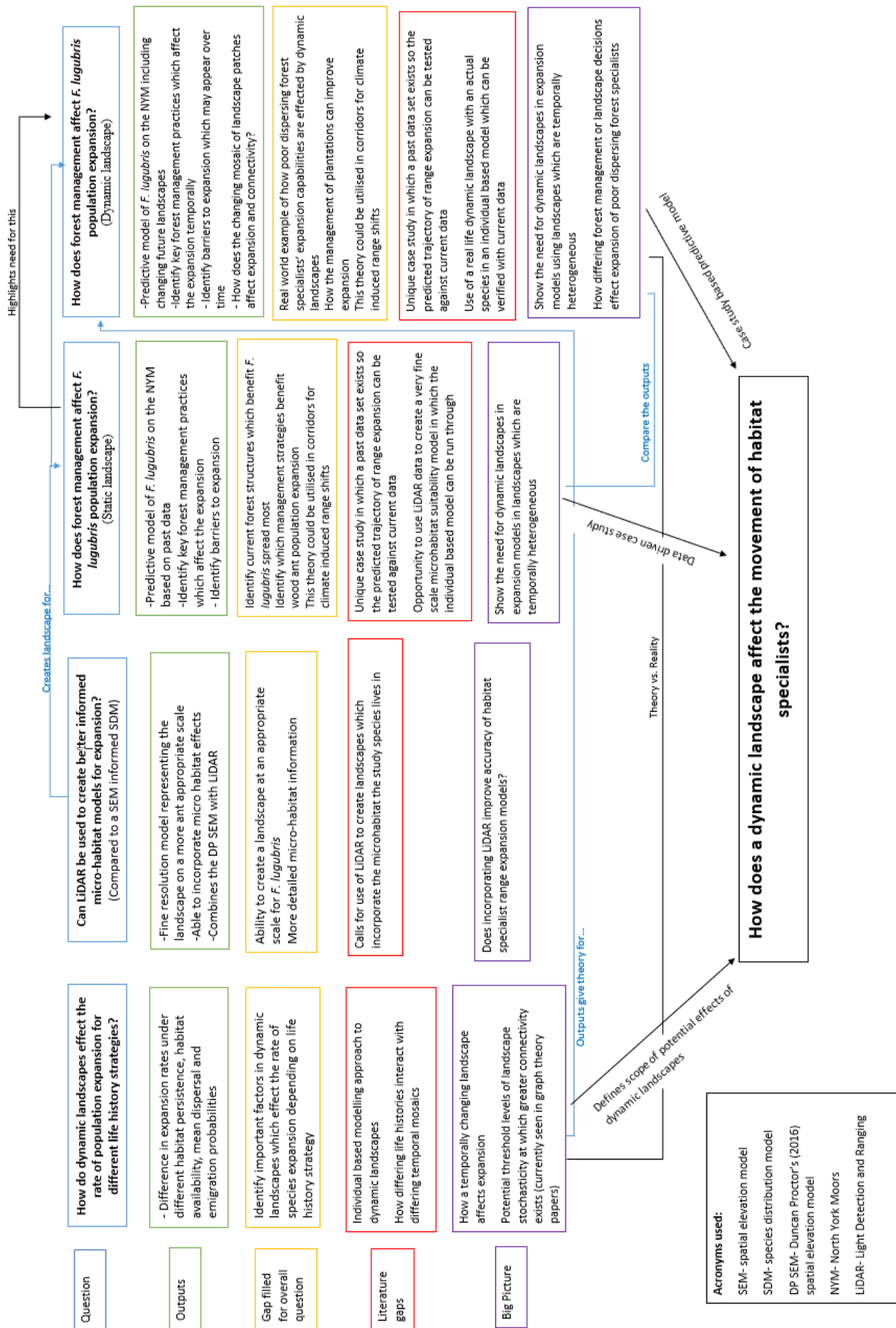NYM- North York Moors
LiDAR- Light Detection and Ranging

Figure 4.1 How the potential future research on this topic could tie together to answer the broader ecological question of 'how do dynamic landscapes affect the movement of habitat specialists?'.

4.7 Conclusion

In this study I have found that *F. lugubris* populations at sites on the North York Moors are continuing to spread and colonise new areas. The surveys of newly colonised row thinned areas at Cropton gave a unique insight into observing a population colonising a new habitat. It also provided an opportunity to see how row thinning positively benefits the wood ants by increasing the heterogeneity of the forest stand and increasing edge habitat. The microhabitat, nest attribute and expansion data collected across three field seasons provides an excellent resource for future research into the dispersal of *F. lugubris* and can inform any future model parametres for wood ants and other poor dispersers. On a local scale, the work has provided evidence of beneficial forest management strategies that can be used to increase the connectivity between isolated wood ant populations.

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