Interactions between the wood ant *Formica lugubris* and plantation forests: how ants affect soil properties and how forest management affects the dispersal of an ecosystem engineer.

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Doctor of Philosophy

Biology

University of York

September 2023

Abstract

Organisms that have a large impact on their environment due behaviours such as constructing biogenic structures, trophic interactions or soil disturbance may be termed ‘ecosystem engineers’. All organisms are dependent on their ecosystem for the provision of resources and habitat, and different characteristics of a landscape may affect organisms’ populations, distributions, and dispersal ability. This means that landscape features and characteristics have the potential to modulate the impacts that ecosystem engineers have on the environment. Due to the large quantities of resources, they transport, and the biogenic structures they create, ants have large effects on soil in their nests, but the effect is not consistent across different species. Using a meta-analytical approach, we investigate how ant species traits can impact the effect they have on soil, and show that ants that build thatched mounds, such as the *Formica rufa* group (wood ants), are associated with large differences between nest and non-nest soils. We suggest that this is due to the concentration of resources in the nest mound, which would correspond to depletion of resources in areas surrounding the nest. In an empirical study of plantation forest sites in the North York Moors where the wood ant *Formica lugubris* is abundant, we compared soils from areas with and without wood ants to investigate if this depletion affects the abundance and distribution of soil resources. We found that *F. lugubris* presence is associated with changes in the spatial variability of several soil resources, probably due to resource removal, resulting in soil heterogeneity reminiscent of later successional stages. In plantations, management decisions can modulate these soil effects by affecting *F. lugubris* abundance and distribution. Using new and long-term data on the population margins of *F. lugubris*, we investigated how width and orientation of linear canopy gaps, such as roads and firebreaks, affects the population dynamics of *F. Lugubris*, and found that the availability of sunlight on N-S or E-W orientated linear gaps facilitates faster dispersal of *F. lugubris* than other orientations. We suggest that, to benefit from the effects that wood ants have on the environment, such as changes to the soil and potential suppression of pest species, forest managers in areas of *F. lugubris* presence should plan plantations in a way that encourages the dispersal of *F. lugubris*.

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Acknowledgments

Throughout writing this thesis and the last four years of work and study for this PhD, I have benefited immensely from the support of many people, and I would not have been able to complete this without their kind attention.

I am very grateful to my supervisors, Elva, Kelly, and Kate, for the advice and support they have given me. I would particularly like to thank my main supervisors, Elva and Kelly, who have always brought unique and complimentary perspectives to the project and advised and supported me throughout the the planning, data collection and writing process, and who have promoted my academic and professional development hugely; I will benefit from what they have taught me for the rest of my career, and I couldn't have wished for better supervisors.

In addition to my supervisors, I have been lucky enough to benefit from the support of many talented and helpful individuals at the University of York. I'd like to thank my thesis advisory panel, Mark, who provided excellent advice and feedback in my TAP meetings, Sándor, whose experience in modelling helped me steer clear of many dead-ends, and Jordan, who helped in the soil lab when the calendar threatened to get the better of me. I would also like to thank everyone in the York Ant Lab; the welcoming atmosphere and helpful input in many lab meetings brightened up Friday mornings, and, during the lockdowns, kept in check my despondency about not being able to get into the field: Eleanor, Dom, Val, Josie, Meg, Georgia, Sándor, Peter, Dan, and Gabby.

Finally, I would like to thank my family and friends, who have made me feel able to complete this thesis: Iulia, Brad, Harry, Simon, Elaine, Tom, Alex and Jack, great friends who always keep me laughing, all of the members of the York University Caving and Potholing Club, University of Bristol Spelaeological Society, and the York University Sailing and Windsurfing Club, who made sure I would always have something to look forward to at the weekend, my wonderful partner Carly, whose unwavering belief that I had everything under control was touching, even though I didn't believe it at the time (this thesis is your vindication), and my wonderful parents, who tolerated jars of insects and mud in the house for too long.

Author 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 a degree or other qualification at this University or elsewhere. All sources are acknowledged as references.

The long-term data used for establishing the population margins in Chapters 3 and 4 were collected by previous researchers in the York Ant Lab: margins data from 2011 and 2013 were collected by Duncan Procter, data from 2018 and 2019 were collected by Meg Holgate, and later years were collected by me.

Analysis of prepared soil samples using the ion chromatograph and the C/N analyser was conducted by Matt Pickering of the Environment Department at the University of York.

Chapter 1 – Introduction

Invertebrates, including ants, are widespread an abundant in most terrestrial zones, and can be the majority animal component of some ecosystems (Hölldobler and Wilson, 1990; Lavelle et al., 2006; Schultheiss et al., 2022). Due to the role that ants play as predators (Hawes *et al*., 2013), bioturbators (Richards, 2009) and agents of resource removal (Griffiths et al., 2018), they have a large potential effect on soil properties. In this first chapter, we discuss how the term 'ecosystem engineer' applies to invertebrates and more specifically to ants; what effects ants can have, and what aspects of ant biology and behaviour result in the altering of soil properties. Finally, we will introduce our study system and the questions that we will aim to answer in this thesis.

1. Ecosystem engineering

The term 'ecosystem engineer' has been broadly and sometimes inconsistently applied, with some definitions overlapping with the 'keystone species' concept (Cottee-Jones and Whittaker, 2012). In order to make meaningful use of the term as a label for species (in our case, invertebrates) with important ecosystem effects, we require a robust definition of the term. As we will see, the effects that invertebrates have on soil are often as a result of the movement of resources, including food (Anderson, 1988). Because of this, we shall use the physical ecosystem engineering concept as defined by (Jones et al., 1997): ''*Physical ecosystem engineers are organisms that directly or indirectly control the availability of resources to other organisms by causing physical state changes in biotic or abiotic materials*", which is most appropriate when considering soil engineers, as soil is such a major reservoir of resources in terrestrial ecosystems. Whilst this definition is generally adequate, we include two modifications to our definitions to make the term more applicable to invertebrates. Firstly, the effects of the species on its ecosystem must be biologically relevant when considered in per-unit engineer biomass terms, rather than per individual; clearly a single elephant will have a greater impact on its environment than a single termite, but termites are far more numerous. A comparison that would better allow us to assess the engineering potential would be per gram of organism biomass. In other words, when organisms have a large impact relative to their total biomass, they may be termed 'ecosystem engineers' (Jones et al., 1997). Secondly, we will exclude purely trophic effects, because all heterotrophs feed and thus would make the term ecosystem engineer so broad as to be meaningless. We can still consider interactions involving food resources where there are effects separate from, or secondary to, consumption alone. For example, wood ants (*Formica rufa* group) consume large quantities of honeydew excreted by the aphids that they protect (Kilpeläinen *et al.*, 2009). Trees in areas near wood ant nests can have reduced growth due to the increased pest burden

(Frouz et al., 2008). The carbohydrate from the honeydew is taken to the wood ant mounds and fed to nest-mates. Feeding on honey dew is not ecosystem engineering under this definition, but the increase in pest burden and the increase in carbon influx to the soil due to the ants taking honeydew into the nest (Finér *et al.,* 2013) is.

2. The impact of invertebrates on soil properties

Soil is of demonstrable importance to almost all ecosystems. It can be a medium for plants and microbes, for animals to dwell and feed in and as a pool for nutrients, organic matter, and water. It is also responsible for ecosystem services that are crucial for agriculture, water quality and carbon budgets (Jónsson et al., 2017). It is estimated that soil invertebrates make up nearly 23% of the diversity of described species (Decaëns *et al.*, 2006). Taking a per-unit-biomass approach, this suggests that even a relatively small effect of a small but numerous invertebrate could have a large overall effect on the soil environment. These changes to soil, whether or not they are adaptive for the invertebrate that caused them, may affect the quality or availability of resources in the environment for use by other organisms, and invertebrates that have attracted particular attention as engineers of soil include earthworms (Babu Ojha and Devkota, 2014), ants (Frouz and Jilková, 2008) and termites (Wood, 1988).

2.1 Soil Structure and porosity

2.1.1 Pores and porosity

The most direct way that soil-inhabiting invertebrates may meaningfully engineer the soil is by changing its physical structure, and many invertebrates modify the soil structure by digging burrows, which increases the porosity and aeration of the soil by introducing voids. Earthworms, for example, have been dubbed by some authors as ‘natural tillers’ (Babu Ojha and Devkota, 2014) due to the effects of both their burrows and casts. Burrowing by earthworms can also result in increased potential for water and air to penetrate the soil and in doing so aerate or drain the soil without changing the overall bulk density of the soil. For example, the increase in the abundance of macropores due to earthworm aggregations under dung pats is counteracted by the compression of the inter-pore soil, so the effect on bulk density remains minimal. These effects remain detectable for over 100 days after the pat is deposited (Knight *et al.*, 1992).

By changing soil pore structure, earthworms also increase water infiltration and decrease run-off in areas of high earthworm density (Knight *et al.*, 1992). These patches of high earthworm density occur under cowpats in cattle pasture. By forming macropores and casts, earthworms may be globally important in facilitating water infiltration and reducing run-off, potentially mitigating some of the effects of compaction on surface water penetration in the world's extensive cattle pastures (Knight *et al.*, 1992). The capacity to increase water infiltration is by no means limited to earthworms: soil-moving activity by various invertebrates can change surface texture and reduce surface run-off (Lavelle *et al.*, 2006). Subterranean termites increase water infiltration by over 50% in areas of minimal vegetation in the Chihuahuan desert (Elkins *et al.*, 1986). By increasing soil porosity, termites may reduce run-off and slow the response of water courses to rain events. Termite activity may even reduce surface run-off to almost negligible rates (Anderson, 1988).

2.1.2 Aeration and aggregate stability

Besides pore spaces, another important structural feature of soil is the material: organic and mineral particles and their aggregates. While the soil's physical characteristics may impact the potential size and stability of these aggregates, the aggregates themselves are often biogenic (Lavelle *et al.*, 2006). Fungi or bacteria may adhere particles to one another through excretion of long-chain polymeric substances, and invertebrates also make long-lasting particles. Earthworm casts, which function as large aggregates, become more resilient to erosion with time, if they are not washed away by rain or fragmented while they are still fresh (Le Bayon and Binet, 1999). Not all earthworms increase the size of aggregates; there are distinct functional groups that either 'compact' or 'de-compact' and the relative dominance of these two groups has measurable consequences for the structure of a particular soil (Jouquet *et al.*, 2006) but both affect the size and stability of aggregates in one way or another. A species of compacting earthworm, *Pontoscolex corethrurus*, completely transforms soil through bioturbation. Its casts accumulate on the surface as an unbroken impermeable layer that reduces water and air infiltration, ultimately reducing the oxygen availability below the surface (Barros *et al.*, 2001). This changes the microbiome and eventually allows anaerobic bacterial and fungal methanogens to proliferate in the top layer of the soil, decreasing the rate of iron oxidisation so that the soil appears grey rather than red (Chauvel *et al.*, 1999; Lavelle *et al.*, 2006)

The feeding activity of soil-dwelling invertebrates may also modulate the effects that bacteria and fungi have on aggregate stability. Selective feeding on fungal hyphae by Collembola, Acari and the larvae of other invertebrates may impact the structure of aggregates stabilised by fungi (Wolters, 1991). Because grazing by some invertebrates can stimulate the growth of basidiomycetes (Crowther et al., 2011), it is likely that the exact effects of invertebrates on fungi-stabilised aggregate formation and longevity will depend on the fungivorous invertebrate community composition.

2.1.3 Soil structure and resource distribution

The impact of soil invertebrates on soil structure through modification of porosity and aggregates can have secondary effects on the distribution of resources. These indirect effects change how abiotic forces redistribute resources and this acts in addition to direct internal or external transport of resources such as food and waste. These two mechanisms can interact; for example, earthworm casts are enriched in phosphorus that is concentrated from their diet (direct) and more exposed to erosion by water run-off (Le Bayon and Binet, 1999), carrying the phosphorous elsewhere (indirect). Because *Aporrectodea caliginosa* and *Lumbricus terrestris* earthworms form patches of high abundance and lower abundance (Knight *et al.*, 1992) the earthworms unevenly facilitate the transport and redistribution of phosphorus in the agricultural environment by concentrating phosphorous in their waste and depositing it in easily weatherable structures. Other invertebrates may also contribute to changes in resource distribution by promoting weathering. For example, termites alter soil profiles through the construction of mounds and clearing of obstructions along their surface trails. Modified soil surfaces respond to wind and water differently compared to undisturbed soil (Anderson, 1988) creating zones where food, materials and soluble nutrients are easily washed away. Through their effects on aggregate formation, porosity and surface texture, soil invertebrates can create patches or layers of high or low nutrient mobility, meaning that the overall distribution of nutrient resources within the soil is in part mediated by the activities of invertebrates, regardless of any effects on the absolute quantities of these nutrients in the soil.

2.2 Resource Availability

Heterotrophs, including soil-dwelling invertebrates, may influence fungal decomposition. Macro-invertebrate (Box 1) grazers can have a large impact on basidiomycete growth (Bardgett and Chan, 1999; Crowther et al., 2011); wood blocks decay quicker when woodlice and millipedes graze on the decomposing fungus because the fungus increases nutrient uptake to regrow lost tissue. Micro-invertebrates (Box 1) have a similar effect on the rate of wood block decomposition, but also increase mycelial growth. The susceptibility of the mycelium to grazing depends on the fungal species, its palatability and growth pattern (Crowther et al., 2011). It seems likely that the abundance and community composition of soil invertebrates will strongly influence decomposition rates in natural

Box 1 – Glossary of terms.

Basidiomycetes: one of two major groups of fungi that includes ‘higher fungi’ characterised by filamentous hyphae.

Mycorrhiza: subsoil symbiosis between fungi and plant roots.

Macro-invertebrate: invertebrates large enough to be seen by the unaided eye.

Micro-invertebrate: invertebrates too small to be seen by the unaided eye.

Soil Mesofauna: soil invertebrates between 0.1mm and 2mm in size

Epigeaic: an organism that lives on the soil surface, as opposed to beneath it (hypogeic) systems because the invertebrate subgroups have differing effects on the basidiomycete growth (Crowther et al., 2011).

Soil invertebrates alter decomposition by bacteria as well as fungi. Changes may occur indirectly due to interactions between the fungal and bacterial communities (Seastedt, 1984). For example, when the only invertebrates in grassland plots were fungal-feeding Collembola, bacterial-feeding nematodes, or both, nematodes alone had no effect on nutrient availability or decomposition relative to the invertebrate free control. However, treatments containing fungal-feeding Collembola had increased nutrient leaching, N mineralisation and shoot N content in the local grass, even when nematodes were also present. In the treatment that contained both nematodes and Collembola, shoot N and P content was significantly greater than the Collembola-only treatment. These results suggest that, because the greatest source of mineral N in the soil was ammonium, which favours fungi, Collembola reduced competition for N by restricting fungal proliferation. The bacterial community grew in response and in the Collembola-nematode treatment nutrients were made more available to plants due to bacterial grazing by nematodes (Bardgett and Chan, 1999). This is a heavily manipulated example, demonstrating the effects of a dramatically simplified invertebrate community; however, it does show that the effect invertebrates have on soil will be dependent on interactions between individual members of the invertebrate community and that changes to the microbial community will have indirect effects on other soil properties, in this case nutrient availability. These indirect effects may also be physical or chemical. For example, microbes may bind particles together with polysaccharides, contributing to aggregate stability and altering the pH and ion balance of soils (Wolters, 1991). Because invertebrates and the structures they create promote particular microbial communities (Lavelle et al., 2006), this regulation of structure and nutrient cycling may inflate or moderate the other physical and chemical effects already discussed, depending on faunal interactions.

Invertebrates mostly affect decomposition by mediating the effects of other organisms. The overwhelming majority of decomposition is microbial, and invertebrate effects contribute less than 10% of total decomposition (Petersen and Luxton, 1982). Nonetheless, micro-invertebrates are responsible for mass loss of organic matter (Seastedt, 1984). The processing of organic matter into smaller particles may facilitate the loss of organic matter in two ways. Firstly, invertebrate activity may increase microbial metabolism; smaller particles have a greater surface area of litter material available for microbes. Secondly, small faecal particles may be lost to lower soil horizons through larger inter-particle space, resulting in a net loss of material for the soil horizon.

2.3 Plants

The effects that soil invertebrates have on higher plants are important to consider because higher plants themselves heavily modify both above and below ground environments. Their roots may increase soil and aggregate stability, they may contribute to weathering, be a major input of organic material into the soil, alter the manner and evenness of precipitation (by catching horizontal precipitation such as mist, for example), stabilise environmental conditions close to the soil surface and alter ion availability leading to other chemical effects (Wolters, 1991).

Lavelle *et al.* (2006) summarised the ways that invertebrates may stimulate primary production:

1. They may increase (or decrease) nutrient release in the plant rhizosphere.
2. Invertebrate activity can enhance (that is, upregulate the effects of) mutualistic micro-organisms, e.g. mycorrhizae (Box 1) and N-fixing microorganisms.
3. The invertebrate community composition can provide protection against pests and diseases, above and below ground, for example by competitive interaction between nematodes and other pests reducing the total pest load (Lavelle *et al.*, 2004).
4. Create a more favourable soil physical structure. For example, increased infiltration by water due to bioturbation discussed earlier may benefit certain plants or habitats.

In addition to these, primary production may be enhanced through other selection mechanisms, e.g. selective seed dispersal of more vigorous species. Ants and termites particularly affect plant survival and distribution. For example, termite presence affected relative abundance of plant species, resulting in a different dominant species, in the Chihuahuan Desert without affecting total plant biomass (Gutierrez and Walter, 1987). In addition to the potential for soil invertebrates to increase primary productivity in certain circumstances, the role that many soil invertebrates play as pest and vectors of disease (McLeod *et al.*, 2005) has negative impacts on plant growth. These are mostly trophic effects and therefore beyond the scope of this chapter; however, they are an important factor in the balance of invertebrate effects on plants. Regardless, because of the impacts that plants have on ecosystems, it is reasonable to consider the impacts of plants an example of indirect ecosystem engineering by invertebrates in situations where the invertebrates may be increasing (or decreasing) primary production (by one of the mechanisms described above) or changing the relative abundances of plant species through, for example, selective seed dispersal.

2.5 Conclusion

Overall, invertebrates may impact the soil in three broad ways. Firstly, they may modify the physical structure of the soil. These modifications can be both direct and indirect: they may build burrows or nests in the soil, change the structure and stability of soil particles by feeding, modify the microbial community, and modify soil surface characteristics (soil texture, flora etc.). These changes to physical characteristics may further precipitate changes in chemical properties of the soil, such as pH and oxidation. Secondly, invertebrates affect decomposition rates in complex and interacting ways, but generally their activity increases it. This can be by stimulating mycelial growth by grazing, regulating competition between microbes, and by increasing the surface area of organic matter available to microbial activity. These effects interact, and the outcomes are highly dependent on the starting soil condition and invertebrate, microbial or plant community. Their impact on decomposition also changes the availability of nutrients to other organisms. Finally, invertebrates may modify the plant community by stimulating primary production, by herbivory, and by selective seed removal or predation.

Though almost all soil-dwelling invertebrates probably have some impact on their surroundings, the three groups that have been most studied and that have the greatest documented effect are earthworms, termites, and ants (Jouquet *et al.*, 2006), and the latter two are eusocial. This eusociality has consequences for how they affect their environment. All individuals in a colony inhabit large nests to which all the resources consumed by the colony are brought. This can result in nutrient hotspots around nests that have different nutrient conditions and flora from the area between mounds (Jones, 1990).

, Ants are found in every major terrestrial ecosystem (Hölldobler and Wilson, 1990), unlike termites (Vander Meer, 2012). Additionally, because they are often predatory, ants may affect the abundance and diversity of other invertebrate, which, as we have seen in the last chapter, can be soil engineers. The following section will explore what makes ants especially important actors in soil ecology and how they may behave as key determinants of the net effects of invertebrates on below-ground systems.

3. Role of ants as soil engineers

3.1 What makes ants important for soil?

There are certain traits that make soil-dwelling eusocial insects, like many ant and termite species, potentially different in their effects on soil from other invertebrates. Firstly, both ants and termites are very abundant in the ecosystems they inhabit (Wilson, 1987). Ants are present almost globally (Hölldobler and Wilson, 1990), so their effects are relevant to most ecosystems. Termites are extremely widespread as well, though are generally restricted to the tropics (Eggleton et al., 1994).

Secondly both ants and termites build and inhabit nests (or bivouacs), to which they bring food and other resources from the surrounding environment. This strategy is known as *central place foraging* and has important consequences for the spatial pattern of any soil effects (Wilby et al., 2001). Finally, eusocial insects that nest in soil will affect its structure. Some ants, for example *Formica* wood ants, also build mounds of organic material above ground (Jurgensen *et al.*, 2008). This has an array of other effects on the soil, as we shall see in the following section. Besides organic mound building and their global range, another difference between ants and termites that changes the way they can influence soil is that many ants can be predators, whereas all termites are herbivores, which means that ants can directly affect the abundance of other soil invertebrates (Frouz and Jilková, 2008). The following section shall address each of these in turn: firstly, we shall discuss the effects of ants of the spatial heterogeneity of the soil environment due to their central place foraging strategy, and the importance of heterogeneity for functioning ecosystems. Secondly, we will look in more detail at the effects of ants on carbon and nutrient cycling and availability. Finally, we will summarise how ants affect other organisms, including soil-dwelling invertebrates, the soil microbiome, and plants.

3.2 The effects of ants

3.2.1 Carbon and Nutrients

3.2.1.1 Carbon and nutrient distribution

Because of their large biomass and centralised foraging strategy, resource selection and transport by social insects will influence the resources entering the soil and create nutrient hotspots, as opposed to the more distributed effects of other invertebrates. Ants alone removed 52% of all food resources added in an experimental manipulation in Malaysia (Griffiths *et al.*, 2018). Where ants were suppressed the overall resource removal decreased, suggesting that no other group can compensate for ant exclusion or remove resources as rapidly and that ants play an irreplaceable role in resource redistribution in this habitat (Griffiths *et al.*, 2018). This study system highlights a similarity between vertebrates and social insects in their role in resource relocation. Solitary invertebrates individually remove very small quantities of resources, process them, and deposit faeces and unused parts randomly and dispersed throughout the habitat. By contrast, both vertebrates and ants may gather resources over a wide area but deposit the faeces and other unused material in a small number of locations, for example in long-term refuse piles near an ant nest (Lenoir *et al*., 2001). In doing so, both groups may contribute to spatial heterogeneity by creating nutrient hotspots (Kristiansen and Amelung, 2001).

3.2.1.2 Carbon and Nutrient Flux

In addition to redistributing nutrients within the soil or across the soil surface, invertebrates can mediate the influx of nutrients into the soil from elsewhere. For example, wood ants (*Formica rufa* group) are major contributors of carbon and nutrient flux into the forest soils that they inhabit (Domisch *et al.*, 2009). The wood ant foragers protect aphids from predation and the aphids, as a by-product of feeding on the tree sap, secrete honeydew, which the wood ants collect. The honeydew is carbohydrate rich and is a major food source for wood ant workers (Domisch et al., 2016). Because of this, ants bring large quantities of carbon directly to their nest-mates in the nest, where it remains in the soil as waste. Prey removed from the soil and relocated to the nest to feed brood is also a major component of the influx of nutrients such as nitrogen and phosphorus into the soil (Domisch *et al.*, 2009). C input is much lower than nutrient (N and P) input by wood ants but is still a modest component of C input relative to litter fall (ant mediated C influx is 2-6% of litter-fall C influx; (Domisch *et al.*, 2009). The impact of the ant-aphid mutualism on plant growth is less clear: in Norway spruce forests in the Czech Republic, tree growth was reduced in the 50m around nests of *Formica polyctena* due to higher aphid densities, though the concentration of nutrients in the nest meant that tree growth was slightly faster within 1m of nests (Frouz et al., 2008). In contrast, the effects of *Formica aquilonia* predation on folivorous invertebrates probably outweigh the negative effects of increased aphid load due to protection by the ants in Finnish mountain birch forests (Punttila *et al*., 2004). Whether ant presence is beneficial to trees or not will probably depend on the relative importance of different kinds of herbivory in a specific environment; when folivory rates are low, the increase in aphid load due to ant presence will have negative net consequences on tree growth but where folivory is, or has the potential to be, a major burden to trees, the overall effect of ants on tree growth will be positive, before the effects on the soil are considered.

3.2.2 Soil organisms

3.2.2.1 Plants

Ants can have a diverse range of effects on plants including on growth and community composition. Harvester ants (*Messor andrei*) can increase the seed production of a species in the community by modifying the soil environment on the mound surface, though this effect was limited to the nest; the plant community in the surrounding environment was not significantly affected by ant exclusion (Brown and Human, 1997). For plants that disperse their seeds by myrmechory, the species composition of the ant community, and the size of the ant species, will strongly affect seed removal and which seeds will survive (Gorb and Gorb, 1999). As a result, ants may indirectly impact the soil by changes to plant community and growth, modulating the effects that plants have on the soil.

Ants are major agents of seed transport in many environments (Del Toro et al., 2012), but they may also modify the distribution of plants by means other than seed transport. The mounds of the harvester ant *Messor andrei* have noticeable effects on the seed production of shining pepperweed, *Lepidium nitidum*, growing on the nests in an experimental manipulation in northern California, compared with the same plant growing on non-nest surfaces, while the mounds themselves can harbour exotic grasses at the expense of forb diversity (Brown and Human, 1997). On the other hand, selective seed removal by the ants had no effect on the plant community over the course of a year-long exclusion experiment, suggesting that the effect of soil changes in and around the mound are of a greater magnitude than the effects of selective seed removal from the wider environment (Brown and Human, 1997). At the landscape scale, the unevenness of this effect on seed production and community makeup is likely to increase the patchiness of plant species distribution. As we will see in the following section, this increase in patchiness is a common effect on soil of invertebrates that are found in high densities at individual locations like ants and termites.

3.2.2.2 Soil Invertebrates

The abundance of other invertebrates also responds to ant presence, and ant mounds can harbour other invertebrates. The favourable conditions inside the mounds of *Formica aquilonia* harbour higher densities of earthworms than the surrounding soil (Parmentier et al., 2014), while the biomass of five species of earthworm found in *F. aquilonia* nests is seven times higher than in soil outside of the nest and the dominant earthworm species in the nest material was also different from the surrounding soil (Laakso and Setälä, 1997). Possibly this is due to the availability of organic matter, low predator abundance and a stable temperature. Because the earthworms can have major effects on the soil, which depend on the earthworm community and the starting soil conditions, the shift in the dominance structure of the earthworm community and the seven-fold increase in biomass could compound the effects that the wood ant nest alone would have on the soil.

Wood ants can also influence the relative abundance of species in the soil invertebrate community inside and outside of the mounds. Mounds of *Formica polyctena* have a high invertebrate species richness, primarily of beetles (Härkönen and Sorvari, 2014); the mound invertebrate community composition is more similar in mounds that are near to one another than ones that are far apart. It follows that, while wood ant nests may harbour a different invertebrate community from the non-nest soil, between-nest similarity does not mask the larger scale heterogeneity of invertebrate distributions in the habitat. Additionally, ant presence does not affect all soil invertebrate groups in the same way: the biomass of predators of epigaeic (Box 1) fauna is lower at high wood ant densities, but there is a greater biomass of mesofaunal (Box 1) predators and epigaeic earthworm reproduction is higher under high ant density conditions (Laakso, 1999). Because the effects of earthworms on soil vary with earthworm community composition (Jouquet *et al.*, 2006), wood ants may regulate the effects of earthworms on soil by changing relative species abundance.

Ant activity may also increase or decrease the density of other arthropods in the soil, which may then further impact soil. Nests of the harvester ant *Pogonomyrmex barbatus* differ greatly from control soils in microarthropod (30 times greater) and protozoa (5 times) abundance (Wagner et al., 1997). Because the effect was seen only in the nest soil, the overall spatial heterogeneity of the grassland is increased. Having been shown to change both the plant and invertebrate community in their nests, which themselves also impact the soil in a variety of ways, harvester ants may begin a positive feedback loop of increasing spatial heterogeneity of the soil, whereby they promote changes in the other agents of soil modification (Jouquet *et al.*, 2006).

Competition from ants may have effects on soil fauna; however, this is highly context specific even between species with similar biology. For example, at high densities, wood ants increase the dominance of the most abundant species of carabid beetle, while supressing medium sized (6-19mm) carabids the most (Hawes et al., 2002). In contrast, short term, small-scale (1.3m plots) artificial exclusion and long-term natural exclusion of *Formica polyctena* had no measurable effects on the soil fauna in Swedish mixed forest (Lenoir et al., 2003). It is probably impossible to make generalisations about the effects of wood ant competition on soil invertebrate communities, and any exact effects are dependent on other factors such as the plant community (Hawes et al., 2002). As a result, any conclusions about the effects of ants will be specific to the study system.

4. Spatial heterogeneity

4.1 Spatial heterogeneity in soil

4.1.1 The role of spatial heterogeneity in soil for ecosystem function

Spatial heterogeneity within an environment is a major predictor of biodiversity (Stein et al., 2014), which is in turn important for ensuring that ecosystem function is robust to change (Oliver *et al.*, 2015). It may even contribute to ecosystem services directly, for example by controlling the spread of forest fires or pest outbreaks in managed forest (Turner et al., 2013). Furthermore, small-scale spatial heterogeneity (tens of metres, as opposed to hundreds or thousands; the scales that ants are active at) could be particularly important for the maintenance of diversity, especially in managed forests such as plantations (Niemelä et al., 2013). Spatial heterogeneity of forest successional stages at the 10-15m scale has the greatest effect on spider, ant, and carabid beetle diversity (Niemelä et al., 2013). This distance is within the typical movement range of these species and so it is possible that the heterogeneity in space creates a greater uniformity of resource availability in time, buffering against times of low resource availability and supporting a greater diversity (Niemelä et al., 2013). This does not necessarily mean that local scale spatial heterogeneity is directly contributing to biodiversity, and caution must be exercised in suggesting a causative relationship between heterogeneity and biodiversity. For example, it could be that local heterogeneity is indicative of later successional stages and less disturbed habitats, and it is successional stage that is affecting biodiversity. We do see small scale spatial heterogeneity in soils of late successional stages. Old growth cove-hardwood forest in the Appalachian Mountains have a greater variance in net N mineralisation and nitrification than previously logged or pastured secondary forest (Fraterrigo *et al.*, 2005). Furthermore, the concentration of nutrients (carbon, nitrogen, and calcium) in the soil shows far greater local (<28m) and medium scale (>150m) heterogeneity in primary forest compared with previously logged forest (Fraterrigo *et al.*, 2005). At the landscape (large) scale, however, previously logged forest shows greater variation nutrient concentration; although large-scale soil nutrient heterogeneity is not greatly affected by prior land use, the local scale heterogeneity is greatly reduced in secondary forest, possibly leaving it more vulnerable to stochastic effects (Oliver *et al.*, 2015). This did not hold true for some nutrients (P, K and Mg) in secondary forests on former pastureland, where nutrient heterogeneity was greater than for some reference soils: this was attributed to the uneven distribution of dung pats from livestock during the pasture phase (Fraterrigo *et al.*, 2005). Even in habitats where spatial heterogeneity has not been shown to directly affect biodiversity or ecosystem function, the above suggests that spatial heterogeneity is at least a predictor of successional stage or relative diversity. As we have seen, the scale at which ants can increase spatial heterogeneity is similar to the fine-scale heterogeneity that is lost in disturbed habitat, for example secondary forest or plantation. This means that ant activity may lead to a nutrient landscape with similar spatial heterogeneity to later successional stages in certain habitats, though it is unclear what effect this would have on the ecosystem.

4.1.2 The effect of ants on spatial heterogeneity in soil

Determining the effects of an ant nest on soil properties requires comparing conditions in the nest with surrounding soil. How ants affect the 'surrounding soil' (away from direct effects of the nest structure) is a gap in our understanding of the ant-soil relationship (Frouz and Jilková, 2008) and is prerequisite to understanding the overall contribution of ants to spatial heterogeneity at different scales. Identifying the size of the 'patches' created by ants is important because, as we have seen, spatial heterogeneity at different scales can have very different consequences for ecosystems. Within the nests, the ants can change the soil properties to a remarkable degree over a small scale. For example, soil from abandoned *F. lugubris* nests, which are typically no more than 1m tall and wide

(Domisch et al., 2016), in Denmark had greater nitrogen and carbon concentrations than the surrounding soil and had greater root density (Kristiansen and Amelung 2001). This effect was still detectable over a decade after nest abandonment. Other soil properties that have been shown to be affected in wood ant mounds include the availability of nutrients (Lenoir et al., 2001; Stadler et al., 2006; Ohashi et al., 2007), nutrient flux (Domisch *et al.*, 2009), pH (Lenoir et al., 2001), physical properties such as bulk density Kilpeläinen *et al.,* 2007) and moisture content (Frouz and Jilková, 2008; Jílková *et al.*, 2017). Some populations of wood ants are polydomous and the high rate of nest relocation and foundation in polydomous ants (Burns *et al.*, 2020) means that they may also have a large effect on the heterogeneity of soil within their range. As a result, all properties of soil that ants can affect within the nest will potentially exhibit increased heterogeneity in ant-modified habitats.

The exact scale of direct nest effects on the soil are unclear. Generally, it seems that the effects of ant nests on soil are local. No significant difference was detected between soil at 1, 2, 4, 8, 12, 20 m from *Formica aquilonia* nests in northern Finland, but foliar nitrogen in trees on the nests (0m) was significantly higher than those at 4, 8, 12 and 20m (Karhu and Neuvonen, 1998). Although soil nutrients did not significantly vary with distance, the authors suggested that this was due to the trees (mountain birch *Betula pubescens*) taking up nutrients more rapidly when they have access to more nutrient rich soil in the ant mounds, masking the response if only soil is measured. They concluded that the radius of birch root networks (5.6 m in southern Finland) was the reason that no effect on foliar nitrogen was found 4 m from the nest (Karhu and Neuvonen, 1998). Even though the biology of the tree species was considered the cause of the radius of effect around the nest, these results have been used as justification for taking soil samples at 3 metres from nests to represent the surrounding soil, (soil supposedly unaffected by ant activity) in managed plantations of Norway spruce (Kilpeläinen et al., 2007). Although it is possible that this assumption is valid, there are two potential problems with it. Firstly, this would mean that the radius of ant effects would be the result of the tree species present, even though the lack of elevated N concentration 1m from the nest was also attributed to the trees, despite the fact that other soil properties are still affected by the nest at this distance (Jílková et al., 2011). It is quite possible that in forests with a different dominant tree species there would be a different radius of effect. Secondly, this assumption excludes the possibility that the ants are affecting the soil by means not directly related to the nest mounds. The ants may forage widely and organic nest building, like that done by these wood ants, requires the materials be brought from the surrounding area. As a result, the ants could change the quantity and type of organic matter entering the soil within their foraging range, which is far greater than 3m.

In conclusion, ants are central place foragers and the effects that they have on soil nutrients and chemical characteristics will be spatially heterogeneous. Not all of the material that ants transport to or near their nests is consumed, and indigestible waste and food parts will accumulate (Wilby et al., 2001). This may serve to change conditions on and near the mound so much that the plant community can be substantially different in terms of productivity and diversity, and this effect can interact with other behaviours such as selective seed harvesting (Brown and Human, 1997). In the case of ants that build surface mounds from organic matter, such as *Formica* wood ants, large quantities of nest building material is also transported (Jurgensen *et al.*, 2008). The movement of both food and non-food resources will change the distribution regime for nutrients and materials; we would expect the soil environment to become patchier and more heterogeneous.

4.2 Spatial heterogeneity within habitats

To answer questions about how ants may affect spatial heterogeneity (of soil), it is important to ask whether existing spatial heterogeneity effects ant presence or abundance. In the simplest sense, more heterogeneous landscapes may harbour more or different species; as discussed earlier, small scale (10-15m) heterogeneity of successional stages has a large effect on spider, ant and carabid diversity (Niemelä et al., 2013). In this example, it is not the invertebrates that are causing the spatial heterogeneity, as may be the case with some of the examples of ant soil modification we have discussed so far, because the successional stage of an area of forest can only be changed by felling or the passage of time. Instead, the structure of the forest changes how the invertebrates can utilise it. Nor is successional change the only major source of structural spatial heterogeneity that might be present in forest; natural features such as rivers, ponds, and geological features in addition to anthropogenic areas like roads, railways, canals, derelict or disused buildings, hedge rows, mineral extraction and other areas of resource exploitation could be sources of heterogeneity. Interestingly, many of these features are linear in shape, meaning that they could be important avenues of species movement if the heterogeneity that they provide is beneficial to a particular species. There is some precedent for linear features effecting communities in this way; in plants, linear forest disturbances may aid wind dispersal of seeds (Roberts *et al.*, 2018) and increase plant abundance and diversity (Suárez-Esteban *et al.*, 2016) and these features can disproportionally benefit generalist plants (Liira and Paal, 2013). This means that plants, and organisms that share some traits with plants (e.g., dispersal ability, reproductive unit effectively sessile) have the potential to greatly benefit from spatial heterogeneity and linear features.

On the other hand, spatial heterogeneity may serve as a barrier to some organisms, and this may be especially true of linear features because a linear feature that cannot be as easily circumnavigated as a, for example, a circular feature of the same area, assuming the organism cannot disperse through either feature. This last assumption will not hold true for all species, and this could mean that this kind of heterogeneity will affect organisms differently. Generalist species of carabid beetles pass through anthropogenic edges more effectively than forest specialist carabids (Magura et al., 2017). Specialists may be negatively affected by interruptions to the habitat they are specialised for, such as the inclusion of another habitat (spatial heterogeneity) or the edge of their habitat (linear feature). A greater proportion of generalist ground-dwelling spiders than forest specialist ones are found as far as 50m into stands of black spruce in eastern Canada, meaning that only forest stands more than 100m wide would favour specialists over generalists (Larrivée et al., 2008). Because pre-existing spatial heterogeneity can differentially effect species, and some of these species may be ecosystem engineers themselves, understanding how structural spatial heterogeneity will affect species distributions is essential to building a complete picture of the relationship between organism and ecosystem.

4.3 Habitat heterogeneity: comparative effects on ants and plants

Ants share some traits with plants which mean that they may benefit from habitat heterogeneity in the similar ways that plants do (Roberts *et al.*, 2018), increasing the reach that their impacts of the soil can have. Although ants may relocate their nest if conditions are unfavourable or the nest is disturbed (McGlynn, 2012), the reproductive females in a colony will never usually leave the nest in most species. This means that the reproductive part of the ant colony is effectively sessile, like a plant. Species that can establish new colonies from a single mated female can disperse widely after nuptial flights, but they still may benefit from linear features in the same way that the seeds of wind dispersed plants do (Roberts *et al.*, 2018). Some species and populations are less effective dispersers, such as the UK populations of the wood ant *Formica lugubris* (approximately 50m per year; Procter et al., 2015), and so the impact of landscape features on their dispersal may be more critical. This is especially pertinent where *F. lugubris* is found in plantation forests because the landscape level heterogeneity in these habitats is determined by management practices. As a consequence, management practices could determine outcomes for wood ant populations that will subsequently have impacts of soil physical and chemical properties.

5. Red wood ants in timber plantations

Many species of social insects that have been called ecosystem engineers, such as termites and leaf-cutter ants, are limited to lower latitudes. Their large biomass and the impressive biogenic structures they create have made them obvious targets for study of the effects that organisms can have on the soil environment (Laakso, 1999; Kristiansen and Amelung, 2001; Lenoir et al., 2001; Risch et al., 2005; Frouz et al., 2008; Kilpeläinen, 2008). At higher latitudes a group of ant species that is of particular interest for its potential effects on ecosystems and soil is the *Formica rufa* group (red wood ants). Like the well-studied leaf-cutter ants of the tropics, they construct impressive nest mounds that can reach heights of 2m and their high population densities in some areas mean that they may monopolise food resources (Jäntti *et al.*, 2001); their impact on invertebrate populations can be so great that they may exclude some insectivorous birds (Haemig, 1994). Many studies on wood ants have been conducted in plantation forest (Kilpeläinen et al., 2007; Frouz et al., 2008; Wardle et al., 2011), especially in Europe, where plantation forests make up approximately 7.1% of Europe's' total of 994.3 Mha of forest land as of 2015 (Payn *et al.*, 2015).

Forestry is a major industry around the globe, valued at approximately $4.5 billion annually (Apsalyamova *et al.*, 2015). The apparent abundance of red wood ants in plantation forests, their potential impacts on soil and nutrients and the wider ecosystem, and large area and value that this anthropogenic landscape represents makes understanding how red wood ants interact with their environment important for understanding the potential economic and conservation impacts of wood ant presence. In this thesis, we leverage available long-term data available on the populations of the northern hairy wood ant, *Formica lugubris,* in the North York Moors to answer some questions that are central to understanding the impact that wood ants have on plantation ecosystems and vice-versa. The biology of *F. lugubris*, and site/population specific detail are explored in the following sections.

5.1 Feeding and nesting biology

In common with all members of the *Formica rufa* group, *F. lugubris* adults' main source of carbohydrate is honeydew from sap-sucking aphids. Plant sap is mostly water, containing 350 g sugar/l phloem sap and very small quantities of protein and other nutrients necessary for growth (Volkl *et al.*, 1999). As the aphids eat nothing else, they must consume large volumes of tree sap to acquire the nutrients necessary for growth and reproduction and they therefore excrete most of the sap by volume as a waste product that still contains sugars (Volkl *et al.*, 1999). Worker wood ants collect this from the aphids, and it is either consumed directly or stored in the ant's crop to share with nest mates by trophallaxis (Domisch et al., 2016). In order to ensure the supply of this valuable resource, the ants provide protection to the aphids, and aphid numbers may be greater on trees tended by ants (Kilpeläinen *et al.*, 2009). As a consequence of the large volume of honeydew harvested by the ants, the ants may be responsible for as much as 0.1–0.7% of the carbon flux into the soil in forests they inhabit (Finér *et al*., 2013). While the adult ants only require carbohydrates acquired from honeydew to survive, the workers also hunt and scavenge invertebrate prey (and occasionally carrion) to provide protein for rearing brood (Domisch *et al*., 2016). The brood are cared for in the nest, so the invertebrate prey that is brought there contributes to a net influx of nitrogen into the nest and soil (Finér *et al*., 2013). As a result, the feeding strategies of wood ants are a major component of their potential impacts on soil and may separate them from other ant species with different feeding biology.

The structure of wood ant nests is very similar between species and unique to the *Formica rufa* group. The nest has below ground tunnels and chambers beneath a large surface mound constructed of excavated mineral soil and organic matter that also contains tunnels and chambers (Wheeler and Wheeler, 1983). This surface mound is covered in leaf letter (Figure 1.1) that is site dependant: in coniferous forests, they use needles, but they can also use catkins, leaves, flowers, cut grass and reeds (Jilkova *et al.*, 2012). The surface layer is actively maintained by the ants and provides insulation and a degree of waterproofing that allows the interior conditions of the nest to be more stable,

Figure 1.1. A wood ant nest on the North York Moors

warmer and drier than the ambient conditions (Kadochová and Frouz, 2013). This thatched nest design is found in all members of the *F. rufa* group and similar behaviours are very rarely found in other ant species (Chapter 2). Because this behaviour causes more organic matter to be removed from the surrounding soil and incorporated into the nest, it indicates a mechanism of ant effects on soil that is largely absent from other species.

5.2 Polydomy

The UK populations of *F. lugubris* are polydomous; one 'colony' occupies multiple nests, with inter-nest trails allowing the movement of workers and the transfer of food (Ellis et al., 2014), such that an individual nest may have no foraging trails of its own (Ellis and Robinson, 2015). These 'colonies' do not form new nests by temporary social parasitism, as is usual in this species (Kilpeläinen, 2008); instead, upon mating, the female reproductive returns to the maternal nest. A mated queen or queens may then disperse on foot with a cohort of workers to build a new nest. As such, polydomous populations of *F. lugubris* are very poor dispersers, with the population margins of expanding populations growing by as little as 50m per year (Procter *et al.*, 2015).

Early in the year, many new nests are made, and nests in good locations, near food resources or with adequate direct sun for example, can quickly grow large as more workers and resources are gathered there. Later in the same season, there is often a consolidation of the nests, with less favourable nests being abandoned and their workers diverted elsewhere, possibly to more favourable nests or the nest of origin. Sometimes, nests in less favourable sites may persist for several seasons before abandonment or be abandoned and reoccupied multiple times (Burns *et al.*, 2020). None of this is possible in monodomous populations, where the failure of a nest would result in either colony death or costly relocation (with colony death potentially resulting). This means that polydomous populations have a far higher rate of nest foundation and abandonment than monodomous ones (Burns *et al.*, 2020), and the lack of aggression between nests means that far higher population densities can be achieved. Polydomy is an important consideration where ecological effects of *F. lugubris* nests are suspected, because it follows that any effects of nests on the environment will be greater where there is a high turnover of nests and a higher total nest abundance (Johansson and Gibb, 2016).

5.3 Study site

The North York Moors are home to several large populations of *Formica lugubris*, with one population north of Helmsley containing nearly 3000 nests in 2013 (Procter *et al.*, 2015). While some areas of Ancient Woodland (woodland that has not been cleared since at least the 15th century (Spencer and Kirby, 1992) remain, some of which contain wood ants, most of the forest cover on the North York

Moors is conifer plantation (Sudd et al., 1977). Much of this plantation is relatively young, being planted within the last 100 years, and planted around the pre-existing areas of Ancient Woodland. Though some of these remnant areas of Ancient Woodland have been connected by plantation forest, and it is possible that this has resulted in several formerly separate populations of *F. lugubris* combining, most of these areas of plantation are separated by open moorland that is unsuitable for wood ants. The slow dispersal of UK populations of *F. lugubris* means that even relatively short gaps in the forest of more than 200m could inhibit their dispersal (Procter *et al.*, 2015). Despite this, the wood ants have colonised much of the areas of plantation forest connected to the likely source populations in remnant areas of Ancient Woodland, and in areas where suitable forest remains un-colonised, such as Broxa and Cropton forests, the population margins have continued to grow over the last 10 years.

5.4 Historic range and utilisation of plantation forests by *Formica lugubris*

From the present extent of *F. lugubris* populations in plantation forests on the North York Moors and the continued expansion of the population margins, it is clear that the non-native coniferous plantation forest is providing suitable habitat for wood ants populations to grow, however historic land use and physical geography explain much of their present distribution on the North York Moors (Procter *et al.*, 2015). Much of the historic extent of forest on the North York Moors was felled before the end of the 19th century and the small areas of forests that were present when the North York Moors reached minimum forest cover remained because it was unsuitable for economic activity, such as farming (Mason, 2007) and escaped felling. The size of the forest remnants was variable (Procter *et al.*, 2015) and it is possible that stochastic factors meant that *F. lugubris* was absent from some of them, or the area was too small to support a viable population. The result is that, while there are many more sites on the North York Moors where plantation forest would be suitable for wood ants to occupy, *F. lugubris* is absent from many of them, and will remain absent without intervention or greater afforestation due to absence of long-range dispersal in UK *F. lugubris* (Sudd et al., 1977; Procter et al., 2015).

5.5 How plantation forest meets the biological requirements of *Formica lugubris*

In addition to the historic and geographic factors that have determined where source populations of *Formica lugubris* currently exist, the suitability of plantation forest for colonisation and the present extent of forest cover have influenced the current extent of wood ant populations in the North York Moors. Plantation forests is typically densely planted and considerably less sunlight reaches the forest floor than in natural or semi-natural forest. *Formica lugubris* nests require some insolation to maintain nest temperature and do not thrive in areas of total shade (Chen and Robinson, 2014). As a consequence, the forest floor within stands of trees in a planation forest, where there is little light, is largely unsuitable for wood ants. The presence of wood ants in plantation forests is restricted to the forest margins and canopy gaps. Most plantation forests do have abundant canopy gaps that are necessary for practical reasons. Firstly, stands of trees are planted at different times for a progressive harvest, resulting in adjacent stands of different ages and heights, causing gaps in the canopy that can let light in. Secondly, modern forestry techniques require there to be many access roads for large machinery and other forest management practices include firebreaks, cut to reduce the spread of forest fires through the crop, and thinned rows or areas of selective harvest, where only part of the crop has been removed to allow light to the forest floor (Demir *et al.*, 2009). Finally, many of these forests are also used for outdoor recreation and have many footpaths and Rights of Way that may also result in breaks in the canopy. This provides the insolation required to make suitable habitat for *F. lugubris* and allows colonisation along these linear features. The plantation forests also provide adequate food for wood ants; sap-sucking aphids are considerable pests of plantation forests, existing at high densities and reducing the rate of growth of the trees (Frouz et al., 2008). Because of the combined presence of coniferous trees hosting aphids and the presence of canopy gaps, the plantations can provide ample suitable habitat for wood ants that has resulted in the expansion of the population margins that have been recorded (Procter *et al.*, 2015).

6. Questions and aims

The available data for the North York Moors *F. lugubris* population make it an excellent study system to answer important questions about the relationship between wood ants and plantation forests. In this thesis, I aim to determine if ants in general, and wood ants in particular, have biologically important impacts on their habitat, with emphasis on the below ground environment. Using new field data, I will then show the impact of wood ants on the soil in their nests and in the wider environment in coniferous plantations. I will also show how the management of plantation forests can impact the spread of these ant mediated effects on soil by influencing their dispersal. Finally, I discuss the implications of wood ant presence in plantation forests from the perspectives of biodiversity, yield and resilience and we will attempt to provide evidence-based advice to forest managers in areas of wood ant presence.

In Chapter 2 I conduct a meta-analysis that explores the effects that ants as a group have on soil in their ecosystem: How is soil altered by ant presence? Which ant traits are associated with changes to the soil and which species have the largest effects? How do wood ants compare to other soil-affecting ant species? This meta-analysis provides context and justification for Chapter 3, an empirical study at sites in the North York Moors. Here I use novel soil sample and historic population margins data to identify the effects that wood ants have on soil inside the nest and in the non-nest soils within their foraging area. I use these data to investigate the role wood ants play in modulating the spatial variability of soil nutrients within plantation forest and discuss the potential mechanisms and outcomes of this. In Chapter 4, we combine historic and newly collected empirical data to close the loop of bidirectional feedback between the wood ants and the anthropogenic environment by investigating how landscape-level forest management decisions can impact the dispersal and abundance of wood ants. Chapters 3 and 4 provide both sides of the picture of how wood ant populations and plantation forests affect one another; the implications this has for the biodiversity, productivity, resilience of planted forests, and recommendations for forest managers in areas of wood ant abundance are discussed in Chapter 5.

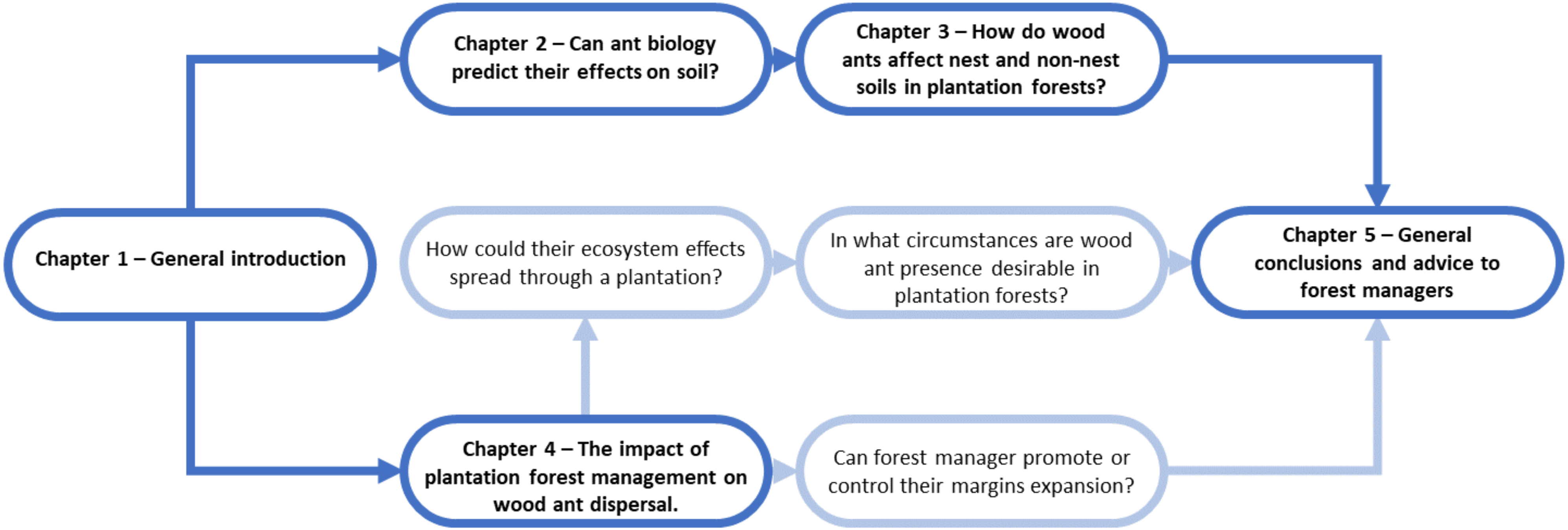

Figure 1.2. Structure of this thesis, with chapters circled in dark blue and questions arising from the data circled in light blue. These are addressed and synthesised in the general conclusions (Chapter 5).

Chapter 2 - Can ant feeding and nesting biology predict their effects on soil?

Abstract

Animals can alter their environment through disturbance, trophic interactions and moving and removing resource, including food and nesting materials. Many species of soil nesting ant change the chemical and physical properties of soils, causing significant differences between the soils within the nest and the soils surrounding it. The changes ants cause to soil are not universal and the differences in the effects of ant nests on soil are driven by the ant's biology, as well as environmental context and initial soil conditions. Our understanding of how behavioural traits, like feeding and nesting biology, modulate the effects that ants have on soil is incomplete. Here we ask how ants' feeding biology and nest structure shape their effects on soil properties. Using a meta-analysis of 64 papers providing 116 comparisons of nest soil with non-nest soil, in conjunction with ant trait data, we find that ants, in general, enrich soil nutrients in their nests: ammonium, nitrate, available and total P, and K were all enriched in ant nests, and the soil in ant nests was more alkaline than the surrounding soil. These effects were not consistent when feeding and nesting strategy were taken into account. Ants that build thatched mounds, such as wood ants of the *Formica rufa* group, increased the concentrations of total P, total N, and total and organic C considerably more than ants with other nesting types, while root-aphid honeydew feeding ants made nest soils much more alkaline while slightly depleting available P, relative to ants with other feeding strategies. Our results suggestthat ant biology is a major factor in determining their impacts on soil, and ants that build complex nests incorporating organic matter or that feed mutualistically on root aphid honeydew are likely to have larger effects on the soil in their nests and contribute more to the nutrient hotspots, than other soil-nesting ant species. The current lack of information on some ants' behaviour and ecology limited our analysis to more commonly reported traits, and this emphasises the need for greater research efforts into less reported species to facilitate a better understanding of potential changes to ecosystem services as a result of changes to species presence.

1. Introduction

1.1 Ant as agents of soil change

Animals affect the chemical and physical properties of their habitat through a variety of different mechanisms; interactions with other organisms (e.g., herbivory), additions to the environment (urine, faeces, and their own carcasses), relocating materials, and destructive interactions like compaction or ground clearing by large vertebrates. These mechanisms can also interact with one another; for example, cowpats increase earthworm density beneath them, which results in more macropores and greater water penetration into the soil (Knight *et al.*, 1992; Lavelle *et al.*, 2006). Animals may also make biogenic structures that modify the local environment for direct adaptive benefits. Biogenic structures may be additive, like many bird nests, whereby material is gathered from the wider area to build a new structure (Sheldon and Winkler, 1999), or they may be subtractive; material is removed or excavated, and the biogenic structure is the void left behind, as in burrows (Begall et al., 2007). Many biogenic structures involve elements of both: most burrowing mammals will excavate soil (subtractive) and line the burrow with insulating nest material brought from elsewhere (additive) (Hansell, 1993; Laundre, 1993). Biogenic structures may also interact with other impacts animals have on their environment; entrances to burrows become areas of high traffic, soil compaction, and are cleared of obstacles, inedible parts of food resources and animal waste may accumulate near a nest, and the burden of herbivory on plants will be greatest near the nest or burrow of an herbivore (Hansell, 1993).

The nests of social insects are biogenic structures that often result in effects on the soil at a large scale; in a population in the southeastern USA, the fungus-growing ant *Trachymyrmex septentrionalis* is estimated to excavate 0.5-1.5 tons/ha of soil every year (Tschinkel, 2015), while the termite *Syntermes dirus* can construct nests 2.5m tall and 9m in diameter (Martin *et al.*, 2018). Social insects exhibit a wide range of nesting strategies resulting in diverse biogenic structures. Bees construct combs out of wax, while wasps make theirs of paper (Hansell, 1993). Termites may produce vast aboveground structures out of mud and saliva, with intricate galleries and a structure that promotes the circulation of air and creates thermally stable conditions within (Korb, 2003). Wood ants construct nests by excavating mineral soil and covering the surface of the mound with organic thatch (Wheeler and Wheeler, 1983). Furthermore, many social insects concentrate their waste in refuse dumps, creating very local impacts on soil nutrients (Lenoir *et al*., 2001). Finally, social insects have a wide variety of diets and foraging strategies that not only shape their interactions with other organisms, but also determine what resources are being brought back to, and concentrated in, nests and refuse dumps. Social insects may feed on wood (Brune, 2014), aphid honeydew, or farmed fungi; they may be nectar feeders, predators, seed harvesters or generalists (Parr *et al.*, 2017). Finally, the number of individuals present in a nest (nests of the leaf cutter ant *Atta cephalotes*, may contain up to half a million individuals) and their biomass within a habitat (globally, termites have a biomass of 100Mt comparable to the biomass of all humans; Bar-On et al., 2018; Rosenberg et al., 2023) mean that even a small effect on the individual or nest scale could be ecologically relevant at the species level. Their biomass, the biogenic structures they create, and the diversity of their foraging strategies have the potential to cause an equally diverse range of effects on their local environment, including the soil, where many of them construct their nests.

Soil is the medium in which many social insects build their nests; approximately 70% of individual ants are epigaeic (Schultheiss *et al.*, 2022). The remaining 30% are arboreal (Schultheiss *et al.*, 2022) and some build no nest at all (Jackson, 1957), but soil-nesting species are of particular interest, not just because of their prevalence, but also because soils can be very sensitive to change as a result of disturbance (Raison, *et al.*, 1987). Incorporation of organic matter can affect nutrient availability (Trofimov, 1997), water retention and pH (McCauley *et al*., 2009), and aeration (Soane, 1990) by the digging of tunnels can bring about changes in the soil microbiome (Lavelle *et al.*, 2006). Furthermore, some social insects actively maintain the temperature of their nests (Kadochová and Frouz, 2013), creating conditions in the nest that are distinct from the surrounding soil. These many changes in the soil chemical and physical properties can impact the plant community (Van der Putten *et al.*, 2013), which can in turn have far reaching impacts on the availability of food resources to other organisms. As a result, the nests of soil-nesting social insects can be very different from the surrounding soil in ecologically significant ways.

Of the social insects, ants have some of the most ecologically important and diverse effects on soil. The majority of soil-nesting social insect diversity belongs to two groups: the ants (family: Formicidae) and the termites (infraorder: Isoptera). Termites have important impacts on the soil and their local environment but are restricted to the tropics (Liu *et al.*, 2022) and feed exclusively on decayed plant matter (Hansell, 1993). Ants, on the other hand, are found on every continent except Antarctica, with a far wider latitudinal range (Schultheiss *et al.*, 2022) and utilise a wide range of feeding strategies (Parr *et al.*, 2017). Because of the diverse range of habitats and latitudes that ants are found in, and the diverse initial soil conditions that this results in, we predict that the effects that ants have on nest soils will vary with location. In addition to this, because of the range of feeding and nesting strategies utilised by ants, we predict that different species of ants will have different effects on soil within the same habitat.

While there are a large number of studies that have quantified the effect that ants have on soil by comparing nest with non-nest soils (Farji-Brener and Werenkraut, 2017), these studies individually focus on one or a small number of species in a particular area, making generalising the effects of particular life history traits on soil difficult. Furthermore, because traits like feeding and nesting strategy do not correlate well with phylogenetic position, drawing broad conclusions about particular taxa without considering the role of ecological traits is flawed; distantly related ants may have similar feeding biology (e.g. though both Myrmicine ants, the seed harvesting ant genera *Messor* and *Pogonomyrmex* are not closely related) while ants in the same genus can have very different nests (*Formica lemani* produces very simple nests with little or no above ground component whereas *Formica rufa* creates complex, thatched mounds with above and belowground components; Seifert, 2018). Clearly this partial independence of nesting and feeding biology from taxonomy means that characterising the effects that ants have on soil cannot rely on classifying ants by taxonomy alone.

Perhaps due to the diversity of both the nesting and feeding biology in soil-nesting ants and the range of habitats that they can live in, different ants affect soil properties in different directions for individual soil parameters. For instance, the nests of the root-aphid honeydew feeding *Lasius flavus* contain higher concentrations of nitrogen than the surrounding soil (Dostál *et al.*, 2005). In contrast, the nests of *Formica polyctena*, which utilises honeydew from arboreal aphids as well as being a generalist predator, contain lower concentrations of nitrogen than reference soils (Jílková *et al.*, 2019). Interestingly *L. flavus* nests can also contain less nitrogen than non-nest soils in other study systems (Wu *et al.*, 2015), showing that location, habitat, and other environmental factors can result in contradictory outcomes within the same species. Different, or even the same, species of ants having differing effects on soil properties is not restricted to nitrogen content alone. For example, the nests of *Solonopsis invicta* (generalist) are more acidic than the surrounding soil (Seaman and Marino, 2003) whereas *Atta robusta* nests are more alkaline (Madureira *et al.*, 2013). Because patterns of soil effects are not consistent across species and studies, to properly synthesise the available information on ant effects on soil, aspects of behaviour, ecology and environment should be included in any analysis. By analysing the effects that ant behaviour, ecology and environment have on soil, predictions can be made about the effects on soil of ant species based on their biology.

1.2 Feeding and nesting strategy

Useful categorisation of the biogenic structures created by ants must, in part, be dependent on the framing of the question. Dividing ant nests into types based on architecture alone might lead to categories which do not differ in their potential effects on the soil. To classify the nests of ants in a way most useful for understanding their effect on soil, we suggest a modification of the definitions of Wheeler (1910) and Wheeler and Wheeler (1983), who proposed 1) crater nests, 2) mound or hill nests and 3) nests under stones, logs etc. Crater nests are piles of excavated material or organic waste around the entrance or entrances to the underground portion of the nests. The aboveground portion of the crater nest has no internal structures except for tunnels accessing the belowground portion of the nest and contains no chambers or galleries. Mounds are constructed of soil, sand or organic matter and differ from crater nests in that the superstructure contains galleries and chambers, and therefore is part of the inhabited portion of the nest. Nests under stones, logs etc. are much the same as crater nests, with no superstructure except for excavated debris, but with an object covering the entrance. We suggest that, to understand the relationship between ant nests and the soil, 'Mounds' be further divided into bare mounds (those without thatch) and thatched mounds. Thatched mounds are mounds with an outer layer of organic plant litter that contains little or no mineral soil and is actively maintained by the ants as part of the nest. This layer acts to insulate or waterproof the nest (Jurgensen *et al.*, 2008) resulting in a higher contrast between the internal and external conditions of the nest than bare mounds, while also incorporating more organic matter. Our categories are thus: 1) simple/no mound (incorporating crater nests and nesting under objects), 2) Bare mound (mound lacking thatch), and 3) thatched mound.

We predict that feeding strategy may also impact the effect that ant nests have on soil, so a system for classifying ant diet that is relevant to soil effects is also needed. Ants that store food underground are likely to affect soil differently from those that do not, and the type of food being stored may also have an effect (e.g., seeds vs. fungus farms). Furthermore, the nature of the waste or indigestible material brought into the nest will be dependent on ant diet. Previous synthesis of ant effects on soil focused on making comparisons between one ant functional group (fungus farming) and other ants, and categorised ant feeding strategies accordingly into leafcutter (fungivore), omnivore or granivore (Farji-Brener and Werenkraut, 2017)

The role of ant natural history traits, especially nest structure, represents a gap in the current synthesis of research on the effects that ant nests have on biologically important soil properties. Some of these ecological traits have not been included in past evidence syntheses (nesting structure) while others (feeding strategy) have been unable to capture the level of detail now available due to recent publications (Farji-Brener and Werenkraut, 2017). We conduct an analysis to 1) determine what the overall effects that ant nest have on soil physical and chemical properties, 2) determine how different feeding and nesting strategies moderate this effect, and 3) use this to predict which ant species have large effects on the soil.

2. Methods

Global Ant Database (Parr et al., 2017) divides ant diet into generalist predator, specialist predator, generalist, seed harvester, seed harvester & generalist, sugar feeder & generalist and fungivore. In this study, we opt for a scheme similar to the Global Ant Database, as it is more exhaustive and does not place emphasis on a particular functional group. We add one further subdivision: we split 'sugar feeder & generalist' into two categories to better capture differences in the transfer of sugar resources to the soil: root-aphid sugar feeder and surface (foliar) aphid sugar feeder. Our final feeding categories, once data availability eliminated some, were therefore: 1) generalist, 2) seed harvester, 3) root-aphid sugar feeder, 4) surface-aphid sugar feeder, and 5) fungivore. Literature contributing to the main data set and to the ant traits data are included in Appendix 1 and 2 respectively.

2.1 Data search

Search terms were developed from the key words of preselected relevant literature (Appendix 3), with additional terms selected based on the investigator’s knowledge of the subject and to include the names of certain key variables (e.g. carbon, nitrogen and phosphorus) that are both ecologically important and commonly reported. All our search terms were in English, and we only included papers written in English. These terms were modified to search strings that would give the maximum coverage (e.g., wildcard characters in place of suffixes) within the three databases used to access the literature: Scopus, Web of Science and PubMed (Appendix 4). Multiple literature databases were used to increase coverage because the overlap of results returned by these search engines is not complete (Martín-Martín *et al.*, 2018). Scopus and PubMed were used because they give more repeatable responses across geographical area to the same search queries than Web of science (Pozsgai *et al.*, 2021). All searches were conducted using Mozilla Firefox browser (84.0.1) in private mode so that cookies and search history would not modify the results returned, increasing repeatability, and the search date, time and location can be found in Table S2 (Appendix 4).

2.2 Data screening

Once the lists of results for each search engine had been gathered, the reference lists were downloaded, duplicates removed, and the title and abstracts of the papers were screened for relevance. This was done systematically using a form to compare the title and abstract to predefined criteria (Figure 2.1).

After title and abstract screening, papers were considered for inclusion based on the contents of the full text. They were included if they compared the N, C or P availability of soil samples taken from within, or adjacent to, the nests of soil-dwelling ants with a ‘surrounding soil’ control; however additional variables were recorded if reported. For papers that sampled various positions within and outside the nest, the data from the sample closest to the centre of the nest was used in the ‘nest soil’ category and the data from the sample furthest from the nest was used in the ‘surrounding soil’ category, except in cases where the furthest sample from the nest was in identifiably different conditions or habitat (e.g. in forest of a different age class), in which case the furthest sample point from the nest in the same site as the nest was used. Likewise, where studies examined the effects of ants on soil in identifiably different conditions (e.g., in forests or different age classes or agricultural vs. natural environment) the treatments were included as separate studies. Although this partially

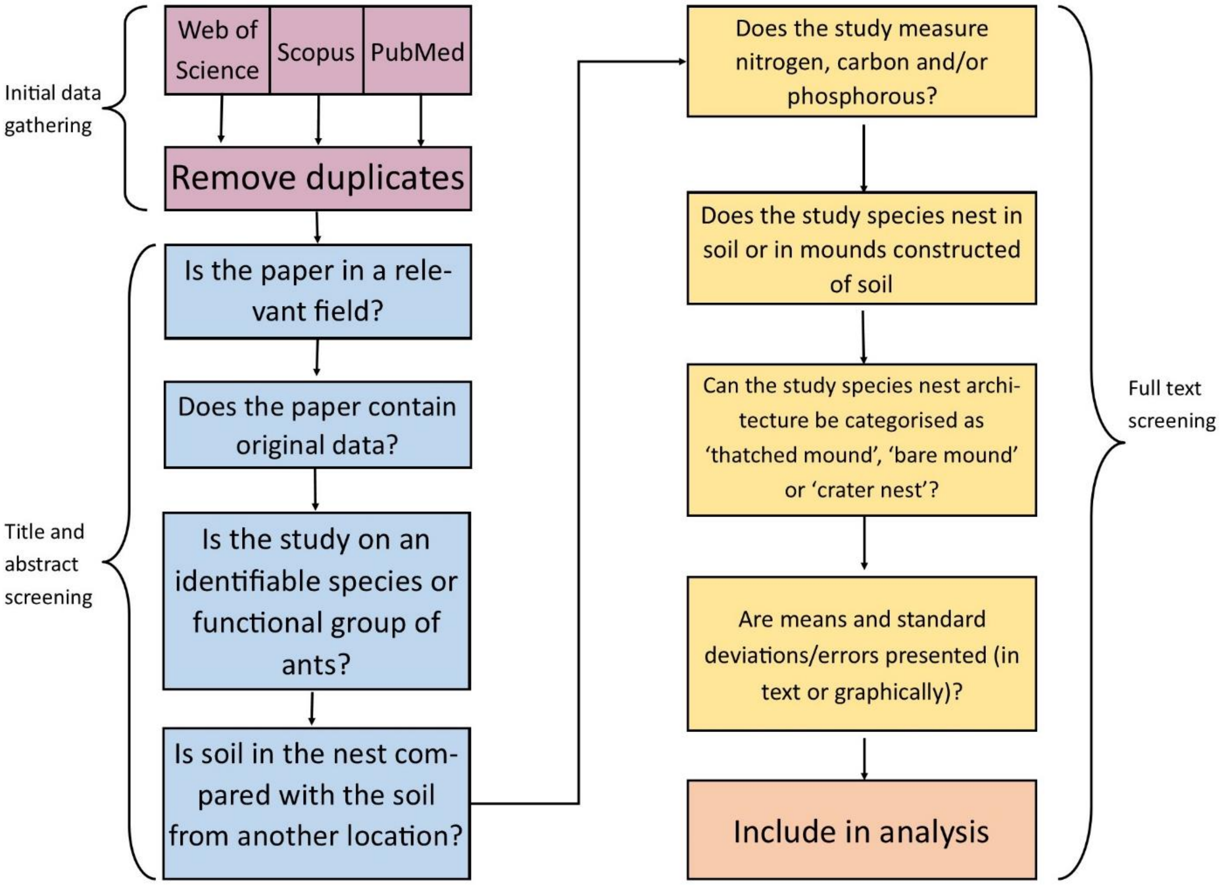

Figure 2.1. The steps of abstract screening and full text screening that was applied to the papers.

breaches the independence of the studies, it is a compromise that allows for a greater sample size and avoids pooling effect sizes that belong to different populations with different mean effect sizes. In the event that the same site was sampled at multiple time points in a study, the last time point was used to reduce the possibility that the nest was newly founded at the beginning of the study, in case the effects of ant on soil increases with time of occupancy. For papers that report multiple depths, we recorded the shallowest subsurface depth.

Because our hypotheses relate to specific ant nesting and feeding traits, we could only include studies that either: a) directly reported the feeding and or nesting biology of the ants at the study site, b) reported the species studied so that the traits could be assigned later (probabilistically for species that exhibit multiple different feeding or nesting strategies in different contexts) or c) reported the species group for species groups that display the same feeding and nesting biology. The trait as reported in the study was always given precedence over the species biology as it appears in other literature, as it was assumed that the description in the study would better reflect the reality at the study location. In fact, feeding strategy was almost never reported in sufficient detail in the studies included, but the nests were adequately described to assign to one of our categories in 71% of studies.

We also recorded taxonomic information, the location of the study, elevation of the site, whether the site was a disturbed habitat or not and whether the ant was in its native range. The location was used to assign the study site to one of the terrestrial ecoregions (henceforth: biomes) according to Olson et al., 2001.

2.3 Data extraction

Each study of ant nest effects on soil was paired with data on the nesting and feeding strategy of the species of ant, from the focal paper if available, otherwise from wider literature (Appendix 2). Where the species: i) adopts multiple nesting strategies and ii) the nest type of the sampled nests was not clear from the original paper, then each nesting strategy used by the species was included as a separate line of data and given a weighting in the final meta-analyses equal to 1 divided by the number of strategies used by the species. Feeding strategy was treated similarly; however, if more than two feeding strategies were commonly reported, these species were assigned the 'generalist' trait.

During the initial data gathering, a separation was made between 'crater nests' and 'nests in soil under objects', following the nomenclature of (Wheeler and Wheeler, 1983). We took the decision to combine these two nesting strategies into the new category of 'no above ground nest structure' (in figures, these are labelled 'simple/no mound' for brevity) for several reasons. Firstly, in the context of potential effects on the soil, there is no ecological reason to think that the two nest types should differ; they are structurally the same, with all of the habitable space belowground, except for the presence of the object covering the entrance in the case of ‘nests in soil under objects’. Secondly, because the type of nest structure was not directly reported in 29% of studies used for the meta-analysis, we would necessarily assign ‘nests in soil under objects’ to a species within a study because this had been reported elsewhere without evidence from the focal study in some cases. Soil sampling with corers in ‘nests in soil under objects’ requires removing the object and seriously disrupting then nest, which would probably be reported in the focal study. As a result, we think it likely that, where the nest type was unreported in the focal study and there is uncertainty whether the nest was ‘crater nests’ or ‘nests in soil under objects’, ‘crater nest’ is more likely. Because this complicates assigning the nest type probabilistically for these two categories, we took the decision to combine them. Finally, by combining these two categories, we increase the sample size of the combined category, resulting in a design that is closer to balanced.

The three main target variables for this meta-analysis were soil N, C and P concentrations, which are commonly measured and ecologically important. We additionally extracted data for other soil properties where they were reported in papers that had passed the screening process. Finally, variables for which we had fewer than 10 replicates (studies) were not analysed. This process left us 12 variables with at least 10 replicates (Table 2.1). For each variable, we calculated Hedge’s g as the measure of effect size because we had sample sizes below 20 for several of our variables.

2.4 Non-independence

Some studies contributed multiple effect sizes to the model. Where a study investigated the effect of multiple species of ant on nest soils, or where multiple sites were sampled that were in different habitats, we did not pool the effect sizes from the study. In cases where multiple species' nest soils were compared to a single reference soil, we risk double counting the control group in this study, causing our pooled effect size to be disproportionately influenced by it. To address this, we divided the sample size of the shared controls by the number of studies they were shared between. Because the reason for not pooling these study effect sizes is because it would either compromise our ability to test our hypotheses (species) or because the separate within-study effect sizes were considered too independent to justify pooling them, we think that this method of managing shared control groups is adequate, despite it not directly addressing the assumption of independence of studies. In order to identify potential publication bias, we inspected funnel plots and tested for asymmetry using Egger's regression test on the effect sizes.

2.5 The model

Our hypothesis was that there would be different effect sizes for populations representing subgroups of ant species with similar feeding and/or nesting strategies. Additionally, we assumed that biome affects soil modification by ants and that nesting and feeding strategy are both taxonomically and regionally biased (Farji-Brener and Werenkraut, 2017). Therefore, in addition to our main hypotheses, we predicted that ant traits (nesting and feeding strategy) would not be independent of biome (fungivory is restricted to the tropics, for example). Because Chi-squared test of independence is sensitive to small sample sizes (some biomes contained fewer than 5 studies) we tested for independence of biome and trait with both Chi-squared and Fisher's exact tests. We examined studies from different regions and species (with different traits), and thus different mean effect sizes, so we used a multilevel model that allowed us to include variability that is not due to individual study sampling error.

2.5.1 Between-study heterogeneity

To account for between-study heterogeneity that may result from taxonomic proximity, or data from the same study, the citations (first author and year) and genus were included as random terms in the three-level model, while nesting and feeding strategy were included as subgrouping variables to allow us to determine how differences in ant ecology impacts soil outcomes. The result was a multi-level model of soil properties with both nesting strategy and feeding strategy as subgroup predictor variables and citation and genus as random effect grouping variables. We used the R package 'esc' version 0.5.0 (Lüdecke, 2019) to calculate Hedges g and 'metafor' version 4.0-0 (Viechtbauer, 2010) to construct our model. The model was fitted using restricted maximum likelihood method. We also fitted a reduced (two-level) model to compare against the Akaike information criterion (AIC) and used a likelihood ratio test to determine if the full model better explained the between-study heterogeneity.

3. Results

3.1 Model selection

After screening the data for inclusion, we had a total of 12 soil variables with sufficient data to include in the analysis: total N, NH_4-N, NO_{3}-N, total C, organic C, total P, available P, pH, Ca, K, Mg, and Na (Table 2.1). Data were tested for independence of nesting/feeding strategies from biome and from each other. The results of both Chi-squared test of independence and Fisher's exact test were significant ($p<0.01$) for all three combinations of biome and strategy, so it is highly likely that these variables were not independent of one another, corroborating visual inspection of the data (Figure 2.7), which should be taken into account when interpreting model results, The full model (with clustering variables of 'citation' and ant genus) had a lower AIC and the likelihood ratio test was significant ($p<0.05$) for the soil variables total N, total C, total P and nitrate (NO_3) N. For all other soil variables, the inclusion of genus and citation as clustering variables did not improve the performance of the model, so the reduced models (cluster variance fixed at 0) were used in all subsequent analyses for these variables.

3.2 Sources of heterogeneity

Of the variables that we fitted to the full model (allowing for between cluster variance), the level 3 variance and I^2 (the percentage of variation due to heterogeneity) for genus as the clustering variable was low (<0.001) for total N and total P, while for total C, nitrate-N the level 3 variance and I^2 for citation clusters (first author and date) were larger than for genus (Table 2.3). This indicates that taxonomy contributed little to heterogeneity, whereas the experimenter/research group may have been a major source of heterogeneity.

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Table 2.1. Only certain combinations of feeding and nesting strategy were available in the data; however, most of those available were represented by data for multiple variables. The numbers in the table represent the number of 'studies' contained in our dataset for each variable. Some papers contributed more than one 'study' if they contained data on multiple species.

Nesting strategy	**Feeding strategy**	**Ca**	**K**	**Mg**	**Na**	**pH**	**Total C**	**Total N**	**Total P**	**Organic C**	**NH_4-N**	**NO_3-N**	**Available P**	**Available N**	**Total**
Bare mound	Aphid + generalist	2	2	1	1	2	0	0	0	0	0	0	0	0	8
Bare mound	Fungivore	6	7	8	5	5	6	6	5	3	5	7	0	0	63
Bare mound	Generalist	9	13	3	7	10	8	10	7	5	12	10	4	0	98
Bare mound	Root aphid + generalist	4	4	5	8	10	5	7	4	3	10	7	4	2	73
Bare mound	Seed harvester	1	1	1	0	1	1	2	1	1	1	2	0	0	12
No aboveground structure	Aphid + generalist	0	0	0	1	1	1	1	1	1	1	1	0	0	8
No aboveground structure	Fungivore	0	0	0	0	0	0	0	0	0	1	1	0	0	2
No aboveground structure	Generalist	7	10	0	2	8	8	8	4	1	9	12	2	0	71
No aboveground structure	Seed harvester	0	0	0	2	3	2	2	2	2	3	3	0	0	19
Thatched mound	Fungivore	0	0	1	0	1	0	0	0	0	1	1	0	0	4
Thatched mound	Generalist	3	3	0	4	3	1	1	1	0	3	2	2	0	23
Total		32	40	19	30	44	32	37	25	16	46	46	12	2	

Table 2.2. For each variable, a 3 level (full) and 2 level (reduced) model was constructed and these models were compared using a likelihood ratio test (LRT) and Akaike Information Criterion (AIC). The better performing model is highlighted in each case, and this model was used for subsequent interpretation (Table 2.3).

Variable	Model	AIC	LRT	p-value
Total N	**Full**	157.440	6.622	0.036 *
	Reduced	160.062		
Total C	**Full**	149.937	7.119	0.028 *
	Reduced	153.056		
Total P	**Full**	164.019	6.255	0.044 *
	Reduced	166.274		
Available P	Full	55.929	0.057	0.972
	Reduced	51.987		
Organic C	Full	82.250	<0.001	≈1.000
	Reduced	78.250		
NH_4-N	Full	124.286	1.962	0.375
	Reduced	122.248		
NO_3-N	**Full**	133.028	5.649	0.059 .
	Reduced	134.676		
pH	Full	167.610	0.131	0.937
	Reduced	163.740		
Ca	Full	86.252	3.834	0.147
	Reduced	86.086		
K	Full	102.868	<0.001	≈1.000
	Reduced	98.868		
Mg	Full	66.639	0.394	0.821
	Reduced	63.033		
Na	Full	43.767	0.337	0.845
	Reduced	40.104		

Table 2.3. The effect sizes (Hedge's g) were calculated for subgroups (feeding and nesting strategy) with genus and citation (first author and year) as random clusters, resulting in a three level subgroup analysis model. Full (three level) and reduced (two level) models were compared (Table 2.2) and the best performing model for each variable is presented. Within and between cluster variance are presented, and correspond to I^2, indicating the distribution of variance across levels; the level 2 I^2 represents the percentage of variation due to differences in true effect sizes (i.e. not sampling error) within clusters, and level 3 I^2 is the percentage due to between cluster variation. The intercept of each model represents the combination of 'Generalist' feeding strategy and 'Bare mound' as nesting strategy. A *p*-value <0.05 in an 'intercept' row indicates that the intercept is significantly different from zero, while *p*<0.05 in a non-intercept row indicates a significant difference between the subgroup and the intercept. Where *p* (subgroup) is less than 0.05 there are significant differences between subgroups not including the intercept subgroups. Pairwise comparisons of the subgroups are included in Table 2.5.

Variable	**Model**	**Subgroup**	**Estimate**	**Z value**	**95% CI**		**Between cluster variance**		**Within cluster variance**	**I^2**			***p*-value**	***p* (subgroup)**
					Lower	**Upper**	**Citation**	**Genus**		**Level 3 (citation)**	**Level 3 (genus)**	**Level 2**		
Total N	Full	Intercept	0.304	0.729	-0.538	1.146	1.169	<0.001	0.091	67.774	<0.001	5.256	0.470	0.154
		Simple/no mound	-0.427	-0.779	-1.536	0.681							0.441	
		Thatched mound	1.117	1.423	-0.470	2.704							0.163	
		Surface aphids + generalist	-0.529	-0.724	-2.007	0.948							0.473	
		Fungivore	0.254	0.386	-1.075	1.582							0.701	
		Root aphids + generalist	-0.923	-1.939	-1.885	0.039							0.060 .	
		Seed harvester	0.447	0.563	-1.158	2.052							0.576	
Total C	Full	Intercept	1.024	1.305	-0.583	2.631	1.763	1.076	0.010	53.926	32.903	0.300	0.202	0.576
		Simple/no mound	0.356	0.335	-1.819	2.532							0.740	
		Thatched mound	1.915	1.513	-0.678	4.508							0.142	
		Surface aphids + generalist	-1.262	-1.151	-3.506	0.983							0.259	
		Fungivore	-1.186	-0.945	-3.758	1.385							0.353	
		Root aphids + generalist	-0.793	-1.184	-2.164	0.579							0.246	
		Seed harvester	-0.870	-0.599	-3.848	2.107							0.554	

Table 2.3. The effect sizes (Hedge's g) were calculated for subgroups (feeding and nesting strategy) with genus and citation (first author and year) as random clusters, resulting in a three level subgroup analysis model. Full (three level) and reduced (two level) models were compared (Table 2.2) and the best performing model for each variable is presented. Within and between cluster variance are presented, and correspond to I^2, indicating the distribution of variance across levels; the level 2 I^2 represents the percentage of variation due to differences in true effect sizes (i.e. not sampling error) within clusters, and level 3 I^2 is the percentage due to between cluster variation. The intercept of each model represents the combination of 'Generalist' feeding strategy and 'Bare mound' as nesting strategy. A *p*-value <0.05 in an 'intercept' row indicates that the intercept is significantly different from zero, while *p*<0.05 in a non-intercept row indicates a significant difference between the subgroup and the intercept. Where *p* (subgroup) is less than 0.05 there are significant differences between subgroups not including the intercept subgroups. Pairwise comparisons of the subgroups are included in Table 2.5.

Variable	**Model**	**Subgroup**	**Estimate**	**Z value**	**95% CI**		**Between cluster variance**		**Within cluster variance**	**I^2**			***p*-value**	***p* (subgroup)**
					Lower	**Upper**	**Citation**	**Genus**		**Level 3 (citation)**	**Level 3 (genus)**	**Level 2**		
Total P	Full	Intercept	1.097	2.067	0.021	2.173	2.359	<0.001	0.179	79.685	<0.001	6.035	0.046 *	0.499
		Simple/no mound	-0.093	-0.158	-1.281	1.096							0.875	
		Thatched mound	1.872	1.600	-0.501	4.246							0.118	
		Surface aphids + generalist	-0.863	-1.438	-2.080	0.354							0.159	
		Fungivore	-0.415	-0.594	-1.833	1.002							0.556	
		Root aphids + generalist	0.342	0.460	-1.165	1.849							0.648	
		Seed harvester	0.239	0.292	-1.421	1.900							0.772	
Available P	Reduced	Intercept	2.412	2.315	0.055	4.768	0.000 (fixed)	0.000 (fixed)	1.764	0.000 (fixed)	0.000 (fixed)	43.656	0.046 *	0.304
		Simple/no mound	0.105	0.059	-3.948	4.158							0.955	
		Thatched mound	-0.593	-0.383	-4.101	2.914							0.711	
		Root aphids + generalist	-2.676	-1.819	-6.005	0.653							0.102	

Table 2.3. The effect sizes (Hedge's g) were calculated for subgroups (feeding and nesting strategy) with genus and citation (first author and year) as random clusters, resulting in a three level subgroup analysis model. Full (three level) and reduced (two level) models were compared (Table 2.2) and the best performing model for each variable is presented. Within and between cluster variance are presented, and correspond to I^2, indicating the distribution of variance across levels; the level 2 I^2 represents the percentage of variation due to differences in true effect sizes (i.e. not sampling error) within clusters, and level 3 I^2 is the percentage due to between cluster variation. The intercept of each model represents the combination of 'Generalist' feeding strategy and 'Bare mound' as nesting strategy. A *p*-value <0.05 in an 'intercept' row indicates that the intercept is significantly different from zero, while *p*<0.05 in a non-intercept row indicates a significant difference between the subgroup and the intercept. Where *p* (subgroup) is less than 0.05 there are significant differences between subgroups not including the intercept subgroups. Pairwise comparisons of the subgroups are included in Table 2.5.

Variable	**Model**	**Subgroup**	**Estimate**	**Z value**	**95% CI**		**Between cluster variance**		**Within cluster variance**	**I^2**			***p*-value**	***p* (subgroup)**
					Lower	**Upper**	**Citation**	**Genus**		**Level 3 (citation)**	**Level 3 (genus)**	**Level 2**		
Organic C	Reduced	Intercept	1.326	0.908	-1.828	4.479	0.000 (fixed)	0.000 (fixed)	2.521	0.000 (fixed)	0.000 (fixed)	43.416	0.380	0.505
		Thatched mound	2.689	1.085	-2.666	8.045							0.298	
		Surface aphids + generalist	-2.490	-0.859	-8.749	3.770							0.406	
		Fungivore	-2.218	-1.292	-5.926	1.491							0.219	
		Root aphids + generalist	-2.880	-1.596	-6.778	1.018							0.134	
		Seed harvester	0.162	0.059	-5.728	6.052							0.954	
NH^4-N	Reduced	Intercept	1.231	2.202	0.077	2.386	0.000 (fixed)	0.000 (fixed)	0.955	0.000 (fixed)	0.000 (fixed)	37.389	0.038 *	0.035 *
		Simple/no mound	1.591	1.576	-0.492	3.674							0.128	
		Thatched mound	2.148	1.398	-1.024	5.321							0.175	
		Surface aphids + generalist	-1.672	-1.129	-4.727	1.383							0.270	
		Fungivore	-1.334	-1.480	-3.193	0.526							0.152	
		Root aphids + generalist	-1.893	-1.790	-4.075	0.290							0.086 .	
		Seed harvester	3.214	1.712	-0.659	7.087							0.100	

Table 2.3. The effect sizes (Hedge’s g) were calculated for subgroups (feeding and nesting strategy) with genus and citation (first author and year) as random clusters, resulting in a three level subgroup analysis model. Full (three level) and reduced (two level) models were compared (Table 2.2) and the best performing model for each variable is presented. Within and between cluster variance are presented, and correspond to I^2, indicating the distribution of variance across levels; the level 2 I^2 represents the percentage of variation due to differences in true effect sizes (i.e. not sampling error) within clusters, and level 3 I^2 is the percentage due to between cluster variation. The intercept of each model represents the combination of ‘Generalist’ feeding strategy and ‘Bare mound’ as nesting strategy. A *p*-value <0.05 in an ‘intercept’ row indicates that the intercept is significantly different from zero, while *p*<0.05 in a non-intercept row indicates a significant difference between the subgroup and the intercept. Where *p* (subgroup) is less than 0.05 there are significant differences between subgroups not including the intercept subgroups. Pairwise comparisons of the subgroups are included in Table 2.5.

Variable	**Model**	**Subgroup**	**Estimate**	**Z value**	**95% CI**		**Between cluster variance**		**Within cluster variance**	**I^2**			***p*-value**	***p* (subgroup)**
					Lower	**Upper**	**Citation**	**Genus**		**Level 3 (citation)**	**Level 3 (genus)**	**Level 2**		
NO^3-N	Full	Intercept	1.226	2.586	0.260	2.192	1.318	0.315	<0.001	64.119	15.332	<0.001	0.014 *	0.123
		Simple/no mound	0.064	0.102	-1.211	1.338							0.920	
		Thatched mound	1.237	1.312	-0.684	3.159							0.199	
		Surface aphids + generalist	-1.035	-1.726	-2.257	0.187							0.094 .	
		Fungivore	-0.170	-0.215	-1.783	1.443							0.831	
		Root aphids + generalist	-0.994	-1.513	-2.331	0.344							0.140	
		Seed harvester	4.374	2.327	0.545	8.203							0.026 *	
pH	Reduced	Intercept	-0.439	-1.044	-1.289	0.412	0.000 (fixed)	0.000 (fixed)	0.882	0.000 (fixed)	0.000 (fixed)	42.593	0.303	0.001 *
		Simple/no mound	0.706	1.154	-0.533	1.945							0.256	
		Thatched mound	1.263	1.337	-0.649	3.175							0.189	
		Surface aphids + generalist	0.560	0.663	-1.150	2.270							0.511	
		Fungivore	0.383	0.554	-1.015	1.780							0.583	
		Root aphids + generalist	3.128	4.915	1.840	4.417							<0.001 *	
		Seed harvester	-0.804	-0.935	-2.544	0.936							0.356	

Table 2.3. The effect sizes (Hedge's g) were calculated for subgroups (feeding and nesting strategy) with genus and citation (first author and year) as random clusters, resulting in a three level subgroup analysis model. Full (three level) and reduced (two level) models were compared (Table 2.2) and the best performing model for each variable is presented. Within and between cluster variance are presented, and correspond to I^2, indicating the distribution of variance across levels; the level 2 I^2 represents the percentage of variation due to differences in true effect sizes (i.e. not sampling error) within clusters, and level 3 I^2 is the percentage due to between cluster variation. The intercept of each model represents the combination of 'Generalist' feeding strategy and 'Bare mound' as nesting strategy. A *p*-value <0.05 in an 'intercept' row indicates that the intercept is significantly different from zero, while *p*<0.05 in a non-intercept row indicates a significant difference between the subgroup and the intercept. Where *p* (subgroup) is less than 0.05 there are significant differences between subgroups not including the intercept subgroups. Pairwise comparisons of the subgroups are included in Table 2.5.

Variable	**Model**	**Subgroup**	**Estimate**	**Z value**	**95% CI**		**Between cluster variance**		**Within cluster variance**	**I^2**			***p*-value**	***p* (subgroup)**
					Lower	**Upper**	**Citation**	**Genus**		**Level 3 (citation)**	**Level 3 (genus)**	**Level 2**		
Ca	Reduced	Intercept	-0.083	-0.216	-0.882	0.715	0.000 (fixed)	0.000 (fixed)	0.404	0.000 (fixed)	0.000 (fixed)	39.791	0.831	0.379
		Simple/no mound	-0.300	-0.491	-1.568	0.968							0.628	
		Thatched mound	1.592	1.134	-1.319	4.502							0.269	
		Surface aphids + generalist	0.668	0.980	-0.746	2.082							0.338	
		Fungivore	0.021	0.036	-1.202	1.244							0.972	
		Root aphids + generalist	1.020	1.683	-0.237	2.276							0.106	
		Seed harvester	0.705	0.945	-0.842	2.253							0.355	
K	Reduced	Intercept	0.900	2.615	0.194	1.606	0.000 (fixed)	0.000 (fixed)	0.420	0.000 (fixed)	0.000 (fixed)	39.636	0.014 *	0.064 .
		Simple/no mound	-0.635	-1.081	-1.840	0.570							0.289	
		Thatched mound	2.842	1.701	-0.586	6.270							0.100	
		Surface aphids + generalist	0.487	0.716	-0.909	1.883							0.480	
		Fungivore	-0.748	-1.303	-1.926	0.430							0.203	
		Root aphids + generalist	0.875	1.667	-0.202	1.951							0.107	
		Seed harvester	0.784	1.159	-0.603	2.171							0.257	

Table 2.3. The effect sizes (Hedge's g) were calculated for subgroups (feeding and nesting strategy) with genus and citation (first author and year) as random clusters, resulting in a three level subgroup analysis model. Full (three level) and reduced (two level) models were compared (Table 2.2) and the best performing model for each variable is presented. Within and between cluster variance are presented, and correspond to I^2, indicating the distribution of variance across levels; the level 2 I^2 represents the percentage of variation due to differences in true effect sizes (i.e. not sampling error) within clusters, and level 3 I^2 is the percentage due to between cluster variation. The intercept of each model represents the combination of 'Generalist' feeding strategy and 'Bare mound' as nesting strategy. A *p*-value <0.05 in an 'intercept' row indicates that the intercept is significantly different from zero, while *p*<0.05 in a non-intercept row indicates a significant difference between the subgroup and the intercept. Where *p* (subgroup) is less than 0.05 there are significant differences between subgroups not including the intercept subgroups. Pairwise comparisons of the subgroups are included in Table 2.5.

Variable	**Model**	**Subgroup**	**Estimate**	**Z value**	**95% CI**		**Between cluster variance**		**Within cluster variance**	**I^2**			***p*-value**	***p* (subgroup)**
					Lower	**Upper**	**Citation**	**Genus**		**Level 3 (citation)**	**Level 3 (genus)**	**Level 2**		
Mg	Reduced	Intercept	0.197	0.536	-0.586	0.979	0.000 (fixed)	0.000 (fixed)	0.231	0.000 (fixed)	0.000 (fixed)	29.874	0.600	0.576
		Simple/no mound	0.151	0.231	-1.237	1.538							0.820	
		Thatched mound	1.959	1.520	-0.789	4.706							0.149	
		Surface aphids + generalist	-0.954	-1.107	-2.792	0.884							0.286	
		Fungivore	-0.023	-0.041	-1.205	1.160							0.968	
		Root aphids + generalist	-0.499	-0.891	-1.693	0.695							0.387	
		Seed harvester	0.372	0.529	-1.127	1.871							0.605	
Na	Reduced	Intercept	0.869	2.061	-0.085	1.822	0.000 (fixed)	0.000 (fixed)	0.199	0.000 (fixed)	0.000 (fixed)	33.177	0.069 .	0.563
		Simple/no mound	0.689	0.834	-1.180	2.558							0.426	
		Surface aphids + generalist	-1.566	-1.680	-3.675	0.543							0.127	
		Fungivore	-0.973	-1.563	-2.382	0.435							0.153	
		Root aphids + generalist	-0.567	-0.918	-1.965	0.830							0.383	
		Seed harvester	-0.860	-1.063	-2.690	0.970							0.316	

3.3 Meta-analytic effect sizes

These models provided us with effect sizes for the difference between nest soils and non-nest soils for each study and pooled effect sizes for each variable, as well as 95% confidence intervals. For every variable, there were studies that provided positive and negative effect sizes and no variable had studies that unanimously indicated one direction of effect (Appendix 6). The pooled effect sizes for K, ammonium-N, nitrate-N, pH, available P and total P were all significantly different from 0 ($p<0.05$; Figure 2.2; Table 2.4) and positive, indicating that the concentrations of these nutrients were higher in ant nests than in the surrounding soil (or that the nest soils were more alkaline in the case of pH). Only organic carbon had a pooled effect size of less than zero, and this was not significantly different from zero.. All variables with effect sizes significantly different from 0 had either medium ($g>0.5$) or large ($g>0.8$) effect sizes based on standard conventions for Hedge’s g (Cohen, 1988).

From the model that included nesting and feeding strategies as subgrouping variables we estimated the intercept (bare mound generalist) from the model and tested whether it was significantly different from 0. In addition, the estimate of the effect of non-intercept subgroups on the overall estimate and the p-value indicating the significance of the difference between the subgroup estimate and the intercept were provided by the model (Table 2.3). This allowed us to calculate the overall effect of each subgroup on the estimate (Figures 2.3-2.6).

3.3.1 Subgroups: nesting strategy

As the nesting strategy that was most well represented in the data set, the pooled effect size for the bare mound subgroup was close to the overall pooled estimate for each variable, so it was used as the intercept in our subgroup models. The pooled effect size was large ($g>0.8$) and positive for the variables total C and P, organic C, ammonium-N, nitrate-N, K and Na; however, none of the pairwise comparisons between nest subgroups were significant ($p<0.05$; Table 2.5; Figures 2.3-2.6). The pooled effect size in this subgroup for total N was small and positive. The effect size for pH in this subgroup was negative (that is, nests were more acidic than surrounding soils) in contrast to other nest types, but small ($0.2<g<0.5$). The same pattern of large positive effects was present for thatched

Table 2.4. The effect sizes (Hedge's g) for all studies were pooled for each variable. The column 'n (of effect sizes)' contains the number of studies that contributed to the pooled effect size. Studies in this case are defined as the combination of paper/species/site (i.e., a paper that investigated the effect of multiple species of ants on soil, or in very different geographical locations, would contribute more than one effect size to the pooled effect). Total sample size is the sum of individual study sample sizes included in the pooled effect. *p*<0.05 indicate that the observed pooled effect size is significantly different from 0.

Variable	**g**	**95% CI**		***p*-value**	**n (of effect sizes)**	**Total sample size**
		Upper	**Lower**			
Total N	0.256	0.795	-0.284	0.345	47	366
Total P	1.107	1.780	0.433	0.002 *	43	527
Total C	0.572	1.533	-0.389	0.235	35	334
Nitrate-N	1.188	1.989	0.387	0.005 *	39	280
Organic C	-0.456	0.710	-1.622	0.422	19	118
pH	0.698	1.265	0.131	0.017 *	45	475
K	1.031	1.444	0.619	<0.001 *	34	456
Mg	0.178	0.511	-0.155	0.278	22	181
Ca	0.270	0.678	-0.138	0.186	29	364
Na	0.306	0.684	-0.072	0.104	16	238
Ammonium-N	1.080	1.812	0.349	0.005 *	31	171
Available P	1.477	2.699	0.254	0.022 *	13	128

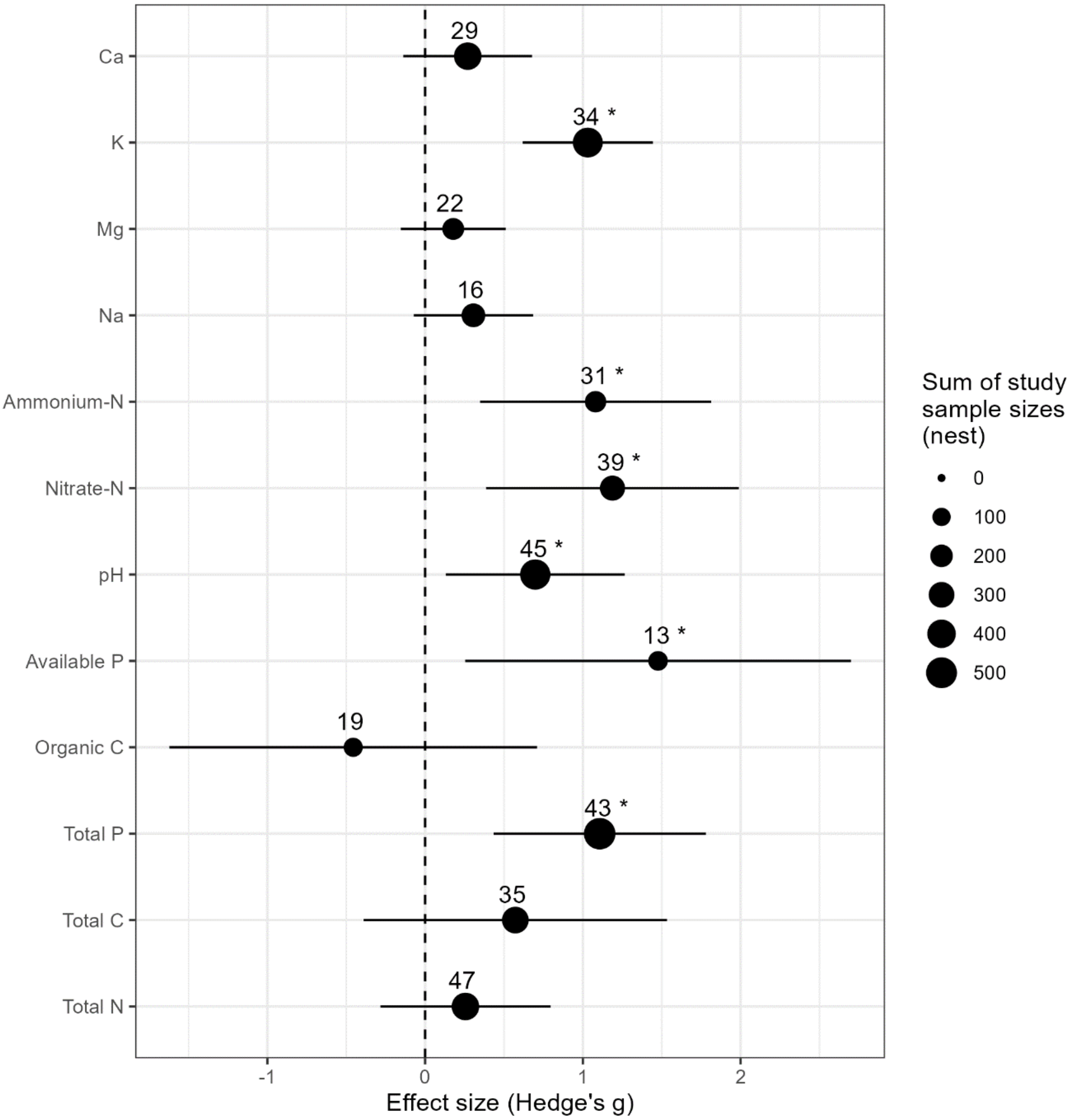


Figure 2.2. Calculated pooled meta-analytic effect sizes (Hedge's g) of the entire data set (no subgroups) for all study variables. Numbers above each data point indicate the number of effect sizes included in the pooled effect size and the radius of each point indicates the sum of the sample sizes (of nest samples). Asterisks indicate pooled effect sizes that were significantly different ($p<0.05$) from 0 (dashed line) and horizontal lines represent 95% confidence intervals.

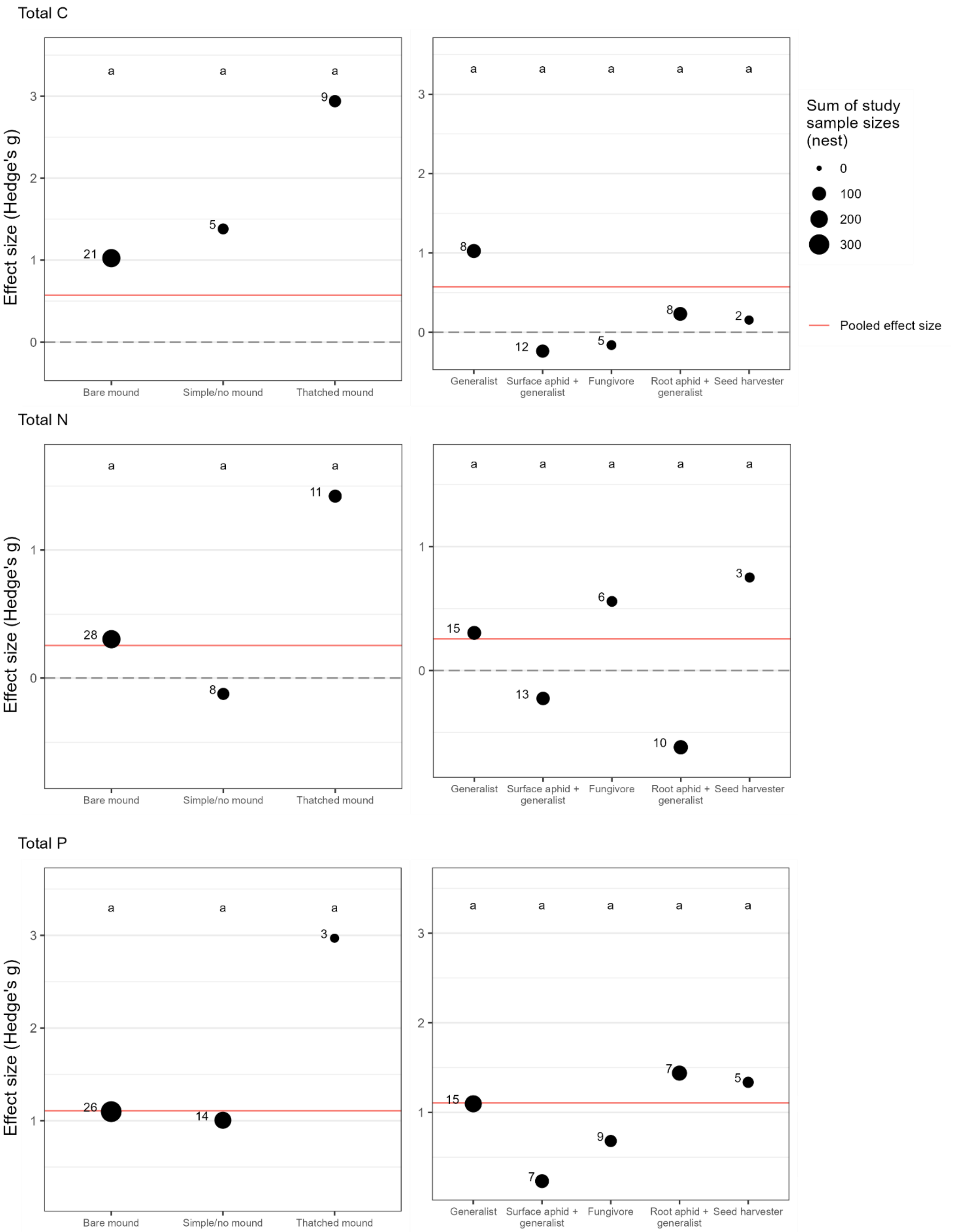


Figure 2.3. Model calculated pooled meta-analytic effect sizes (Hedge's g) for the variables total P, total N and total C for the subgroups of nesting strategy and feeding strategy. Plots on the left show pooled effect sizes for each subgroup of nesting strategy (assuming feeding strategy is 'generalist') and plots of the right show the pooled effect sizes of each subgroup of feeding strategy (assuming nesting strategy is 'bare mound'). The numbers annotating each point indicate the number of effect sizes included in the pooled effect size and the size of the points indicates the sum of sample sizes (of nest samples). Letters at the top of each figure indicate whether subgroups are significantly different ($p<0.05$) with differing letters based on pairwise Tukey comparisons (adjusted). Pairwise with $0.05 < p < 0.1$ are also included in Table 2.5. The dashed line at 0 (no effect) provides reference while the salmon line is the pooled effect size for all studies for all subgroups of both nesting and feeding strategy (total P based on 43 effect sizes from 30 studies, total sample size 527; total N based on 47 effect sizes from 28 studies, total sample size 366; total C based on 35 effect sizes from 20 studies, total sample size 334).

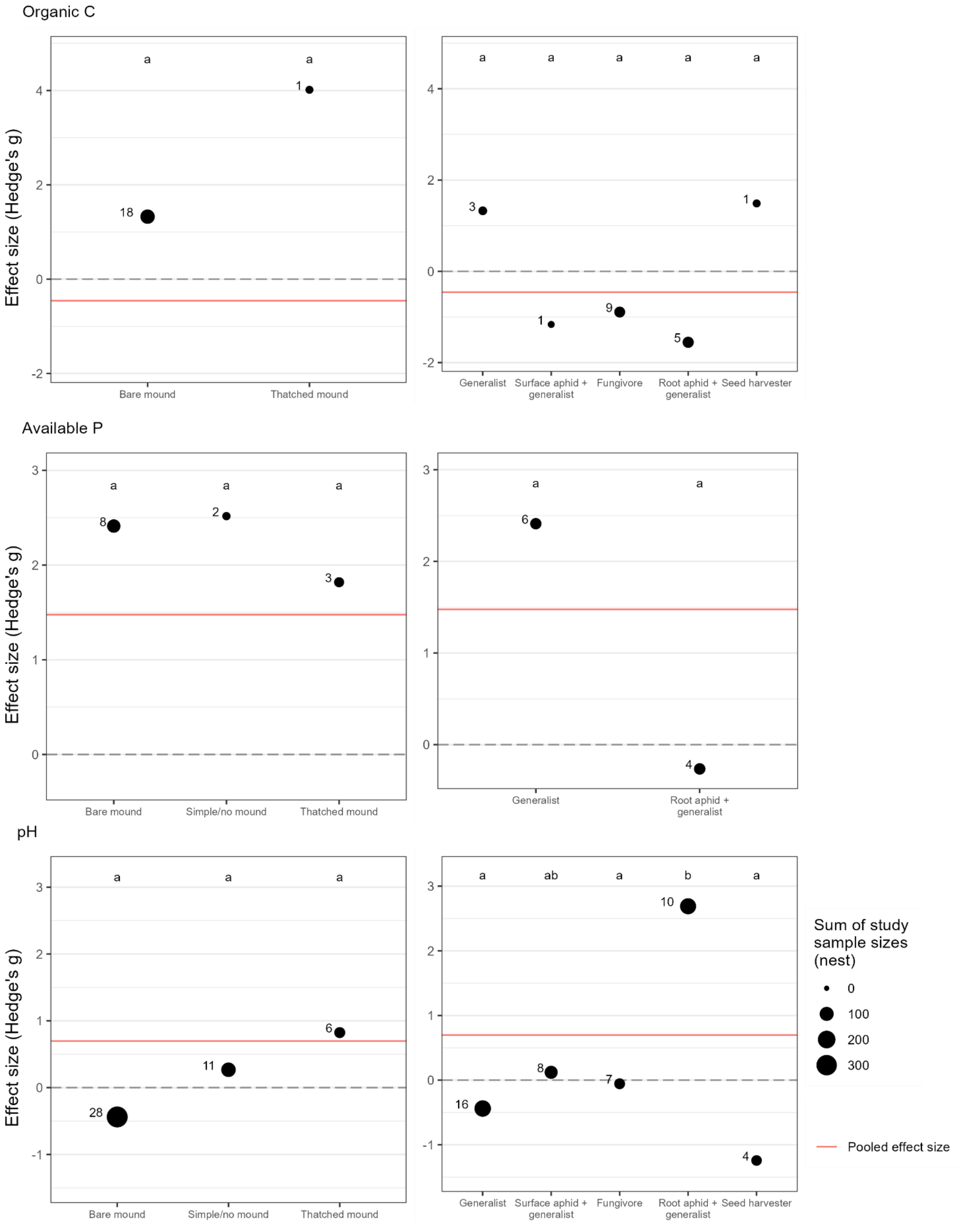


Figure 2.4. We calculated pooled meta-analytic effect sizes (Hedge's g) of variables available P, organic C and pH for the subgroups of nesting strategy and feeding strategy within our model. Plots on the left show the pooled effect sizes for each subgroup of nesting strategy (assuming feeding strategy is 'generalist') and plots of the right show the pooled effect sizes of each subgroup of feeding strategy (assuming nesting strategy is 'bare mound'). The numbers annotating the points indicate the number of effect sizes included in the pooled effect size and the size of the points indicates the sum of the sample sizes (of nest samples) in those studies. Letters above the subgroups indicate that the subgroup is significantly different ($p<0.05$) for subgroups with differing letters based on pairwise Tukey comparisons (adjusted). Pairwise with $0.05 < p < 0.1$ are also included in Table 2.5. There is a dashed line is at 0 (no effect) for reference and the salmon line is the pooled effect size for all studies for all subgroups of both nesting and feeding strategy (organic C based on 19 effect sizes from 10 studies, total sample size 118; available P based on 13 effect sizes from 8 studies, total sample size 128; pH based on 45 effect sizes from 30 studies, total sample size 475).

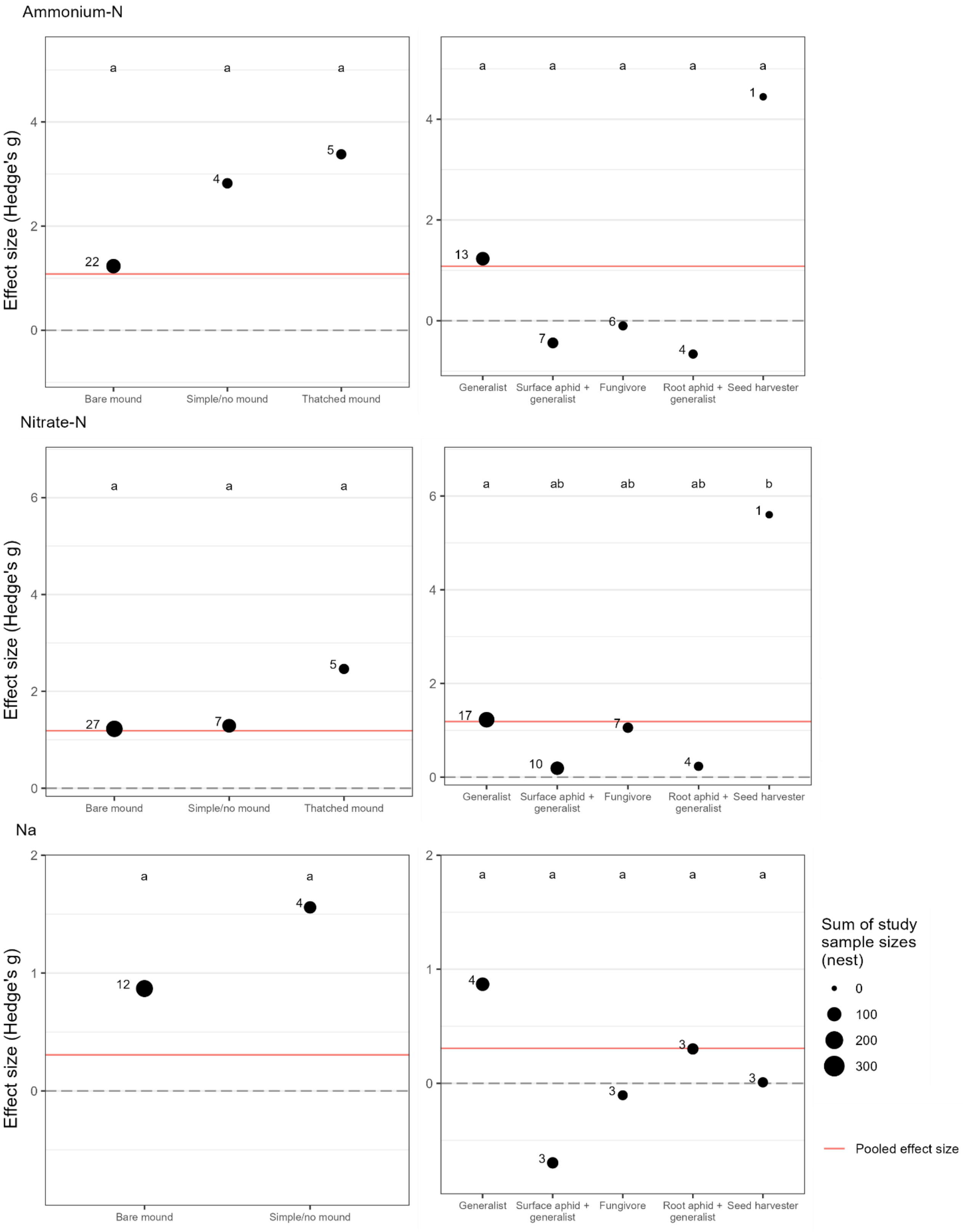


Figure 2.5. We calculated pooled meta-analytic effect sizes (Hedge's g) of variables ammonium-N, nitrate-N and Na for the subgroups of nesting strategy and feeding strategy within our model. Plots on the left show the pooled effect sizes for each subgroup of nesting strategy (assuming feeding strategy is 'generalist') and plots of the right show the pooled effect sizes of each subgroup of feeding strategy (assuming nesting strategy is 'bare mound'). The numbers annotating the points indicate the number of effect sizes included in the pooled effect size and the size of the points indicates the sum of the samples sizes (of nest samples) in those studies. Letters above the subgroups indicate that the subgroup is significantly different ($p<0.05$) for subgroups with differing letters based on pairwise Tukey comparisons (adjusted). Pairwise with $0.05 < p < 0.1$ are also included in Table 2.5. There is a dashed line is at 0 (no effect) for reference and the salmon line is the pooled effect size for all studies for all subgroups of both nesting and feeding strategy (ammonium-N based on 31 effect sizes from 17 studies, total sample size 171; nitrate-N based on 39 effect sizes from 22 studies, total sample size 280; Na based on 16 effect sizes from 13 studies, total sample size 238).

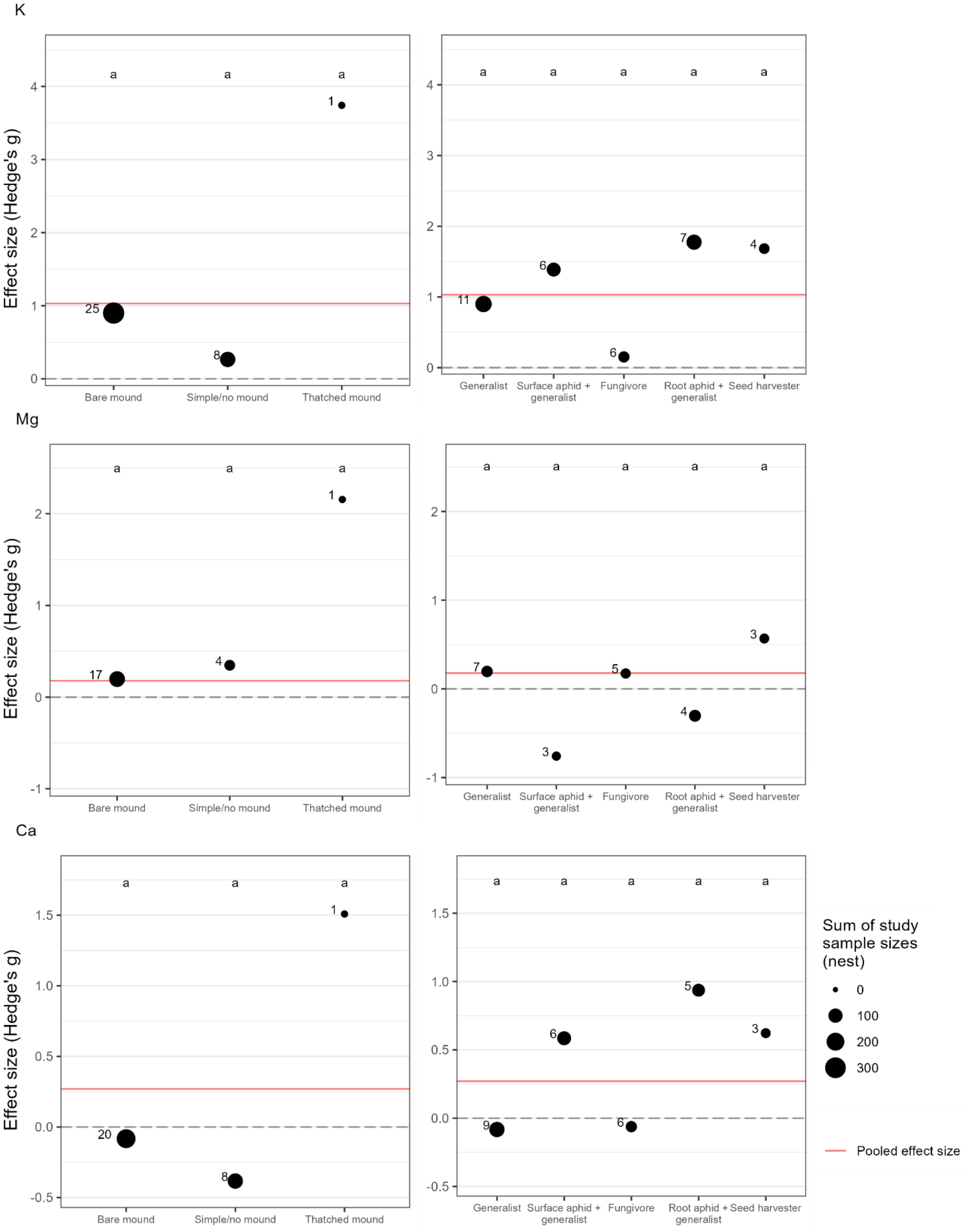


Figure 2.6. We calculated pooled meta-analytic effect sizes (Hedge's g) of variables K, Mg and Ca for the subgroups of nesting strategy and feeding strategy within our model. Plots on the left show the pooled effect sizes for each subgroup of nesting strategy (assuming feeding strategy is 'generalist') and plots of the right show the pooled effect sizes of each subgroup of feeding strategy (assuming nesting strategy is 'bare mound'). The numbers annotating the points indicate the number of effect sizes included in the pooled effect size and the size of the points indicates the sum of the samples sizes (of nest samples) in those studies. Letters above the subgroups indicate that the subgroup is significantly different ($p<0.05$) for subgroups with differing letters based on pairwise Tukey comparisons (adjusted). Pairwise with $0.05 < p < 0.1$ are also included in Table 2.5. There is a dashed line is at 0 (no effect) for reference and the salmon line is the pooled effect size for all studies for all subgroups of both nesting and feeding strategy (K based on 34 effect sizes from 24 studies, total sample size 456; Mg based on 22 effect sizes from 16 studies, total sample size 181; Ca based on 29 effect sizes from 20 studies, total sample size 364).

Table 2.5. Subgroups included in the model were tested for pairwise differences (Tukey), with adjustments for multiple comparisons, and those comparisons with *p*<0.1 are presented below. In addition, subgroups significantly different from the model intercepts (Bare mound, Generalist) have been repeated below for comparison. The estimate may be positive or negative and indicates the direction of the difference; a positive estimate means that the effect size for subgroup in the second column was higher than the subgroup in the first.

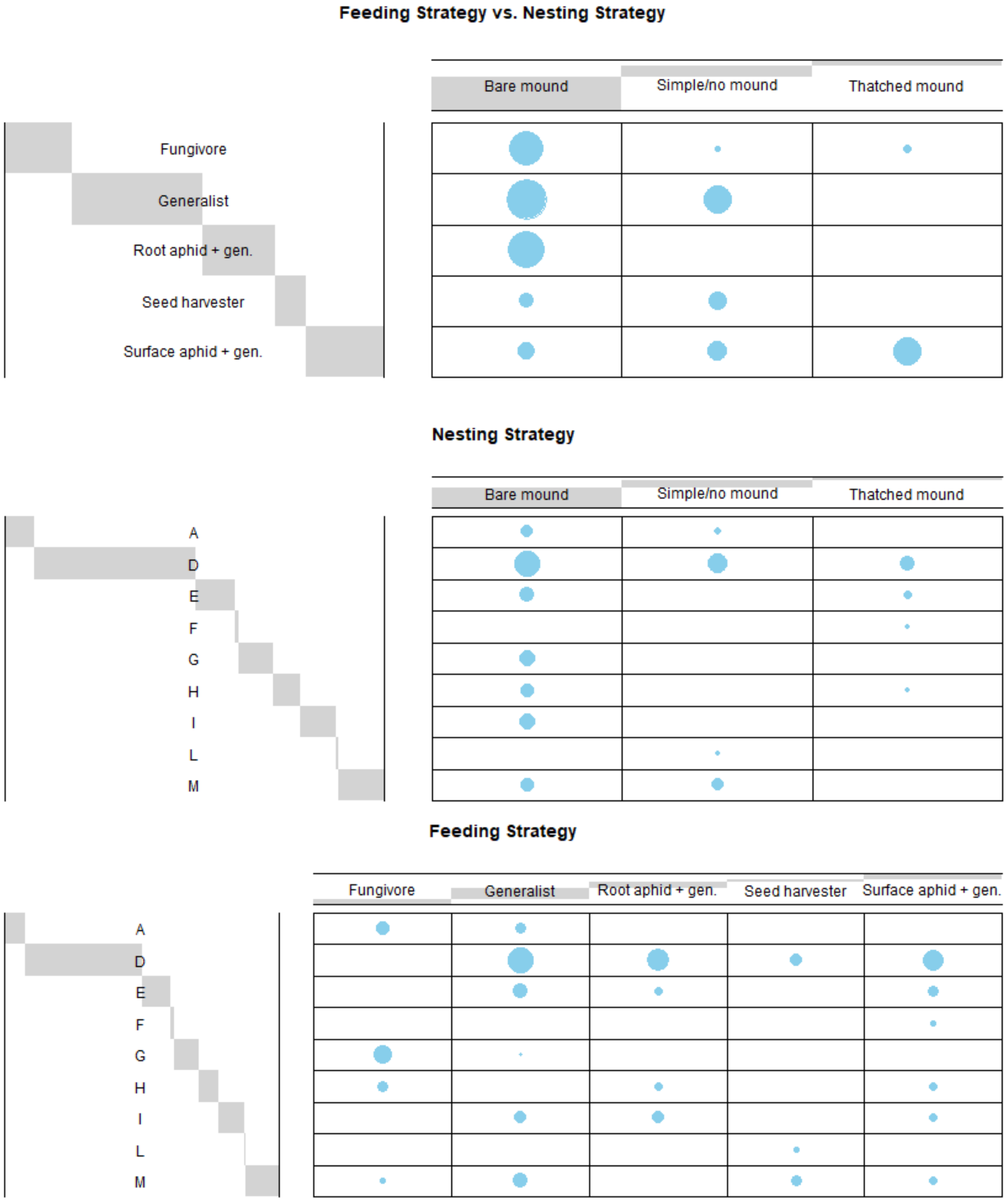
Significant pairwise comparisons		**Variable**	**Estimate**	**Z value**	***p*-value**
Intercept (Generalist)	Root aphid + generalist	pH	3.128	4.915	<0.001 *
Intercept (Generalist)	Root aphid + generalist	Total N	-0.923	-1.939	0.060 .
Intercept (Generalist)	Root aphid + generalist	NH_4-N	-1.893	-1.790	0.086 .
Intercept (Generalist)	Seed harvester	NO_3-N	4.374	2.327	0.026 *
Intercept (Generalist)	Surface aphid + generalist	NO_3-N	-1.035	-1.726	0.094 .
Seed harvester	Surface aphid + generalist	NO_3-N	5.409	2.776	0.07 .
Seed harvester	Root aphid + generalist	NO_3-N	5.368	2.721	0.081 .
Seed harvester	Root aphid + generalist	pH	-3.973	-3.924	0.001 *
Root aphid + generalist	Fungivore	K	1.623	2.674	0.088 .
Root aphid + generalist	Fungivore	pH	2.799	3.562	0.006 *
Root aphid + generalist	Surface aphid + generalist	pH	2.709	2.799	0.067 .

mounds, but more extreme: in addition to the large effect sizes observed for the bare mound subgroup, the pooled effect size of Ca concentration for the thatched mound subgroup was large and positive. Similarly, the direction of the effect size of pH for this subgroup was large and positive (that is, nests were more alkaline). It is important to note that the thatched mound results are based on fewer studies than the bare mound subgroup and are, as such, less reliable; the pooled effect size for the thatched mound subgroup of organic C, K, Mg and Ca are based on a single study (Figures 2.3-2.6). The nesting strategy subgroup 'simple mound' was generally not different from bare mound.

3.3.2 Subgroups: feeding strategy

Pooled effect sizes of feeding strategy subgroups generally appeared to be clustered randomly around the overall effect size; however, some exceptions were apparent from the pairwise (Tukey) analysis of model subgroups: root aphid + generalist is significantly different ($p<0.05$) from other subgroups for soil pH, and shows significant pairwise differences for the variables K, nitrate-N, ammonium-N and total N. While most other subgroups had little or no effect on soil pH (except seed harvester, which had a large negative ($g<-0.8$) but non-significant effect on pH), the pooled effect size for root aphid + generalist is large ($g>0.8$), positive and significantly different ($p<0.05$) from the intercept. Additionally, the subgroups seed harvester and surface aphid + generalist had a pooled effect size close to zero, significantly lower than the intercept for the variable nitrate-N. Other pairwise differences are listed in Table 2.5.

Every feeding strategy that was included as a subgroup variable was seen paired with bare mound nesting strategy in at least one study and only root aphid + generalist was not paired with simple/no mound in at least one study (Figure 2.7). With the exception of one leaf cutting ant (*Acromyrmex lobicornis*) that built nests meeting our criteria for the thatched mound nesting strategy, all of our thatching mound species belonged to the *Formica rufa* group wood ants and therefore all used the surface aphid + generalist feeding strategy.


Feeding Strategy vs. Nesting Strategy

Nesting Strategy

Feeding Strategy

Figure 2.7. Balloon plots to visually represent the independence of feeding and nesting strategies, and biome. Larger balloons indicate more data fell into the intersecting categories. Biomes are labelled alphabetically for brevity, and correspond to Olson et al. 2001 Terrestrial Ecoregions (A- Tropical and subtropical moist broadleaf forests, D - Temperate broadleaf and mixed forests, E - Temperate coniferous forests, F - Boreal forests/taiga, G - Tropical and subtropical grasslands, savannahs, and shrublands, H - Temperate grasslands, savannahs, and shrublands, I - Flooded grasslands and savannahs, L - Mediterranean forests, woodlands, and scrub or sclerophyll forests, M - Deserts and xeric shrublands)

3.4 Bias, sensitivity and influential outliers

The geographic coverage of studies included in this meta-analysis was fairly broad, however Asia and Africa were very poorly represented in the dataset (Figure 2.8). There was a higher density of studies in central and northern Europe than elsewhere and lower in tropical America, Africa and south-east Asia, where the highest diversity and abundance of ants are found. Nonetheless, we obtained a good representation of most terrestrial ecoregions (Olson *et al.*, 2001) where ants are abundant (Figure 2.8) despite the representation having geographic bias.

Egger's regression (Table 2.6) showed little asymmetry in the funnel plots for all variables except for K, Na and nitrate-N, suggesting that there was unlikely to be -study effect bias due to limited publication/study numbers for soil variables, except for these three.

One effect size from Boulton et al. 2003 (total N) was excluded our models on the basis that the result was likely to be a measurement or calculation error in the original paper (effect size more than 10 times the interquartile range of the pooled effect size). In order to check that our model results were robust and not dependent on individual extreme values, all models were fitted first to the full data set and then to data with outliers removed based on the following pre-set criteria. Any study with a Cook's distance more than 3 times the mean was removed, and the model rerun to see if our results were robust. This process resulted in the removal of 1 outlier from total C, organic C, NO_3-N, pH and Ca, and 2 removed from NH_4-N. The removal of the outlier from pH resulted in the p-value for the subgroup 'no above ground structure' to increase above 0.05 and for the p-value of the 'generalist' feeding strategy to increase from 0.07 to >0.1.

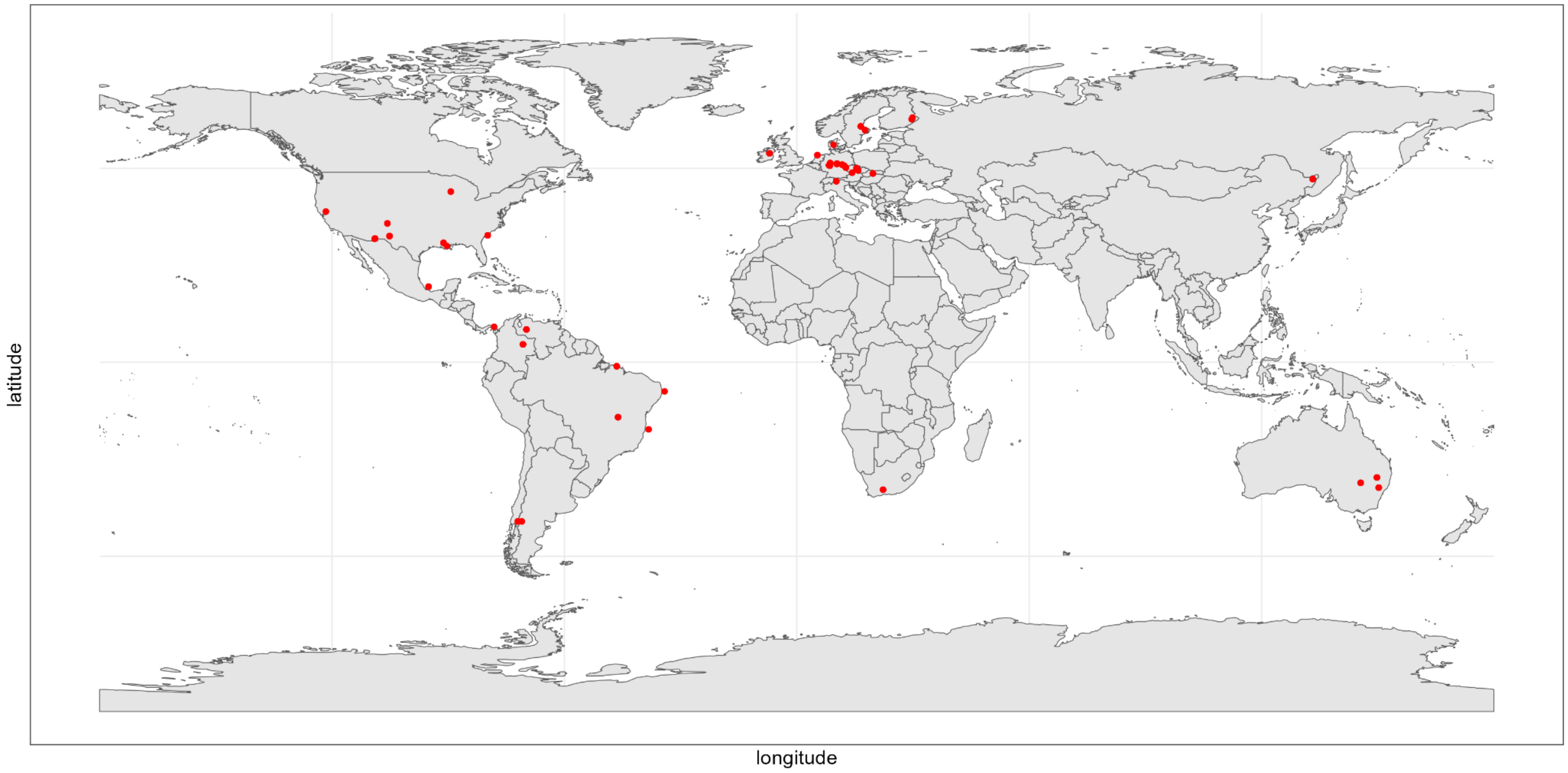


Figure 2.8. The studies used in the meta-analysis were globally distributed, with at least one study from every continent where ants are found.

Table 2.6. We conducted Egger's regression to test for asymmetry in funnel plots of each of the variables included in the meta-analysis to identify small-study effects, which may indicate publication bias.

Variable	**Intercept**	**95% CI**		**t**	***p*-value**
		Lower	**Upper**		
Total N	-0.263	-2.154	1.629	-0.272	0.787
Organic C	-0.849	-4.172	2.474	-0.501	0.623
Total P	1.063	-0.451	2.577	1.376	0.176
pH	1.001	-0.638	2.639	1.197	0.238
Total C	0.376	-1.258	2.010	0.451	0.655
K	2.977	1.156	4.798	3.204	0.003 *
Mg	-1.732	-3.417	-0.047	-2.015	0.057 .
Ca	0.146	-1.558	1.850	0.168	0.868
Na	-2.059	-3.653	-0.466	-2.533	0.025 *
NO3N	1.764	0.240	3.287	2.268	0.030 *
NH4N	1.194	-0.549	2.937	1.342	0.190
Available P	1.786	-0.917	4.490	1.295	0.224

4. Discussion

Our results show that the impact that ants have on the soil can be large and is consistent for multiple soil variables. In line with our hypotheses, the nests of ants have significantly higher concentrations than reference soils of most nutrients and cations for which data were available. This enrichment effect is most likely due to foraging, nest building and hygiene behaviours of ants concentrating nutrient rich material in the nest structure. The magnitude of some of these effects is striking; the Hedge's g of the pooled effect size of available P was approximately 1.5, nearly double the 0.8 standard generally considered a 'large' effect (Cohen, 1988). The magnitude of these effects was partly determined by the nesting and feeding strategy of the ant species but with variable impacts across different nutrients. Nest type and feeding strategy also influenced pH; while ant nests generally have a higher pH than reference soils, this effect was most marked in thatched nests and root-aphid sugar feeders. By including nesting and feeding strategy, this meta-analysis highlights the aspects of ant biology that modulate their effects on soil.

We found that biogenic structures of soil nesting ants were significantly enriched in many nutrients. This effect has also been recorded for refuse dumps, where some species of ants deposit dead ants and other waste material that may pose a pathogen risk to the colony (Farji-Brener and Werenkraut, 2017). This enrichment of nest soils, while consistent among the majority of studies, is not uniform; for each variable there was at least one study that indicates the opposite, depleted, effect. These 'nest-depleted' results are not linked to particular nesting or feeding strategies; all nesting and feeding strategies that showed significant pooled effects were characterised by nest enrichment. This broad consistency matches our hypothesised mechanisms of nutrient enrichment in ant nests. Foraging and, in the case of thatching ants, gathering of nest materials from the surrounding environment, increases the abundance of nutrient-rich material, such as indigestible or otherwise inaccessible food, ant waste and organic matter used in nest construction, inside the nest. Here, the stable soil temperature and moisture conditions within the nest allow bacteria and fungi to break down the nutrient-rich material (Kadochová and Frouz, 2013) while the activity of the ants prevents plants from growing on the nest structure itself (Dean, Milton and Klotz, 1997), meaning that these liberated nutrients accumulate in the nest soils rather than being absorbed by plant roots. This mechanism suggests that more complex nests that are constructed of material brought from elsewhere, rather than merely excavated, and that provide more stable, ant-managed, conditions, will have the largest effect on nutrient concentrations in nest soils. Our results confirm this; thatched mounds have larger effect sizes than either bare mounds or simple/no aboveground nests, though our results also show that there are far fewer papers published on the soil impacts of thatched mound constructing ants than on other nesting types. This highlights the importance of continued work on the nests of ants using this strategy.

The ecological effects of ant nests as hotspots of nutrients are complex. On the one hand, these hotspots create gradients of nutrient concentration centred on the nests with the potential to create microhabitats and heterogeneity in the soil landscape, and these hotspot effects can persist long after nest abandonment (Kristiansen and Amelung, 2001). Spatial heterogeneity can be an important predictor of biodiversity within a habitat (Stein *et al*., 2014), which has downstream consequences for ecosystem function and resilience (Oliver *et al.*, 2015) in addition to its advantages for conservation of species. On the other hand, it is unclear whether the gradients and hotspots created by ant nests lead to microhabitats that would have any meaningful effect on biodiversity. Many ants keep their nest entrances and mound surfaces clear of vegetation (Dean *et al*., 1997), so the nutrients concentrated in the nest are largely unexploitable while the nest is occupied. As such, the potential niche creation for organisms other than myrmecophiles (Kronauer and Pierce, 2011) is limited. This is not always the case, however: the nests of *Lasius flavus* have continuous cover of plants, and harbour different flora to the surrounding grassland (Dauber *et al*., 2006). The presence of plants on the surface of *L. flavus* mounds is partly a consequence of their feeding strategy too. Because these ants feed on the honeydew of root aphids, they are rarely seen aboveground at all (King, 1977) and therefore do not clear the surface of their mound of vegetation, demonstrating the potential for the feeding and nesting strategy to interact in their effects on the soil nutrients. For ants that do keep the nest surface vegetation free, the ecological effects of these nutrient hotspots will depend on how large the area affected is, and how far beyond the nest margin the nutrient concentrations are elevated. While synthesising the effect of distance from an ant nest on nutrient concentration or plant performance is beyond the scope of this study, there are cases where plant growth has been shown to be greater near ant nests; spruce trees 0-1m from nests of *Formica polyctena* had significantly wider tree rings than trees growing 3-50m from the nearest nest (Frouz *et al.*, 2008). It is likely that the concentration of nutrients in nests, and the effect on pH will have an impact on the flora, at least at small distances from nests, and this will have downstream effects on invertebrates and other animals on top of the effect that the ants may directly have on these organisms. On top of this, the nesting and feeding strategy of the ant, and the interaction of the two, may impact not only the effect on the soil chemical and physical properties, but also how (or how much) these changes to the soil affect other organisms.

The effect that ant life history traits have on soil suggests that conserving functional diversity of ant assemblages in natural or semi-natural habitats and promoting functional diversity in already degraded habitats can increase spatial heterogeneity in those habitats. The benefits that spatial heterogeneity in soil resources can bring by creating microhabitats and promoting diversity are highly variable. This study investigated nesting and feeding strategy, and previous work has included diet (Farji-Brener and Werenkraut, 2017), but there are doubtless other aspects of ant natural history that modulate ant effects on soil that we were unable to include here. The differential impact of ant feeding and nesting strategy indicates that high functional diversity of ant species within a habitat will have a range of possible effects on the soil, different in magnitude and nature. This may create many different microhabitats and gradients of nutrient availability, adding to the complexity (and therefore resilience; (Oliver *et al.*, 2015) of the habitat. Whilst this should be expected as the natural state in undisturbed habitats with high levels of existing functional diversity, many agricultural landscapes, such as palm oil or timber plantations, waste ground and pasture may have a very low ant functional diversity on top of the lack of heterogeneity resulting from intense management (Scott-Shaw *et al.*, 1998; Wilcove and Koh, 2010). Spatial heterogeneity in these landscapes may provide additional resilience (Turner *et al.*, 2013) on top of potential pest outbreak mitigation provided by predatory ants (Karhu and Neuvonen 1998). On the other hand, presence of some ant species may reduce yields in certain contexts (Frouz *et al.*, 2008). Whether high ant functional diversity is desirable in agricultural habitats will be dependent on many factors including the crop (whether the crop is vulnerable to ants), the relative risk of pest outbreak (is the loss of yield due to the ants an acceptable trade-off for reduced damage in the event of a pest outbreak) and the species of ants that may colonise (are they likely to cause damage or are they beneficial). In heavily disturbed land that is otherwise unused, no such trade-offs exist, and here functional diversity of ants may be to the overall benefit of the habitat by restoring lost complexity; translocations of the harvester ant *Messor barbarous* to a formerly oil-degraded site resulted in an increase in soil fertility and small-scale spatial heterogeneity (De Almeida *et al.*, 2020). Where the trade-offs in agricultural land are found acceptable, and ant diversity is promoted, the increased diversity of microhabitats may be an added benefit, while ants could play a role in regaining some ecosystem function in heavily degraded sites with restoration potential. In order to understand the dynamics of ant introductions to modified landscapes, more study is needed on both neglected species and habitats, especially in anthropogenic environment.

While the general pattern of nest enrichment appears to be consistent for different nesting and feeding strategies, some subgroups stand out. Not only did thatched mounds generally have a larger effect on the nutrient concentration than other mound types, but thatched mounds were also more alkaline (compared to the surrounding soil), whereas bare and simple mounds were more acidic (Figure 2.3). This disparity may be explained by the soil pH of the woodlands in which wood ants are studied. Wood ants are the most data-rich group of thatched mound nesting ants, and many of the available studies on wood ant nests were conducted in coniferous plantations (Lenoir *et al.*, 2001; Risch et al., 2005; Kilpeläinen et al., 2007; Berg-Binder and Suarez, 2012; Jilkova et al., 2013), that typically have highly acidic soil (Armolaitis *et al.*, 2011). It has previously been proposed that the soil in the nests of many ant species is closer to neutral in pH, rather than the nests having an explicitly directional effect (Frouz and Jilková, 2008). This would mean that it is far more likely that a positive effect size would be observed in already acidic soils, as effect sizes on soils with a pH above 7 (alkaline soils) would have to be negative to correspond to a more neutral pH in the ant nest. This would cause the difference between thatched mounds and other nest types in the case of pH.

Root-aphid sugar feeding ants inverted the general trend for both pH and available P; the soils in their nests were less acidic than surrounding soil, where ants with other feeding strategies either had no effect on the pH of nest soils or made them slightly more acidic, while available P was slightly depleted in the mounds of root-aphid sugar feeders, in contrast to the enrichment of available P in the nests of ants with other feeding strategies. Of the 15 studies on root aphid feeding ants, all but one was *Lasius flavus* (the other being *Aphaenogaster barbigula*). *Lasius flavus* builds mounds that are usually covered with vegetation and are often studied in calcareous grassland, where they can be very abundant (King, 1977). Soils in calcareous grassland are typically alkaline; however, all but one of the studies included in our analysis were conducted in soils with a baseline pH of less than 7. This result is consistent with the idea that ants' nests are more neutral than surrounding soils (Frouz and Jilková, 2008) and, crucially, shows that this is true for both acidic and alkaline soils.

While overall geographic coverage of the meta-analysis is satisfactory, there were gaps indicating understudied areas. Africa and much of Asia were very poorly represented in the dataset, highlighting the need for more research in these regions. Equally, practical considerations meant that we conducted the synthesis with studies published in English only, which likely reduces coverage of certain regions (Angulo *et al.*, 2021). One important and unexpected result is that the heterogeneity in the model that was explained by taxonomy was dwarfed by the heterogeneity associated with the year and authorship of the paper. There are many potential causes of the substantial differences in the results found by different research groups (e.g. site-specific effects), and whilst we cannot make clear conclusions about the cause of these disparities, the use a standardised approach for soil analysis methods would eliminate one potential source of between study variation.

We were unable to include worker and colony size (as a proxy for biomass), whether the ant was polydomous (colonies split across multiple nests), or whether the study site was disturbed or natural in our analysis because there was insufficient data available, either in the focal studies themselves, or in the broader literature on the natural history of the ants. There are currently major range changes for many invertebrates, due to introductions, invasions and the changing climate, and an ongoing decline of many species of invertebrate (Habel *et al.*, 2019), yet fieldwork-based ecology papers such as species lists and natural histories are declining as a proportion of the total number of papers published (Ríos-Saldaña *et al*., 2018). Our meta-analysis shows that, without detailed and up to date data on the behaviour and life histories of ants, quantifying their role in ecosystems is difficult and will inevitably lack some of the resolution required to identify which species invasions or losses will be disruptive. Increasing the attention paid to research traditionally considered 'low impact', such as species lists, is essential to better understand their role in a changing world.

It is clear that the effect of ant nests on local soils is shaped by the biology of the ants in question. Diet and habitat can influence the magnitude of their effects on soil (Farji-Brener and Werenkraut, 2017) and the diversity of biogenic structures they create (Wheeler and Wheeler, 1983) can also influence their roles in altering soil chemical and physical properties. Here we also show that certain groups of ants with specific feeding and nesting strategies stand out as influencing soil particularly strongly, and thus as being worthy foci for further investigation. Ants that feed on root aphids seem to have a particularly strong (and atypical) effect on chemical characteristics of soil such as pH; however, the overwhelming majority of work on root aphid feeders has been conducted on *Lasius flavus* and the ability to generalise these findings requires further study of other root aphid feeding ants. Similarly, thatching ants seem to have a far greater effect on the soil than ants with other nesting types but have been the subject of less research on their effects on soil than some other ant groups. Overall, this synthesis demonstrates the major and trait dependant effects that ants can have on the soil by creating enriched hotspots and highlights the importance of continued work researching the natural history of understudied ant species to better understand their role in changing environments.

Chapter 3 - How do wood ants affect nest and non-nest soils in plantation forests?

Abstract

Ants are ecosystem engineers and can have wide ranging effects on habitats, especially in soil. Although spatial heterogeneity in an ecosystem is an important indicator of biodiversity and resilience, the ability of ants to modify spatial heterogeneity of ecosystems has been less well studied. The population margins of the wood ant *Formica lugubris* are expanding into areas on coniferous plantation forest at some sites in the North York Moors, providing an opportunity to study their effects on soil and compare similar areas with and without wood ants. Here we investigate how the soil in nests of *Formica lugubris* differs from the surrounding soil and how they impact non-nests soils in coniferous plantation forests in the North York Moors, England. Using these data, we quantify the contribution that wood ants make to the spatial heterogeneity of soil properties. We find that soils in wood ant nests are significantly enriched in organic matter and several bioavailable nutrients compared with soil 3m from the nest, and that non-nest soils in ant-occupied areas are significantly depleted of nitrite. Other variables measured were not significantly different in ant occupied forests compared to forest stands where they are absent, but our simulations indicate that total nitrogen and total carbon was more variable in soils of ant-occupied forests than forests where wood ants are absent, while the variability of phosphate and nitrate concentrations was greater where wood ants were absent. Interestingly, this difference in heterogeneity was driven by the non-nest soils rather than the ‘hotspot’ effect of the nests. We suggest that this is because the area occupied by the nest structures is relatively small, even in densely populated forests, meaning that the direct effect of nests on spatial heterogeneity is negligible compared to the effects of resource removal by ants. Overall, wood ant colonies increase the spatial heterogeneity of plantation forest soils, leading to a soil nutrient landscape that may resemble later successional stages.

1. Introduction

Spatial heterogeneity within an environment is a major predictor of biodiversity (Stein et al., 2014), which is in turn important for ensuring that ecosystem function is robust to change (Oliver *et al.*, 2015). For example, spatial heterogeneity of forest successional stages at the 10-15m scale has a greater effect on spider, ant, and carabid beetle diversity than other scales in the 5-75m range (Niemelä et al., 2013). While the correlation between spatial heterogeneity and biodiversity is documented observationally, the relationship is not predictable by plot size (Lundholm, 2009), especially at smaller scales (Tamme *et al.*, 2010), and is not necessarily causative; increased heterogeneity is characteristic of later successional stages and less disturbed habitats, themselves hotspots of biodiversity.

Ecosystem engineers can modify the physical environment in a way that can impact other organisms and spatial heterogeneity (Cottee-Jones and Whittaker, 2012). They do this by changing the availability of resources required by other organisms; their effects on resource availability may not be consistent across space and time and may even outlast the organism itself (Hastings *et al.*, 2007). By unevenly affecting the distribution of resources in space and time, ecosystem engineers can increase spatial heterogeneity (Jones *et al.*, 2006) and, in doing so, ecosystem engineers may indirectly bring about the benefits of spatial heterogeneity to an ecosystem, such as increased biodiversity or resilience.

Wood ants (*Formica rufa* group) have ecosystem engineer traits and have a high potential to affect soil and heterogeneity. By constructing large, long-lasting nest mounds, wood ants of the *Formica rufa* group can cause changes in local soils, most substantively within the bounds of their nest (Finér et al., 2013; Jílková et al., 2017; Kilpeläinen et al., 2007; Lenoir et al., 2001; Ohashi et al., 2007). This group of ants share aspects of their nesting behaviour that contribute to their effects on soil; they construct large mounds (sometimes over 1m tall; Klimetzek, 1981) that incorporate a mixture of excavated mineral soil and organic matter and with a constructed layer of ‘thatch’ on the outside of the nest. This thatch is made of organic matter such as pine needles, grass, leaves and twigs and functions to insulate the nest, leading to a nest interior that varies much less in temperature and moisture content than the above and below ground surroundings. In addition to this, the ants use both metabolic heat from microorganisms and the ants themselves, as well as active construction behaviours, to maintain the temperature conditions (Frouz, 2000). These factors combine to make the conditions within the nests different from the surrounding soil, with the potential to affect microbial activity and decomposition in nest soils (Jílková and Frouz, 2014; Jilkova et al., 2018), potentially facilitating ecologically important changes to the availability of soil nutrients to the local ecosystem (Wardle *et al.*, 2011).

By bringing large quantities of food and nesting materials into the mound, wood ants concentrate resources in the nest resulting in ‘hotspots’ of nutrient concentration that can have measurable ecological effects. In Norway spruce forests occupied by *F. aquilonia*, the input of honeydew and invertebrate prey into nest mounds can be as high as 39kg ha^{-1} $year^{-1}$ for 100-year-old stands (Domisch et al., 2009). Although the small area occupied by a single nest relative to the forest in general means that the contribution by wood ants to regional nutrient influx is small, this does result in higher concentrations of total available nitrogen and carbon in soil from nests compared with the surrounding soil (Domisch et al., 2009; Finér et al., 2013). Pools and flux of other important nutrients such as phosphorus and potassium are elevated with the nests (Finér et al., 2013; Jílková et al., 2017; Kilpeläinen et al., 2007; Ohashi et al., 2007), but others are not (e.g., calcium Finér et al., 2013; Jílková et al., 2017; Ohashi et al., 2007). Even in abandoned nests, where the moisture content and thatch are no longer maintained by ant activity, N concentration may be elevated in nests for 20 years after abandonment (Kristiansen and Amelung, 2001). The redistribution of nutrients can affect the wider forest ecosystem, for example Norway spruce trees within 1m of *F. polyctena* nests, where the concentration of P, K and NO_3 were higher, grew more quickly than those of trees growing 3-50m away from ant nests (Frouz *et al.*, 2008). Together with both positive (Karhu and Neuvonen, 1998) and negative (Frouz et al., 2008) impact of wood ants on herbivorous invertebrates, this highlights the ecological and, in plantation forests, agricultural relevance of the impact that wood ants have in the soil.

While evidence indicates that wood ants alter the soil within their nests, there is comparatively little research on the effects that wood ants have on soils outside of the nest structure, through mechanisms such as resource removal. Ants are major agents of resource removal in tropical (Griffiths *et al.*, 2018), arid (Luna *et al.*, 2021) and temperate grassland (Ohwada and Yamawo, 2021) ecosystems. The magnitude of resource influx into the nests of wood ants suggests that they are performing a similar role in resource removal in northern coniferous forests. We know little about the effects of wood ants on soil beyond their nest, where their role as agents of resource removal and as predators of invertebrates may deplete soil nutrients or prevent their depletion by other organisms (Wardle *et al.*, 2011). Long-term exclusion (6 years) of *F. aquilonia* from forest plots decreases carbon and nitrogen storage, possibly because wood ants suppress other invertebrates that consume organic matter in the soil. This changes the microbial community by making the organic matter more readily available to bacteria (Wardle et al., 2011). However, the effects of ant presence or absence on the non-nest soils in an exclusion scenario may well be different from the effects of wood ants in real world forests, highlighting the need for studying the effects of wood ant activity on soils beyond their nests.

With well-established effects of wood ants on nests soils and the potential for effects in non-nest soils, it is important to consider the interaction between the two: by affecting nest soils and soils outside the nests differently, wood ants may impact spatial heterogeneity in the soil environment. Wood ant nest densities of 3.9 mounds ha^{-1} have been recorded (Kilpeläinen *et al*., 2007) and a landscape dotted with hotspots of nutrients (Lenoir *et al.*, 2001) at this density could have a greater spatial heterogeneity of soil resources than where wood ants are absent, especially as even long abandoned nests show significant differences between nest soil and soil outside of the nest (Kristiansen and Amelung, 2001). Equally, the large volumes of organic material and food resources removed from the areas around the nest (Domisch *et al.*, 2009) could contribute to spatial heterogeneity in the non-nest soils. By causing increased heterogeneity of soil resources, wood ant activity may modify the soil-nutritional landscape of early succession, heavily disturbed or plantation forests to resemble later successional stages and less disturbed forest more through greater soil spatial heterogeneity (Tamme *et al.*, 2010). This may impact biodiversity and resilience within the habitats they occupy (Stein *et al*., 2014; Oliver *et al.*, 2015) making their presence desirable in degraded or disturbed woodland ecosystems such as plantation forests.

The conditions, including soil properties, in plantation forests (under management for timber production) differ from natural woodland and such plantation forests occupy large areas in many countries; sometimes far more land area that natural woodlands do (Defra, 2021). Generally, the bulk density of soils in plantation forests is higher, and the concentrations of many nutrients are lower (Liao *et al.* 2012), while intensive management of plantation forests can lead to soil compaction and erosion, as well as disruption of soil structure (Worrell and Hampson, 1997). This results in the soil conditions of a large areas of tree cover (59% of woodland in the United Kingdom is considered managed; Defra, 2021) being substantially different from the conditions in soils of natural forests, where the native forest soil invertebrate community would have evolved.

Wood ants can be abundant in planation forests (Frouz *et al*., 1997), and the margins of some populations are expanding from natural woodland into areas of plantation in some areas (Procter *et al.*, 2015) so their potential to cause change in forest soil could have ecologically important consequences for this major forest habitat. The creation of mound structures that act as nutrient hotspots (Lenoir *et al*., 2001) may mitigate the nutrient depleting effects of plantation (Liao *et al.* 2012), or the removal of resources from the surrounding soil by the ants may exacerbate it. It is important that we understand the interaction between wood ants and the soil environment in plantation forests to better predict the effects that their arrival (Procter *et al.*, 2015) or translocation (Nielsen *et al.*, 2018) may have for plantations and the other organisms that occupy them.

The aim of this study is to quantify the effects of wood ants on nest and surrounding soils, and their influence on the spatial heterogeneity of soil properties at the scale of whole plantation forest. The North York Moors contains large areas of coniferous plantation forest where *Formica lugubris* is abundant (Procter *et al.*, 2015). In some of these forest sites, there are areas where a colonisation lag has occurred because of rapid afforestation outpacing ant expansion from forest refugia, containing the source population of *F. lugubris* (Procter et al., 2015). This has resulted in adjacent areas of long term, recent, and no *F. lugubris* presence. By collecting soil samples from the non-nest soils in these three conditions and from wood ant nests directly, we quantify the impact of wood ant nests on overall soil heterogeneity in North York Moors managed forest plantations. Specifically, we i) assess how nest soils differ from non-nest soils; ii) quantify differences in ecologically important soil properties between areas with long-established wood ant populations, recently arrived wood ant populations and no wood ant nests and iii) quantify the overall contribution of wood ants to spatial heterogeneity of soils in plantation forests.

2. Methods

2.1. Study sites

We conducted the study in the North York Moors National Park in the northeast of England at two plantation forest sites: Cropton Forest (54° 19' 9” N, 000° 50' 22” W) and Broxa Forest (54° 19' 51” N, 000° 32' 17 W). There are many areas of woodland in the North York Moors where *F. lugubris* is present, but these two were chosen because the population margins are still expanding at these sites (Procter *et al.*, 2015). This expansion arises from colonisation lag after rapid afforestation due to the short dispersal distances of *F. lugubris* (Procter *et al.*, 2015). At each site, we confirmed that *F. lugubris* was the only species of wood ant present. We conducted all the sampling on land managed as plantation by the Forestry Commission. These forests have been planted with conifers over the last 100 years, including areas of Sitka spruce, *Picea sitchensis,* Scots pine, *Pinus sylvestris*, Japanese larch, *Larix kaempferi* and Hybrid larch, *Larix x leptolepis* (Procter *et al.*, 2015).

2.2 Population margins mapping

The population margins of *F. lugubris* on the two North York Moors sites are subject to long term monitoring and were surveyed in 2011, 2013 (Procter *et al.*, 2015), 2018, 2019 (Holgate, 2021), 2020 and 2021 following the same protocol (Procter et al. 2015). Due to the habitat requirements of *F. lugubris* and the importance of direct sunlight for maintaining nest temperature, 78.5% of nests are within 10m from the edges of forests (Chen and Robinson, 2014; Procter *et al.*, 2015). The previously recorded extent of the populations was used to identify all the forest edges that lay on the population margins. ‘Edges’ included roads, footpaths and firebreaks that cause canopy gaps, or the edges of forest stands themselves. The population margins were areas where wood ants were present, and where you could travel 200m in at least one direction without getting closer to any other wood ant nests. Any nests beyond this 200m buffer are assumed to belong to a different subpopulation of ants. On the edges at the population margins, we conducted 10m long transects perpendicular to the edge every 5m, recording the nest locations using a handheld GPS (models: Garmin eTrex H, 2011-19; eTrex

32X, 2020-21). Where the understory was sparse enough to allow 5m visibility, a single transect running 5m behind the edge and parallel to it was conducted, followed by a second running along the edge itself, providing the same coverage as the 10m long transects. This was done along the whole edge, starting 50m behind the previously mapped population margin, or until no wood ant nests were encountered for 200m. Some areas where wood ants were present were either recently felled/planted, semi natural, or contained mature trees sufficiently spaced to allow canopy gaps throughout. In these cases, we conducted transects every 10m all until we had a) not encountered a nest for 200m or b) encountered a previously mapped area or nest or c) encountered the edge of the stand. Our aim was to determine the extent of the wood ant populations year on year, not the exact location of every nest. Therefore, we did not resurvey the interior of the populations each year; we started the survey 50m back along the edge from the previous years' population margin and worked outwards.

2.3 Sampling design

2.3.1. Occupancy effects

To compare between areas with long-established ant occupancy, recent ant occupancy, and areas beyond the margins of the current populations, we identified subsite triplets. Each site (Cropton and Broxa) was divided into four subsites, each of which provided three levels of occupancy within approximately 400m^2: i) long-term occupancy, where ant nests had been present for at least 8 years (recorded in 2013); ii) recent occupancy, i.e. nests present at least 3 years (presence recorded in 2018 but not 2013) and iii) ant-absent woodland, where no wood ants have been recorded as present (2013-2021) and at least 50m from the nearest nest. This wood ant population spreads by local nest budding, thus these sites without wood ants are beyond the expansion front of the colonising population (Procter *et al.*, 2015). For each combination of subsite and occupancy condition, we took five soil samples along a transect running parallel to the colonised edge, 10m from the canopy gap, at 10m intervals. If a potential sampling point along a transect fell within 3m of an active or abandoned wood ant nest, the sample was taken at the nearest point to the line of the transect that was greater than 3m from a nest, to avoid any potential effect of run-off from the nest. For each sample, we recorded the distance to the nearest nest, the distance to the nearest tree greater than 5cm diameter at breast height, ground cover and precipitation. PVC corers (45mm external diameter, 42mm internal diameter, 375mm long), were driven to a maximum depth of 20cm. At these sites, we found this adequate to collect the entire O (organic) horizon and the top of the A horizon. We recorded the depth to which the core was driven, and the internal depth to soil surface, allowing calculation of compression ratio for dry bulk density and depth of O-A horizon transition calculations. Cores were extruded in the field and the O horizon discarded. The top 2cm of the A horizon were retained in a sealed plastic bag for analysis, after recording the depth at which the A horizon started. We chose to sample the A horizon because the O horizon at these sites was very inconsistent in thickness and state of decay and was often highly compressible and seasonally variable, whereas sampling the top of the A horizon provided a consistent structure to sample from that was comparable between cores. The O and A horizons at the sites were visually distinctive and the two layers readily separated. Soil temperature, percentage canopy cover and the location of the sample were recorded at each soil sampling site. This sampling was performed once in June/July (early summer) and once in September (late summer) for a total of 240 samples (Table 3.1). Two samples from Broxa (2013/2018) were unusable due to mislabelling, leaving 238 soil cores which were analysed for nutrient content, depth of O-A horizon transition, bulk density, and pH.

Table 3.1. The number of soil cores collected in each sampling period in the occupancy experiment. Sampling was carried out once in June/July (early summer) and once in September (late summer) 2021, resulting in 240 soil cores in total.

	Cropton			Broxa		
	Ant-absent	2018	2013	Ant-absent	2018	2013
Subsite 1	5	5	5	5	5	5
Subsite 2	5	5	5	5	5	5
Subsite 3	5	5	5	5	5	5
Subsite 4	5	5	5	5	5	5
Total = 120	20	20	20	20	20	20

2.3.2 Direct nest effects

In order to determine how soils in wood ant nests differ from the surrounding soil, we collected soil cores underneath 20 active, established (present since at least 2018, at least 1m across) nests, comprising 10 nests at each site (Broxa and Cropton). To do this with minimal disturbance to the ants, the corer was driven from the edge of the mound (where the thatch transitions to unmaintained leaf litter) at 45 degrees from the horizontal and towards the centre of the nest, down to a depth of 20cm. A selected, standardized depth, the 8-10cm section, of these cores was retained for analysis. This standardized depth, as opposed to a depth relative to the A horizon, was used for these samples because the mixing of the soil by the ants in the nest samples eliminates the distinction between soil layers within the nest. Internal and external core depths were measured for soil compaction calculations, as above. Each nest sample was paired with a control soil sample collected 3m from the nest collected using the same methods resulting in 40 samples in total.

2.4 Soil analysis

Bagged soil samples were transported in coolboxes and stored at 6^{o}C in the lab until processing. We recorded the mass of the 2cm section of fresh soil for bulk density calculations. A suspension of 1g of fresh homogenised soil in 10ml of deionised water was prepared. We agitated the suspension for 30 seconds and then centrifuged at 4000 rpm for 10 minutes before passing the supernatant through a 0.2 um filter in preparation for the ion chromatograph (Dionex ICS-2000 ion chromatograph fitted with a EGC III KOH Eluent generator cartridge, ADRS 600 2 mm suppressor, DS6 heated conductivity cell and AS40 autosampler; Dionex IonPac AS18 2x 250 mm analytical column fitted with an IonPac AG18 2x 50 mm guard column) to determine extractable nitrite, nitrate and phosphate concentrations. A second 1:10 suspension was made in 0.1M KCl solution and the pH of this measured directly using a Jenway pH Meter 3310. We recorded the mass of the remaining fresh soil and placed in the oven at 70^{o}C, weighing at 24 hr intervals until the mass lost in a 24hr period was less than 0.05g. The resulting mass loss was used to calculate the water content and correct dry bulk density. The sample of the dry soil was prepared for C/N analysis (Thermo Flash EA 1112 NC analyser), using aspartic acid as a standard.

2.5 Data analysis

2.5.1 Field data

The data for all soil samples were plotted and inspected for normality. To compare the direct nest samples to the control soils, we conducted non-parametric Wilcoxon signed rank test on variables that breached assumptions of normality (pH, nitrate, and phosphate concentrations) and parametric paired T-tests on the rest (dry bulk density, total N, total C, pH when split by site; Table 3.2). To test the effect of age of wood ant occupancy, we used a nested ANOVA design with fixed and random effects (occupancy + collection period + site:subsite). No non-parametric equivalent of this test exists, so we used the same analysis for all variables, but tested for normality and homogeneity of variance using Shapiro-Wilk normality test and Levene's test respectively in order to inform our interpretation of the results. All analyses were conducted in RStudio (R version 4.2.1). The data were tested for homogeneity of variance (Levene's Test; Table 3.2) prior to analysis with a nested ANOVA (formula: *variable occupancy + collection period + site:subsite* with subsite nested within site as random effects). Prior to transformation (natural log), phosphate and nitrate did not display homogeneity of variance and therefore breached the assumptions of a parametric test. Post transformation, variance was homogenous, so lnPhosphate and lnNitrate were included in the ANOVA instead of the untransformed values.

The ANOVA residuals were tested for normality with a Shapiro-Wilks test (Table 3.3). In this model, only the depth of the A horizon had normally distributed residuals (Shapiro-Wilks, W=0.997, p=0.884; Table 3.3). The residuals of all other measured variables were non-normally distributed (Shapiro-Wilks, p<0.01 in all cases), breaching the assumptions of the model. This potentially presents a dilemma for the analysis, since there are no non-parametric equivalents of a mixed effects ANOVA with nested random effects. We do not think that this is a significant concern for this analysis,

Table 3.2. Physical and chemical data from nest and control soils were normality tested (Shapiro-Wilk of difference between paired samples) after inspection of histograms to observe breaches of test assumptions. The data were tested with either paired t-test or Wilcoxon signed ranks test. Bulk density (B.D), phosphate, total N, and total C were all significantly different in the nest soils compared with control soils 3m away and pH was significantly different at Broxa but not Cropton or overall.

Shapiro-Wilk normality test	W	p-value	Test	Test statistic	df	p-value	p<
Dry B.D. (g/cm^3)	0.92552	0.1432	Paired t-test	t = 5.498	18	**<0.0001**	**0.01**
pH NYM	0.85199	**0.005756**	Wilcoxon signed rank test	V = 103	19	0.9563	1
pH Brox.	0.94594	0.6208	Paired t-test	t = -3.0359	9	**0.01411**	**0.05**
pH Crop.	0.95124	0.6831	Paired t-test	t = 1.4521	9	0.1804	1
Nitrate NYM (ppm)	0.40073	**<0.0001**	Wilcoxon signed rank test	V = 62	19	0.114	1
Nitrate Brox. (ppm)	0.78525	**0.009592**	Wilcoxon signed rank test	V = 11	9	0.1055	1
Nitrate Crop. (ppm)	0.57257	**<0.0001**	Wilcoxon signed rank test	V = 22	9	0.625	1
Phosphate (ppm)	0.7571	**0.0002117**	Wilcoxon signed rank test	V = 11	19	**0.000105**	**0.01**
Total N (%)	0.98005	0.9347	Paired t-test	t = -4.0035	19	**0.00076**	**0.01**
Total C (%)	0.97524	0.8593	Paired t-test	t = -3.5014	19	**0.002388**	**0.01**

Table 3.3. Soil variables from cores taken in three different ages of occupancy in the North York Moors were analysed using a nested ANOVA design, and the assumptions of this design were tested.

	Shapiro-Wilk normality test				***Levene's test***		
	df	W	p-value	p<	F value	p-value	p<
Depth of A (cm)	2	0.99658	0.8844	1	0.1278	0.8801	1
Dry bulk density (g/cm^3)	2	0.94102	**<0.0001**	0.01	0.3351	0.7156	1
pH	2	0.75567	**<0.0001**	0.01	1.4303	0.2413	1
Soil nitrite (ppm)	2	0.25364	**<0.0001**	0.01	1.703	0.1843	1
Soil nitrate (ppm)	2	0.71521	**<0.0001**	0.01	2.74	0.06662	**0.1**
Ln of nitrate	2	0.97313	**0.0001627**	0.01	0.6121	0.543	1
Soil phosphate (ppm)	2	0.54732	**<0.0001**	0.01	3.8958	0.02164	**0.05**
Ln of phosphate	2	0.87869	**<0.0001**	0.01	0.5841	0.5584	1
Total N (%)	2	0.9776	**0.0008081**	0.01	0.6592	0.5182	1
Total C (%)	2	0.9806	**0.002404**	0.01	0.1699	0.8439	1

however, for two reasons: firstly, the robustness of ANOVAs to breach of the assumption of normality is well documented (Blanca *et al.*, 2017). Secondly, main risk of breaching the assumption of normal residual is an increase the rate of type 1 errors (Keselman, 1996). Since we found no significant effect of occupancy on any measured variable, type 1 error is impossible in this case. Additionally, we fitted a logistic model to investigate any interaction between variables (Occupancy ~ the interaction between all measured soil variables). All interactions were statistically non-significant.

2.5.2 Simulating composite landscapes

In order to investigate the effect that wood ant nests and wood ant foraging activities might have on the spatial variability of soil parameters, composite landscapes were simulated by combining synthetic data. These data were sampled from artificial distributions with the same statistical properties as field data from a) the ant-absent forest soils b) non-nest soils in wood ant occupied areas and c) nest soils. For the simulated ant-occupied landscapes, both data from nest soils and from non-nest soil were included, with the number of nest-soil data points determined by sampling from an artificial distribution of nest densities. This nest density distribution was generated using real data of nest abundance in 1km^2 grids over the survey areas.

2.5.2.1 Generating distributions

The empirical data for each variable and occupancy condition combination were used to generate distributions to sample from. Three simulated habitats were created: 'Absent' represents a forest where no wood ants were present; 'Occupied-no nests' represents only the non-nest soils in a forest where ants are present and 'Occupied represents soils in a forest where ants were present and includes the nests (Figure 3.1). 'Absent' and 'Occupied-no nests' simulated habitats were generated by sampling a distribution fitted to real data from soils sampled in forests where wood ants were absent (n=79-80; Table 3.4), or present (n=175-180; Table 3.4) respectively. The 'Occupied' simulated habitat was generated by sampling a distribution fitted to empirical data from cores taken inside wood ant nests (n=20; Table 3.4) combined with data sampled from the fitted distribution based on empirical data from the surrounding soil where wood ants were present. Firstly, the distribution type and parameters were determined using the fitDist() function from the gamlss package version 5.4-3 (Rigby and Stasinopoulos, 2005)and these parameters were used to generate distributions using functions from the gamlss.dist package version 6.0-3 (Rigby and Stasinopoulos, 2005). We corroborated the choice of distribution type by inspecting Cullen and Frey graphs generated using the fitdistrplus package version 1.1-8 (Delignette-Muller and Dutang, 2015) and compared the resulting distributions to the real data. This was done be visual inspection of histograms, Levene's test and Kolmogorov–Smirnov test between the real and simulated data. Total C:Ant-absent consistently failed the KS test ($p < 0.05$) and the Nitrate:Nest distribution showed nonhomogeneity of variance (Levene’s test, $p < 0.05$) but were deemed acceptable for inclusion based on visual inspection across multiple simulations

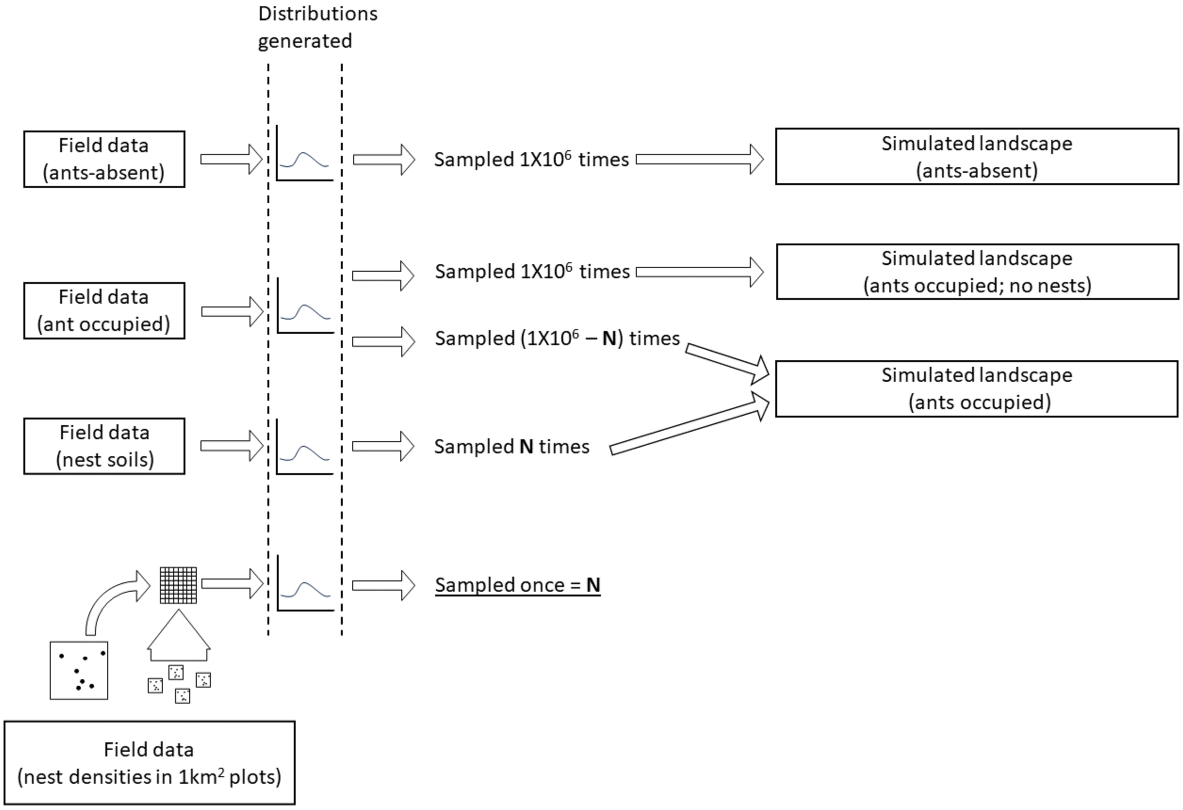


Figure 3.1. Three simulated landscapes were generated: one drawn from a distribution generated from field data in ant-absent forests (ant-absent), one drawn from a distribution generated from field data in occupied forests sampled from non-nest soils only (ant occupied; no nests), and one drawn from a distribution generated from field data of wood ant nest soils at a frequency determined by a distribution generated from field data of ant nest densities at the study site combined with the 'ant occupied' simulated data (ant occupied), for a total of 1x10^6 datapoints per simulated landscape.

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Table 3.4. The sample sizes of the dataset used to generate the simulations presented in Figure 3.5. Only simulated data that fell within the specified confidence intervals were used for pH, nitrate and phosphate to keep the results constrained to real world values.

Variable	N of real data used to generate simulation			Confidence intervals
	Absent	Present	Nest	
B.D.	79	175	20	
pH	80	178	20	.99
Nitrate	79	175	20	.99
Phosphate	80	180	20	.95
% N	80	178	20	
% C	80	178	20	

2.5.2.2 Simulated landscapes

The simulated 'Occupied' landscape was a composite of simulated data from empirical data for both nest soils and non-nest soils in ant-occupied forests, and our simulated landscapes represented a 1km x 1km square where a soil sample had been collected in each $1m^2$. For the purpose of these simulations, the mean area of soil under the direct influence of a nest was assumed to be $1m^2$. The data used to generate the nest density distribution was gathered by overlaying the study area with 1km in QGIS (version 3.32.2) and calculating the number of wood ant nests that fell within each 1km square. Squares outside of the wood ant population margins were excluded, and the resulting nest data were used to generate a distribution of nest density using the methods described above. The simulated landscapes were then generated: for each iteration, a data point was sampled from the nest density distribution. This number would determine the number of times the 'nest soils' simulated data would be sampled, and the dataset would be made up to $1x10^6$ points by sampling from the 'ant occupied' simulated data. An 'Occupied-no nests' and an 'Absent' simulated landscape were generated by sampling all $1x10^6$ points from the ant occupied and ant-absent forest soil data distributions respectively (Figure 3.1). To exclude scientifically invalid values (e.g., pH>14, ppm>$1x10^6$), only data within the 99% (pH, nitrate) or 95% (phosphate) confidence intervals of the simulated data were included in the final simulated habitats (Table 3.4).

2.5.2.3 Coefficient of variation ratio

By calculating the coefficient of variation ratio (Nakagawa *et al*. 2015) of 100 iterations of these simulations, it was possible to quantify the contribution of nest and non-nest soils to variability at the landscape scale. Coefficient of variance ratio (COVR) was calculated as: $COVR = \ln\left(\frac{CV_E}{CV_C}\right)$ (Nakagawa *et al.*, 2015), where CV_E and CV_C are the coefficients of variance ($s/\bar{x}$) of experimental and control group respectively (other terms simplify to zero when the sample sizes are equal). A positive COVR indicates that the numerator has greater variance; a negative value indicates that the denominator has greater variance, and a value of zero means that there is no difference in the variances of the two groups. As a result, the COVR can be used as a stand in for effect size in this simulated data. However, statistical hypotheses testing on simulated data is unsound and the methods used here to generate an effect size for the difference in variance between our simulated landscapes do not offer rule-of-thumb distinctions between large or small effect sizes (Nakagawa *et al.*, 2015), which should be taken into consideration when interpreting the results.

3. Results

3.1 Differences between nest soils and surrounding soils

Bulk density (BD) was significantly lower in nest soils than non-nest soils (paired t-test, df=18, t = 5.498, p<0.01; Table 3.2; Figure 3.2) at both sites. Total Nitrogen (TN) and total carbon (TC) were higher; the median was more than twice as high in the nest soils than the control soils for both (Figure. 3.2). Additionally, for BD, TN and TC, the paired data points consistently trended in the same direction with very few exceptions. Phosphate also differed significantly (Wilcoxon signed rank test, df=19, p<0.01; Table 3.2), being higher in nest soils. When the data from both Cropton and Broxa were analysed together, neither soil nitrate nor pH differed between nests and control soils. The two sites are both on the North York Moors and generally have the same underlying geology (Long Nab Member; sandstone, siltstone and mudstone; British Geological Survey, 2019). We also analysed Cropton and Broxa samples separately for pH and nitrate and confirmed that the significant difference was consistent between sites for other variables; there was no difference in nitrate between treatments at either site (Wilcoxon signed rank test, p>0.1 in both cases). pH at Cropton was highly variable (though never alkaline) and there was no significant difference between the nest and control soils. In contrast there was very little variability in the pH of Broxa samples (Figure 3.3) and a small but significant difference between the nest soil and the control soil pH was found, with the nest soils less acidic than controls (Paired t-test, df=9, t = -3.04, p<0.05; Table 3.2).

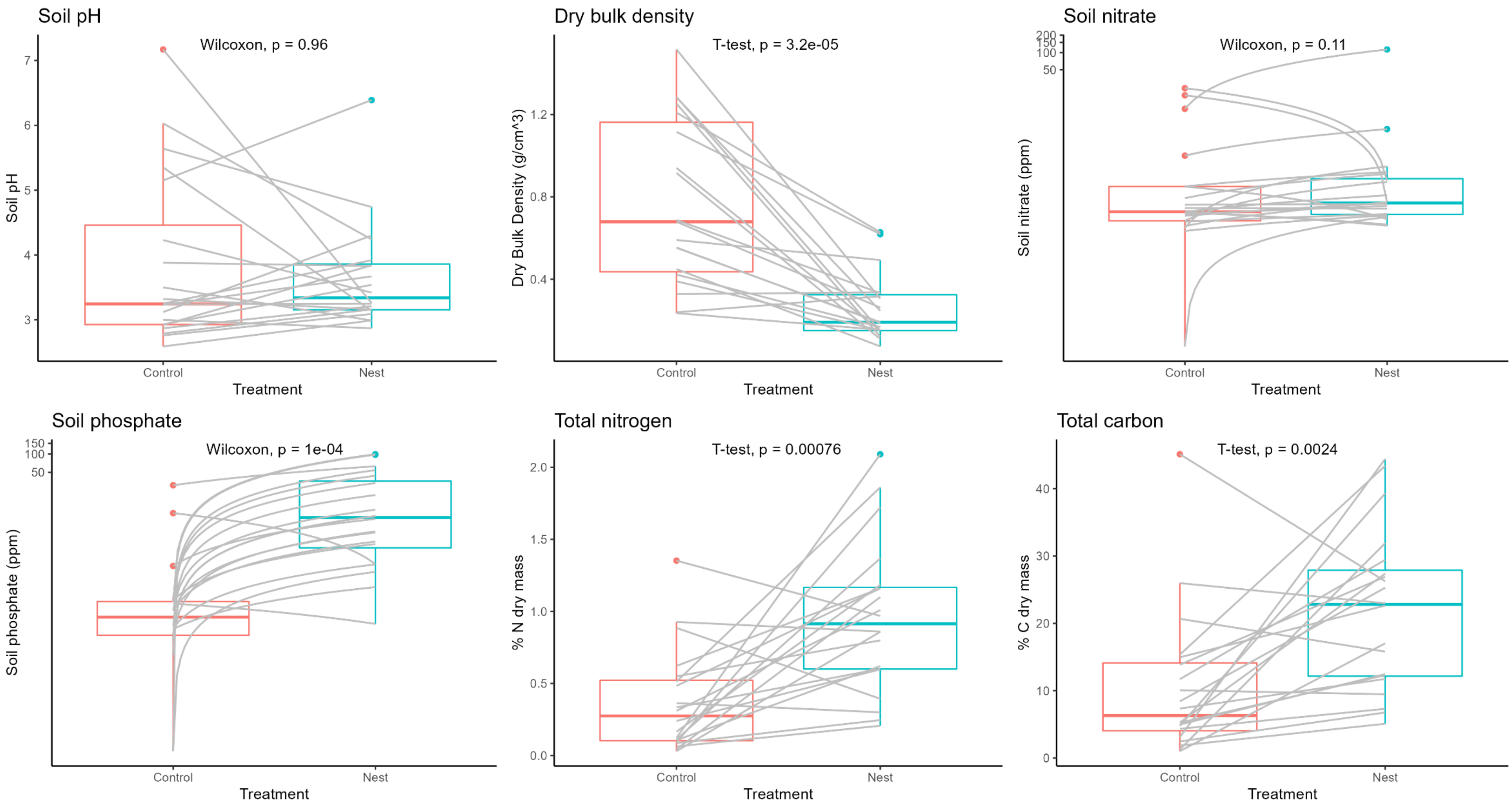


Figure 3.2. Pairs of soil cores were taken from *F. lugubris* nests and control locations 3m from each nest and analysed for 7 soil chemical and physical properties (nitrite omitted above). Nitrate and phosphate are plotted on a Log10 scale (note the curved lines). Lines link paired data. See Table 3.2 for statistical details.

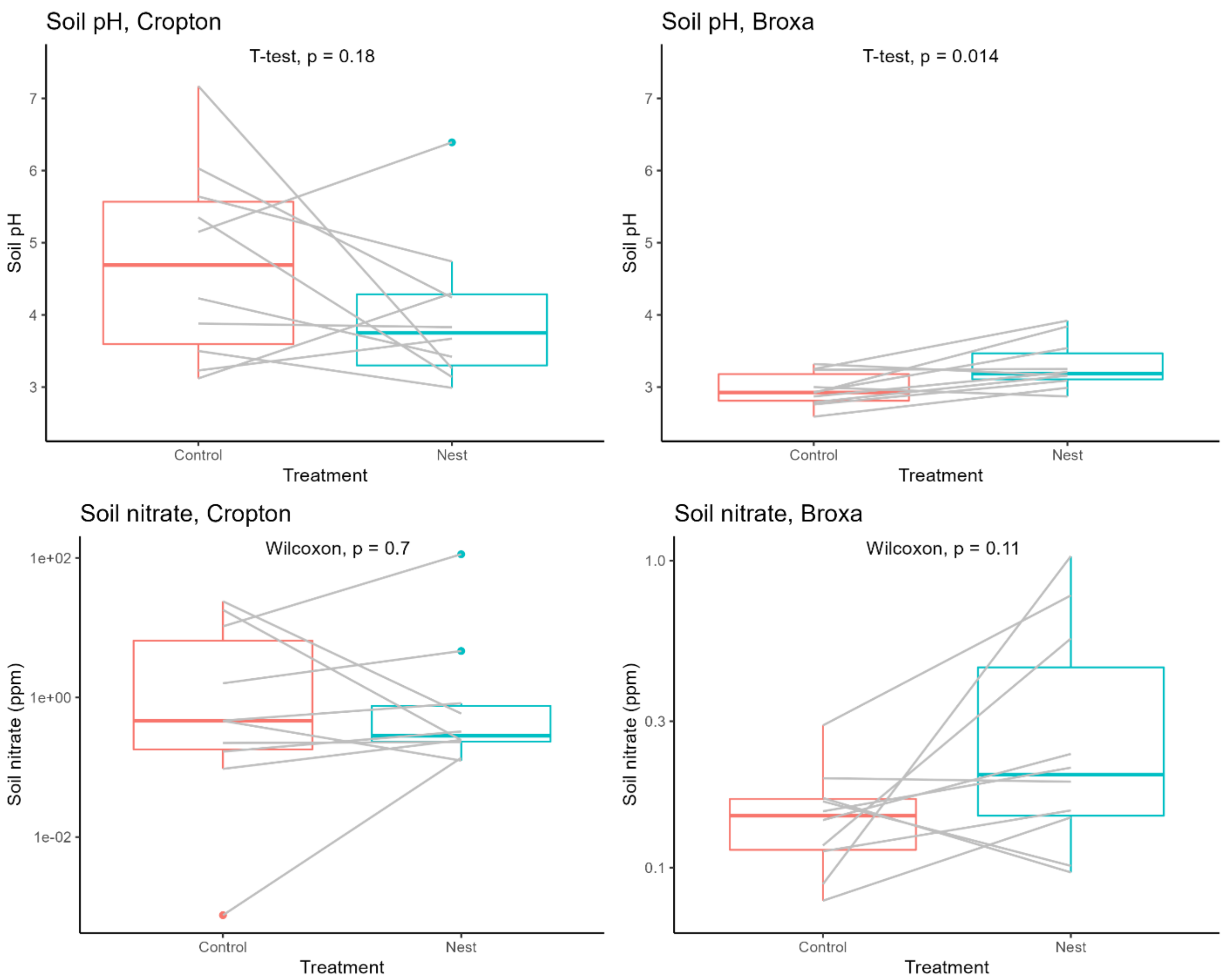


Figure 3.3. Soil core data (paired nest and control soil cores) were collected at 2 sites, Cropton and Broxa forests. Combining data across sites revealed no significant difference between nest and control soils for pH or nitrate (Figure 3.2; Table 3.2); however, patterns were not consistent between the two sites, so the data are presented here separated by site. Lines link paired data. See Table 3.2 for statistical details.

3.2 Effects of wood ants on non-nest soils

Site (i.e., Cropton or Broxa) and/or subsite (sampling region within the two forests) had a statistically significant effect on every variable measured (Table 3.5), suggesting a high level of location-dependant spatial variation in the soils. The depth to the A horizon, pH, and water extractable phosphate were all significantly different between the summer (July) and autumn (September) samples. Only phosphate and nitrate differed significantly between occupancy ages (Nested ANOVA, $p<0.05$; Table 3.5; Figure 3.4) when untransformed. This difference, between 18 and N in both cases, is not apparent from the boxplots of the data (Figure 3.4). This is likely a type 1 error due to the breach of the assumption of homogeneity of variance for both of these variables (Levene's test, $p<0.05$; Table 2). When the data were transformed (natural log) the variance was homogenous, but the difference non-significant (Table 3.5). We collected soil cores from two different sites on the NYM: Cropton (blue) and Broxa (orange).None of the other variables were significantly different between occupancy treatment (nested ANOVA; $p>0.05$ in all cases; Table 3.5).The highly skewed nature of the nitrite data in the long-term occupancy and Broxa recent occupancy (Figure 3.4) suggested that differences between the treatments were not picked up by the initial model; the nested ANOVA does not perform well with highly skewed data and no non-parametric alternatives are available. We therefore attempted several different analyses to rule out the possibility of a type 2 error. A simplified model (formula: nitrite ~ occupancy) using an alternative non-parametric test indicated a statistically significant difference between the occupancy treatments (Kruskal-Wallis, x^2= 81.853, df = 2, $p<0.0001$); however, this model did not include location or season as factors. While transforming the data (natural log) did not result in ANOVA residuals that were not significantly non-normal (Shapiro-Wilks, W = 0.255, $p < 2.2e-16$), a histogram of the residuals (Appendix 1) indicated that they are visually approximate to normal with a right-hand tail. The original model, using the natural log transformed data, showed a significant difference between occupancy treatments, site and site:subsite ($p<0.0001$ in each case). A post-hoc Tukey HSD test showed that all pairwise comparisons were significant, and the effect size was greater between endpoint treatments (N-13) than other combinations, with 2018 treatment being intermediate between the other two treatments (Table 3.6). This is consistent with the hypothesis that wood ant presence is affecting forest soil because the magnitude of the difference between ant occupied and ant-absent forests increases with longer term ant occupancy.

3.3 Estimating wood ant impacts on spatial heterogeneity

Our simulations contained three types of landscape ('Occupied', 'Occupied-no nests', and 'Absent', constructed from our original data;Figure 3.1). Total carbon and total nitrogen were less variable in the 'Absent' landscape, as shown by the high COVR for the 'occupied/absent' and 'no nests/absent' comparisons (Figure 3.5B&H, TC: COVR = 0.24; Figure 3.5C&I, TN: COVR = 0.38) compared with the ‘occupied/no nest’ COVR, which was near 0 in both cases. In contrast, nitrate and phosphate were considerably more variable in the simulated ant-absent landscapes; the ‘occupied/absent’ and ‘no nests/absent’ comparison COVRs were negative and large (Figure 3.5E&K, nitrate: COVR = -0.11; Figure 3.5F&L, phosphate: COVR = -0.2 to -0.3) compared with a ‘occupied/no nest’ COVR of near 0 for nitrate and 0.05 for phosphate. The contribution of the nests to heterogeneity of all variables measured in forest soils was negligible; Plots G-I (Figure 3.5) show that, for pH, total C and total N, the wood ant nests make very little contribution to the variance (COVR for ‘Occupied/No nest’ was near 0) and that the ant occupied habitats are more variable than where wood ants are absent in this simulation (medians: pH=0.17, TC=0.24, TN=0.38). Plots A-C (Figure 3.5) corroborate this; there is less spread in the data for ‘absent’ than the other two groups. Bulk density and nitrate show the opposite trend; Figure 3.5J and K show that ‘absent’ landscapes are more variable, but the difference is relatively small for bulk density (COVR > -0.05). The ‘occupied/no nests’ COVR is still near zero, indicating that the nests are not affecting the variance. This pattern is also visible in single simulation plots 5D and 5E (note the log scale compressing the upper quartile for nitrate; Figure 3.5E). For phosphate (Figure 3.5F and L), the nests introduce occasional extreme values causing COVR for ‘occupied/no nests’ to be slightly greater than zero. Only in extreme cases is this sufficient to affect the relationship between the variances of ‘occupied and’ ‘absent’, where ‘absent is still the more variable (COVR < -0.2). Generally, the soil properties that are likely to be driven by ant nest related processes, such as the incorporation of organic matter into mineral soils, were similarly variable in both ant-occupied and ant-absent simulated landscapes. The COVR of ‘occupied/absent’ and ‘no nests/absent’ comparisons for bulk density were between -0.04 and 0, and 0 and 0.17 for pH as compared to near 0 for ‘occupied/no nest’, indicating that the difference in variability between the simulated landscapes (bulk density slightly more variable in ‘ant-absent’ landscape, pH slightly less variable in the ‘ant-absent’ landscape) is small relative to other variables

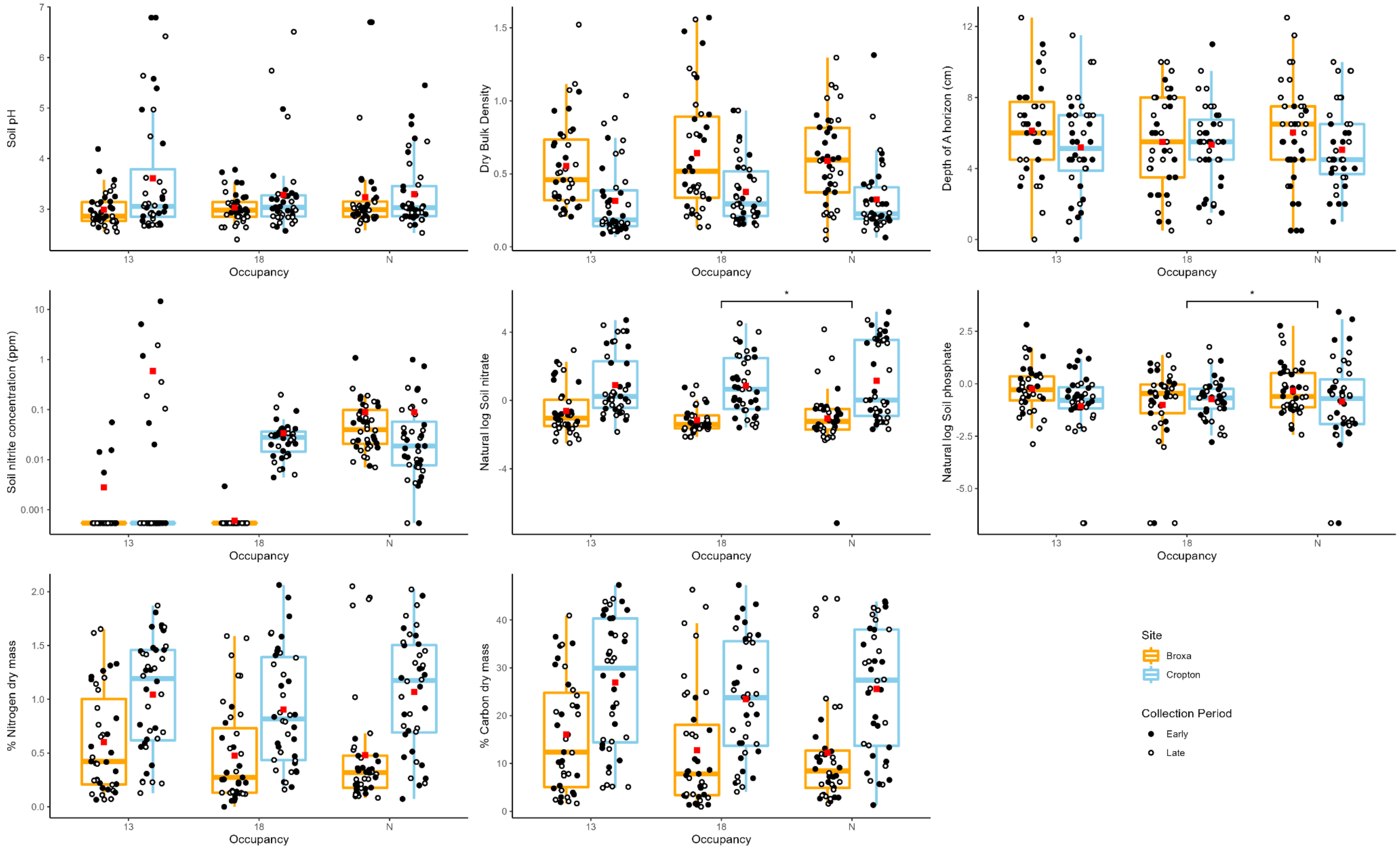


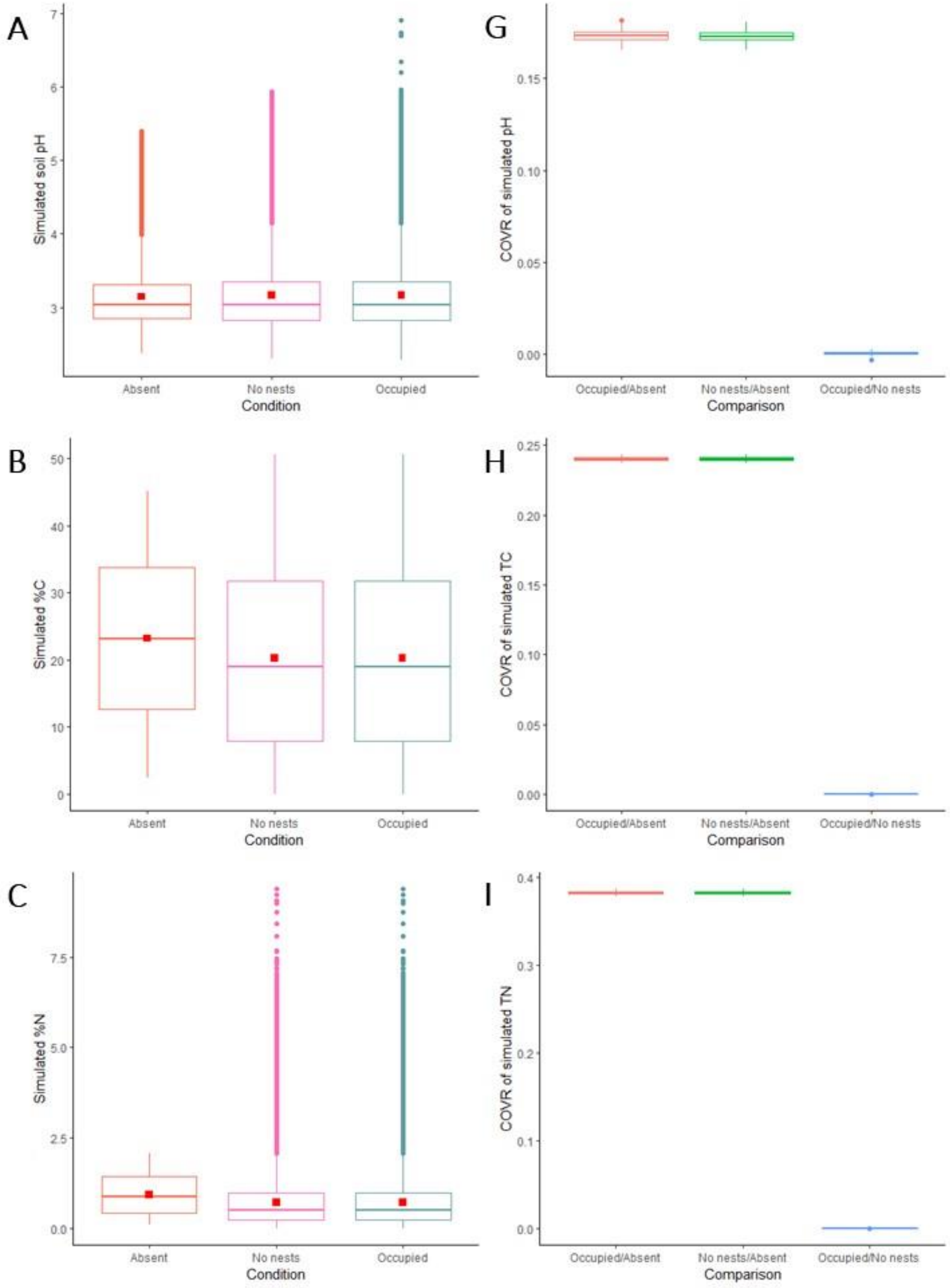
Figure 3.4. 238 soil cores were collected from three different ages of wood ant occupancy (ant-absent: N; 18: *F. lububris* recorded since 2018; 13: since 2013) at two forest sites in the North York Moors and analysed for chemical and physical properties. The points are coloured by collection period (Early/July = solid, Late/September = circle). pH and DOA significantly differed between collection period, and un-transformed phosphate (Table 3.5). The red square indicates the mean value for each combination of site and age of wood ant occupancy. Note logarithmic scale for nitrate, nitrite, and phosphate.

Table 3.5. Soil core data from the forests of different occupancy ages were analysed using a nested ANOVA with fixed and random effects. The model constructed was *occupancy + collection period + site:subsite* with subsite nested within site as random effects. In every case, subsite nested within site and/or site alone was significant (p<0.05), indicated a high degree of within and between site variation. Only nitrate and phosphate were significantly different between occupancy treatments. In both cases, the ant-absent and 2018 occupancy treatments differed significantly. When transformed (Ln) to meet the assumptions (Table 3.2), neither difference is significant. Excluding un-transformed phosphate and nitrate, only the depth of the A horizon and pH significantly differed with collection period.

Nested ANOVA with fixed and random effects	Model:	*occupancy + collection period + site:subsite*						
Variable	***Source of variation***	***df***	***Sum of squares***	***Mean square***	***F-ratio***	***P-value***	***p<***	***Normal residuals***
Depth of A (cm)	occupancy	2	1.1	0.54	0.095	0.90896	1	Yes
	collection_period	1	165.1	165.05	29.026	**<0.0001**	**0.01**	
	site	1	27.4	27.42	4.822	**0.02911**	**0.05**	
	site:subsite	6	114.3	19.05	3.351	**0.00349**	**0.01**	
Dry bulk density (g/cm^3)	occupancy	2	0.25	0.125	1.574	0.209	1	No
	collection_period	1	0.003	0.003	0.036	0.849	1	
	site	1	3.855	3.855	48.643	**<0.0001**	**0.01**	
	site:subsite	6	2.399	0.4	5.045	**<0.0001**	**0.01**	
pH	occupancy	2	0.92	0.46	0.832	0.436632	1	No
	collection_period	1	2.36	2.364	4.272	**0.039873**	**0.05**	
	site	1	5.67	5.666	10.237	**0.001573**	**0.01**	
	site:subsite	6	16.15	2.692	4.864	**0.000107**	**0.01**	
Soil nitrite (ppm)	occupancy	2	3.29	1.6464	1.724	0.1806	1	No
	collection_period	1	1.78	1.7847	1.869	0.1729	1	
	site	1	2.52	2.5226	2.642	0.1054	1	
	site:subsite	6	13.7	2.2827	2.391	**0.0293**	**0.05**	
Ln nitrate	occupancy	2	4.0	2.00	0.709	0.493	1	No
	collection_period	1	0.3	0.35	0.123	0.726	1	
	site	1	244.2	244.20	86.384	**<0.0001**	**0.01**	
	site:subsite	6	86.6	14.43	5.103	**<0.0001**	**0.01**	
Ln phosphate	occupancy	2	4.9	2.442	1.118	0.3286	1	No
	collection_period	1	7.7	7.677	3.515	0.0621	0.1	
	site	1	3.9	3.912	1.791	0.1821	1	
	site:subsite	6	148.9	24.821	11.366	**<0.0001**	**0.01**	
Total N (%)	occupancy	2	0.7	0.349	1.422	0.24331	1	No
	collection_period	1	0.41	0.41	1.669	0.19776	1	
	site	1	14.16	14.157	57.62	**<0.0001**	**0.01**	
	site:subsite	6	4.65	0.774	3.152	**0.00547**	**0.01**	
Total C (%)	occupancy	2	503	251	1.658	0.1928	1	No
	collection_period	1	177	177	1.168	0.281	1	
	site	1	8075	8075	53.253	**<0.0001**	**0.01**	
	site:subsite	6	2465	411	2.709	**0.0147**	**0.05**	

Table 3.6. The mixed model ANOVA of transformed (natural log) nitrite data was analysed with a post-hoc Tukey multiple comparison of means. The samples for the recent occupancy forest (18) were intermediate between long-term occupancy (13) and ant-absent (N) stands, and all pairwise comparisons were significant. 95% confidence intervals are also presented.

Comparison	Difference	Lower	Upper	Adjusted p
18-13	1.006	0.353	1.658	0.001
N-13	3.109	2.459	3.759	<0.001
N-18	2.103	1.452	2.753	<0.001


A
Simulated soil pH
7
6
5
4
3
Absent
No nests
Occupied
Condition
G
COVR of simulated pH
0.15
0.10
0.05
0.00
Occupied/Absent
No nests/Absent
Occupied/No nests
Comparison
B
Simulated %C
50
40
30
20
10
0
Absent
No nests
Occupied
Condition
H
COVR of simulated TC
0.25
0.20
0.15
0.10
0.05
0.00
Occupied/Absent
No nests/Absent
Occupied/No nests
Comparison
C
Simulated %N
7.5
5.0
2.5
0.0
Absent
No nests
Occupied
Condition
I
COVR of simulated TN
0.4
0.3
0.2
0.1
0.0
Occupied/Absent
No nests/Absent
Occupied/No nests
Comparison

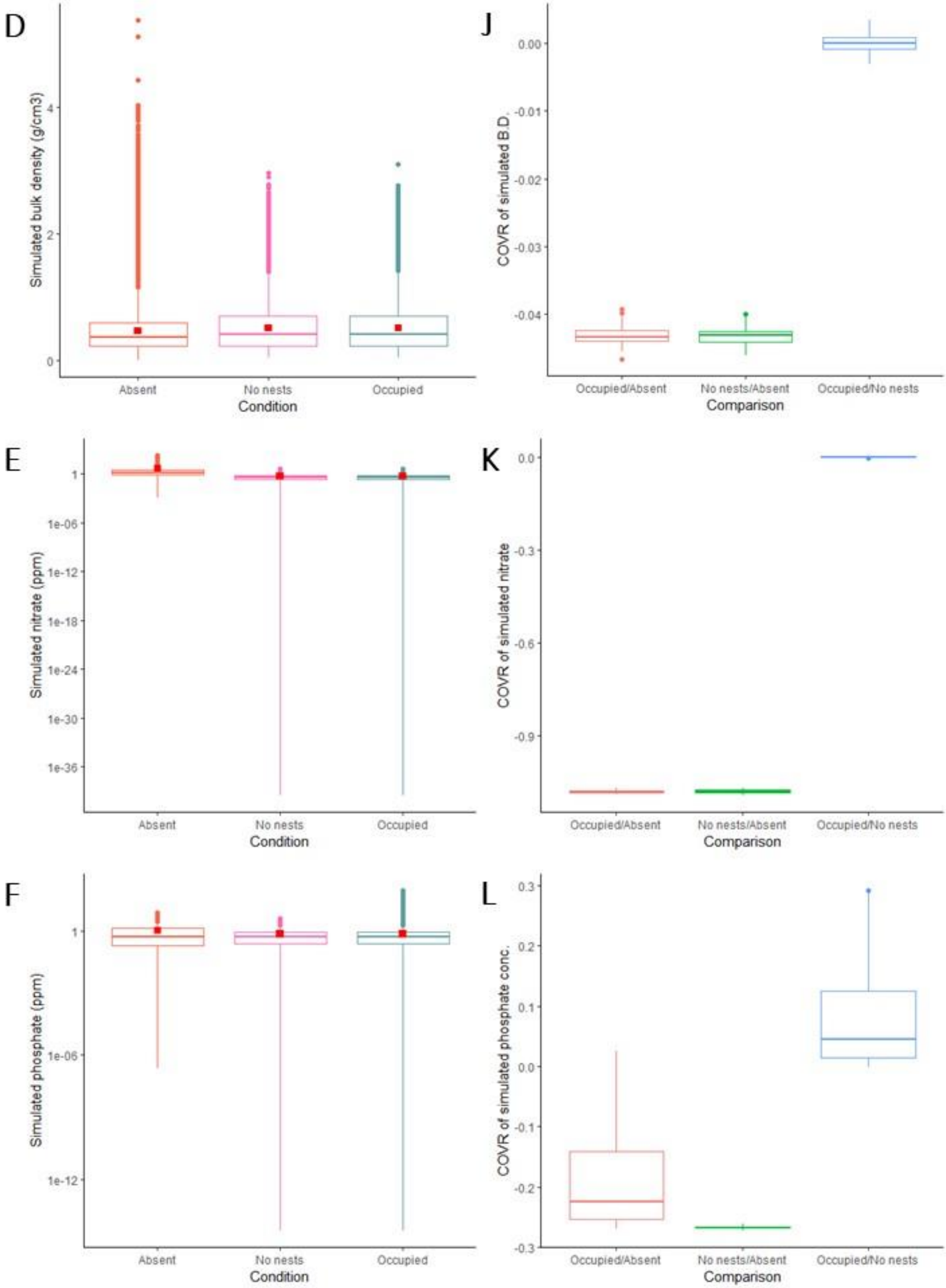

D
Simulated bulk density (g/cm3)
0
2
4
Absent
No nests
Occupied
Condition
J
COVR of simulated B.D.
0.00
-0.01
-0.02
-0.03
-0.04
Occupied/Absent
No nests/Absent
Occupied/No nests
Comparison
E
Simulated nitrate (ppm)
1
1e-06
1e-12
1e-18
1e-24
1e-30
1e-36
Absent
No nests
Occupied
Condition
K
COVR of simulated nitrate
0.0
-0.3
-0.6
-0.9
Occupied/Absent
No nests/Absent
Occupied/No nests
Comparison
F
Simulated phosphate (ppm)
1
1e-06
1e-12
Absent
No nests
Occupied
Condition
L
COVR of simulated phosphate conc.
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
Occupied/Absent
No nests/Absent
Occupied/No nests
Comparison

Figure 3.5. A single simulation of soil variables in three habitat conditions (A-F) and the coefficient of variation ratio (COVR) of pairwise comparisons between simulated habitat conditions, replicated 100 times (G-L). In each case, 1x10^6 samples were sampled from the fitted distributions. Red squares in A-F represent the group means for the individual simulation. For the COVR plots (G-L) positive values mean that the numerator in the comparison (comparisons on the x-axis) was more variable, while a negative value means that the denominator was more variable and a value near 0 means that there was no difference. The simulated landscapes are: 'occupied' = simulation using data from nest soil and non-nest soils in ant occupied forests, 'no nest' = simulation using data from non-nest soils in ant occupied forest only, and 'absent' = simulation using data from forests with no wood ants only.

4. Discussion

Our results show a clear difference between the soil in wood ant nests and the surrounding soil, with the nest soils being enriched in some bioavailable nutrients and organic matter (measured as TN and TC) and a lower bulk density. We also found that nitrite was depleted in the non-nest soils where wood ants were present, and this effect was greater with longer term occupancy, while other soil properties did not differ between the non-nest soils and soils where ants were absent. While there was no difference in the means of most soil variables between ant occupied and ant-absent forests, our simulations showed that, given our empirical data, the organic matter components TN and TC were more variable in ant occupied than ant-absent forest and the inverse was true for the bioavailable nutrients phosphate and nitrate. These differences in spatial heterogeneity were driven by variability in non-nest soils, rather than the presence of nest 'hotspots' in the landscape.

4.1 Differences between nest soils and surrounding soils

Our data are consistent with established ideas about wood ant nests as nutrient hotspots (Lenoir et al., 2001; Risch et al., 2005; Kilpelainen et al., 2007). Total carbon and total nitrogen were consistently higher in the wood ant mounds than the surrounding soils at our sites. This is likely due to the incorporation of organic matter, mostly leaf litter used in nest building, into the soil in the ant mounds, and the mounds relative protection from the leaching effects of rainfall (Kilpelainen *et al.*, 2007). The incorporation of organic matter would similarly explain the lower bulk density in ant mounds found here and the percent total nitrogen and carbon in nest material (medians approximately 1 and 24% respectively) were similar to concentrations found by other studies on closely related species in mixed woodland (Risch *et al.*, 2005; Finér *et al.*, 2013).

The difference enrichment of phosphate in nest relative to control soils could be driven by several non-exclusive mechanisms. Firstly, the accumulation of phosphorus-containing organic matter in the mound results in a greater total quantity of P in the nest, while the increased decomposition rate in the mound converts phosphorus into bioavailable phosphate (Frouz et al., 1997). Secondly, concentrations of available phosphorus may be modified by different pH conditions in the nests; phosphorous, in comparatively neutral conditions such as those often reported in ants' nests (when compared to nearby soils), does not bind as readily to other elements that would make it unavailable to plants (Frouz et al., 2005). Finally, the higher concentration of phosphates in wood ants' nest could be a result of reduced uptake of phosphate by plant roots similar to mechanisms suggested for nitrate (Lenoir et al., 2001). The surfaces of active wood ant mounds are mostly free of herbaceous plants, while the tree root biomass and the occurrence of ectomycorrhizal exploration types is no greater in nest material than surrounding soil (Jilkova *et al.*, 2017). As a result, a small increase in the concentration of total phosphorus in the ant mound because of the accumulation of organic matter will build up because even normal rates of decomposition will outpace the reduced rate of absorption by plants. In fact, the nests of wood ants are generally enriched in plant-available forms of phosphorus compared to reference soils and total phosphorus is enriched to a lesser extent (Frouz et al., 2005). In the present study, we only considered certain plant available forms of phosphorous (phosphate) and found the concentrations to be much greater in the ant nests with comparatively little overlap between nest and control soils. Nearly all soils at these sites were highly acidic, with several samples having $\mathrm{pH} < 3$ for both nest and non-nests soils, and the pH of nest and non-nest soils did not differ when we considered the data as a whole. Only at Broxa was there a difference between nest and non-nest soils, this was very small; the nests were slightly less acidic. The between site differences may be due to differences in historic land management, forest age, and other variables that were not recorded. Although nests soils are closer to neutral in this case, as predicted by Frouz et al. (2003), the small effect size and site dependency of this finding, along with generally very acidic soil, suggests that the phosphate accumulation in ant mounds found in this study is not a result of wood ant mediated changes to pH. More likely, our results were because of accumulation and faster decomposition of organic matter and/or reduced absorption by plant roots.

4.2 Effects of wood ants on non-nest soils

In this our study we found that, excluding nitrite concentration, wood ants did not affect the average concentrations of soil nutrients in the surrounding non-nest soils. Wood ants do, however, affect the spatial variability of these nutrients, and our simulations show that these impacts can result in landscape-level effects on the spatial heterogeneity of the soil. It appears likely that ant effects on non-nest soils are limited to small but abundant patches, allowing them to increase the variability of soil variables without having measurable effects on the regional means of these values. This would explain the different results obtained by an earlier study that focussed on areas of $1.5\mathrm{m}^2$ (Wardle *et al.*, 2011). In this exclusion experiment, C and N mass lost from litter bags was less when ants were present and there was a corresponding increase in C and N storage (Wardle *et al.*, 2011). This predicts that the presence or absence of wood ants alone would have an impact on total C and N in soil surrounding nests. This was not the case for our data. When comparing non-nest soils from areas of forest with different ages of presence or absence of wood ants, we found that sites varied considerably and there was an effect of season on some variables, but not of occupancy (except for nitrite). The effects of wood ants on soil can be highly site specific due to, for example, stand age (Kilpelainen et al., 2007) or other geographic factors (Lenoir *et al.*, 2001) and our study incorporated considerable within-site and between site variation that may have masked effects similar to those found by (Wardle *et al.*, 2011). Our finding that soil properties were more variable in ant occupied sites suggests that wood ants are modifying the availability of soil resources in a “patchy” way at scales closer to 1.5m^2 (Wardle *et al.*, 2011) than our landscape level study. At the small scale, sampling within an ant modified patch might lead to the conclusion that wood ants change the mean nutrient concentrations in soils, whereas sampling at the landscape scale (for example, 50m; the length of our transects in this study) may lead to the pooling of modified and unmodified patches and the conclusion that ants do not change mean concentrations of nutrients in soils at the landscape scale. Neither of these conclusions would be wrong, but both would be incomplete. This study highlights the necessity of examining the effects that ecosystem engineers have on their environment at multiple spatial scales where possible, to build a complete picture of the impacts.

Our clearest evidence for a landscape scale impact of wood ant on the surrounding soil comes from our measures of nitrite (NO_2). Our results showed nitrite concentrations in soils from areas with long-term wood ant occupancy were considerably lower than in areas where the wood ants were absent; where wood ant occupancy was recent (<8 years) nitrite concentration was partly site-dependant, but generally lower in the wood ant occupied sampling sites relative to ant absent sites. This is striking, because the concentration of nitrate (NO_3), which nitrite is the precursor to in the soil nitrogen cycle, was not affected at this scale. One possible mechanism for this is that wood ant foraging removes high-quality organic matter (nest material and honeydew through-fall, for example), causing less high-quality organic matter to enter the soil. This removal will have effects on the microbial community in the soil (Wardle *et al.*, 2011), potentially leading to changes in the rate of nitrification (Laganière et al., 2009) that could in turn lead to the reduced production or depletion of nitrite we observed, while nitrate uptake may be limited by the plant root absorption rates. If this were the case, further work would be required to determine if this was due to a change in the rate of microbes nitrifying ammonia to nitrite or the rate of nitrite to nitrate nitrification. Our highly skewed data indicate that even nitrite had a patchy distribution in the soil; where wood ants were present, the majority of soil samples had near-zero concentrations of nitrite with a small minority containing as much as 10ppm of nitrite. This suggests that nitrogen-rich material is highly clumped in wood ant occupied forests, and these patches could be areas rich in invertebrate prey or carrion, as both are nitrogen rich and high value food resources for the wood ants. Because wood ants can discriminate between good and bad food patches (Lenoir, 2002) they may remove many of these good patches by recruiting large numbers of workers to them. Newer, less accessible, or undiscovered, patches would remain and result in the patterns we observed in the data. It may be that that wood ant foraging behaviour is responsible for changes in the nitrite dynamics in wood ant occupied forests.

While foraging behaviour may be the cause of differences between ant occupied and ant-absent forest stands, it remains unclear exactly how the lower input of higher quality organic matter would lead to the necessary changes in the microbial community to cause such a reduction in nitrite concentration. This effect could instead be related to the wood ants' role as predators of soil invertebrates. Reduced soil invertebrate abundance slows decomposition rates (Figueroa et al., 2021). Conceivably, the wood ants could suppress soil invertebrates through predation, downregulating their role in processing soil organic matter and making it available to microbial metabolism. If this were the case, we might expect that the lack of invertebrate procession of organic matter might lead to less surface area available for microbial colonisation and therefore slower rates of decomposition, ammonification, and nitrification. This could cause the lower observed concentrations of soil nitrite in ant occupied forests. The literature does not support this hypothesis, however; the effect of *Formica* wood ants on soil-fauna is negligible (Lenoir et al., 2003) and where effects are reported, only larger, predatory invertebrate abundance and diversity is suppressed (Laakso, 1999) either by direct predation or interference competition (Thunes et al., 2018). On the other hand, soil communities with a high abundance of macroinverebrates may have a faster rate of organic matter cycling than a similar one with lower macroinvertebrate abundance (Laganière et al., 2009). If *F. lugubris* suppresses larger invertebrates in this system, this mechanism might explain the lower nitrite concentrations via slower cycling of organic matter upstream of microbial processes, assuming the ants themselves do not compensate the lost function of other macroinvertebrates in this system. Either way, the very rapid rate of nitrite conversion to nitrate in the soil (Isobe *et al.*, 2012) and the high nitrite consumption to production ratio in acidic soils such as our study sites (Yang *et al.*, 2018) suggest that even small changes to the mechanisms regulating nitrite concentrations could have large magnitude effects. Because toxic nitrite rarely accumulates on soils, its presence in the ant-absent forests potentially indicates the degradation of the soil in plantation ecosystems (Shen, Ran and Cao, 2003). Because nitrite accumulation was lower in ant occupied forest stands, we suggest that the presence of wood ants is causing the nitrite dynamics of plantations forests to resemble less degraded ecosystems.

4.3 Effect of wood ants on spatial heterogeneity of soil properties

Our simulations used field data from nests, ant occupied forests and forests without wood ants to simulate the effects of ants on spatial heterogeneity of soil properties at the landscape scale, and we found that some bioavailable nutrients were less variable in availability where wood ants were present, but organic matter content was more variable. Wood ants have been suggested to contribute to spatial heterogeneity due to the 'hotspot' effects of their nests. (Lenoir et al., 2001; Jílková et al., 2011; Jílková et al., 2020). Because the resulting heterogeneity of simulated ant occupied landscapes was no different with or without nest data included, it seems that the nests found at our sites, while numerous, are insufficiently abundant for the differences between nest soils and non-nest soils to contribute detectably to spatial heterogeneity at the landscape scale. Instead, the landscape-level differences in spatial heterogeneity we observed were driven by the non-nest soils. In our empirically grounded simulations, organic matter content (here measured as total C and total N; Saini, 1966), was more variable where wood ants were present, and this increased variability is likely to be driven by the displacement of organic matter by the ants. The content of organic matter in soils increases with distance from nests of *Formica polyctena*, and needles are removed from a diameter of up to 8m from the nest (Jílková et al., 2011). This strongly indicates the existence of a 'shadow' around the nest, where litter removal for mound building results in the soil being depleted of organic matter over an area much larger than the nests themselves. Whereas the nests themselves occupy too small an area to have measurable effect on the spatial heterogeneity for the scales we considered, this large 'shadow' might result in the increased variability in simulated Total C and N where wood ants are present because nest-building organic matter is an abundant and low value resource that the ants are unlikely to carry great distances, creating an area near the nest slightly reduced in organic matter.

In our empirical data, we found that wood ant presence had an effect on the variability of nitrate and phosphate concentration, and our simulations show that this effect is big enough to be ecologically relevant; both were more variable where ants were absent than where they were present. Organic matter from plant sources, such as needle litter is less rich in N and P that animal sources (Mattson, 1980; Elser *et al.*, 2000; Fagan *et al.*, 2002; Woods *et al.*, 2004; Bertram *et al.*, 2008) and the quantity of N and P input to wood ant nest from invertebrate prey is greater (per gram of dry mass) than from honeydew (Domisch *et al.*, 2009). Because wood ants can judge the quality of food patches (Lenoir, 2002), the ants will exploit resources such as larger invertebrates or carrion that may serve as a source of valuable protein for raising wood ant brood. In doing so, they may remove what would otherwise become patches with elevated P and N after decomposition and we would have detected the bioavailable portion of this in our sampling as nitrate and phosphate peaks. This is also consistent with the reduced accumulation of nitrite we observed in ant-occupied areas from our empirical data, indicating that resource removal is the mechanism of effects on soil properties in non-nest soil. Our field data of phosphate and nitrate were highly skewed, with a small number of extremely high values and this was reflected in our simulations. Similar to nitrite, this indicates a spatially heterogeneous nutrient landscape that was dominated by a small number of very nutrient rich patches. By removing dead matter, the ants remove the patches and reduce the number of extremely high values in the dataset, resulting in lower variance. In this way, wood ants could be reducing the spatial heterogeneity of soil nutrients where they are present. The ratios of N and P in invertebrates and needle litter suggest that the removal of necromass may be contributory to this effect. Nitrate concentration was many times more variable than phosphate in our simulated ant-absent landscape, the high N:P ratio in our empirical data is indicative of invertebrate, rather than plant, origin for the extremely high values;

needle litter has a N:P of 17 (Scots Pine; Berg and Staaf, 1980) whereas the N:P of an invertebrate is closer to 30 (Texas field cricket, *Gryllus texensis*; Bertram et al., 2008).

Alternatively, both the observed reduction in variation and frequency of extreme values of nitrate and phosphate could be explained by the displacement of other insectivores, as another potential source of extreme values is faecal matter from birds and small mammals. The Eurasian treecreeper and several species of tit forage for less time in trees where wood ants are present (Haemig, 1992, 1994; Jäntti *et al.*, 2001) and high-density wood ant populations may reduce bird abundance and diversity of birds via competition for insect prey (Catzeflis, 1979). If insectivorous birds spend less time in areas with high ant densities, their faeces will be less abundant in these areas. Whether directly or indirectly, it seems likely that the reduction of the spatial heterogeneity of nitrate and phosphate concentrations is driven by wood ant predation and scavenging.

Based on our empirical data and simulations, wood ants have little impact on the spatial heterogeneity of bulk density and pH; the variability is similar with or without ants. The pH (Jílková et al., 2011) and bulk density (Saini, 1966) of soil samples are indirectly affected by the organic matter content. While the contribution of wood ants to C flux into nest soils as a proportion of total needle litter fall is large relative to the area of the forest floor the nest cover 2-6% (2-6%; Domisch et al., 2009), it is small compared with the total mass of organic matter entering the soil and indicates that displacement of organic matter alone by the ants is inadequate to drive much change in these two variables.

4.4 Soil properties in ant inhabited landscapes

Overall, the effect that wood ants have on the soil environment is more complex than previously thought. As a result of the contrasting direction of effect on spatial heterogeneity that we found for phosphate and nitrate compared to total carbon and nitrogen, some areas would see high heterogeneity of low-quality resources at the expense of high-quality resources, while other areas, where ants are absent, would see the reverse. In this way, the presence of wood ants may make a meaningful contribution to plantation forest heterogeneity, resulting in a soil landscape that exhibits the high levels of variability reminiscent of natural woodland. *F. lugubris* presence usually results in a landscape dotted with their nests, and these will be enriched in plant-available P, C and N as a result of the incorporation of organic matter. The area around the nest is slightly reduced in N and C, indicative of the removal of needle litter. The removal of protein sources by the ants may reduce the spatial heterogeneity of phosphate and nitrate in the non-nest soils of ant occupied forests, directly or by their interactions with vertebrates. As a result, it seems that ants promote the spatial heterogeneity of low quality (slow to decompose) soil resources and reduce the spatial heterogeneity of high-quality resources. We could not detect an effect of wood ants on absolute values of soil properties at the landscape scale, in contrast to previous studies on small scales, and we suggest that this is because wood ants impact soil in a way that is patchy on scales smaller than 50m. Because the wood ants are unable to utilise large areas of the interior of these plantation forests due to shading (Chen and Robinson, 2014; Procter et al., 2015), their real effect on spatial heterogeneity is likely to be greater, since their nests are not uniformly distributed within their populations.

Many ant species have been shown to alter the soil in their nests (Farji-Brener and Werenkraut, 2017) and this is partly due to their role as major agents of resource removal (Griffiths et al., 2018). What we have shown here is that the resource removal has impacts on the heterogeneity of the nutrient landscape at a scale larger than the nests, but smaller than the forest stand scale. This scale of heterogeneity has been shown to be important for invertebrate (Niemelä *et al*., 2013) and plant (Ozinga *et al*., 1997) diversity, both of which could be important contributors to biodiversity in species poor ecosystems, such as those under intensive management.

Overall, we highlight the importance of studying ecosystem engineers at a variety of spatial scales where possible to build a complete picture of the effects that ecosystem engineers have on their environment. Finally, we suggest that wood ants could play a role in changing the soil of heavily disturbed and managed plantation forests to a state more closely resembling late successional stages in the accumulation of toxic nutrients and in the spatial heterogeneity of soil resources.

Chapter 4 - Wood ants on the edge: how do the characteristics of linear edges effect the population dynamics of an edge specialist?

Abstract

The dispersal of species is influenced by the landscape structure, as some features present less of a barrier to to species movement than others, while some may facilitate dispersal. Slow-dispersers and species with specific habitat requirements will be most affected by landscape heterogeneity because they are less likely to encounter suitable habitat within their limited dispersal radius. Edge specialists require two adjacent habitats and are therefore often affected by local topography and the land management practices. The northern hairy wood ant, *Formica lugubris*, is a slow dispersing edge specialist that requires adjacent forest and open habitat to access aphid honeydew, invertebrate prey, and direct sunlight for thermoregulation, so typically only occupies canopy gaps in plantation forests. The predominating form of canopy gaps in plantation forest are paths, firebreaks, and roads (collectively termed 'rides'), and their orientation will determine the shade distribution. Using 10 years of population mapping in conjunction with recent data collection, we ask how properties of rides, such as bearing and width, affect the distribution and dispersal of wood ant populations in the North York Moors. We found that nests were more abundant on the north side of rides, where they receive more sunlight, for canopy gaps of all orientations and that nests were generally larger on narrower rides. Furthermore, we found that *F. lugubris* dispersed approximately 3 times as fast along rides that were oriented along cardinal bearings (N, S, E, W) than on ones oriented along intercardinal bearings (NE, SE, SW, NW) although N-S bearings were used more symmetrically than E-W bearings, where the south facing side was predominantly used. Given the slow documented rate of dispersal for this species (approximately 50m/year), this difference is ecologically significant. Due to the role that wood ants can have in the mitigation of defoliating pests, the effect of ride orientation on wood ant spread likely has forest management implications. Additionally, the dispersal of other edge-specialist species that utilise linear canopy gaps could be affected in the same way as *F. lugubris*, having consequences for conservation and silviculture that should be considered when planning new areas of plantation forest.

1. Introduction

1.1 Why does species movement matter?

The ability of species to move through a landscape can have major implications for the conservation of biodiversity, and for preventing species loss in a changing climate (Mendenhall *et al.*, 2014; Lenoir and Svenning, 2015). How porous a landscape is to species movement will also affect the dispersal of species, and this porosity may be determined by the contrast between one habitat and the next. Low contrast edges between forest patches and agricultural land in Costa Rican countryside ecosystems are more porous to bats than high contrast edges between forest patches and open water in Gutan Lake, Panama, and forest patches in the agricultural ecosystem harbour higher bat species richness as a result (Mendenhall *et al.*, 2014). The permeability of habitats to species may become even more important as a result of climate change induced range shifts along latitudinal or altitudinal gradients (Lenoir and Svenning, 2015). This highlights the critical role that species movement can play in the conservation of biodiversity, in contrast to the well documented negative economic (Cuthbert *et al.*, 2022) and environmental (Pyšek *et al.*, 2020) effects of species invasions.

Natural linear features such as rivers, coasts, habitat edges, and mountain ranges, or anthropogenic ones such as roads, railways and canals can be major facilitators of species movement and invasion, providing corridors of suitable habitat for certain species through otherwise inhospitable areas. For example, wind-dispersed seeds and their proxies travelled nearly four times further along linear forest disturbances than in undispersed forest (Roberts *et al.*, 2018) while, in a meta-analysis, 70% of studies indicated that either plant abundance or diversity was higher along linear gaps and verges than habitat interiors (Suárez-Esteban *et al.*, 2016). By facilitating the dispersal of food plants, linear features can indirectly promote the dispersal of invertebrate herbivores. Ragworts (genus: *Senecio*) disperse along anthropogenic linear features (e.g., oxford ragwort dispersal along railways; Harris, n. d.), while the cinnabar moth (*Tyria jacobaeae*) is more successful at dispersing and laying eggs on their host, *Senecio jacobaeae*, in alpine areas with roads and valleys than in areas where no linear features exist (Brunzel et al., 2004), suggesting that invertebrates may derive similar benefits from linear features as their plant hosts.

The role that linear features can play in the movement of species can be exploited for conservation purposes, as in the use of habitat corridors to connect smaller areas of protected land and reserves (Bennett, 1990; Brito *et al.*, 2017). However, benefits of habitat corridors to some species have been questioned, due to the potentially asymmetry in their benefits to habitat generalist and specialists: landscape corridors connecting areas of fragmented forest in south-eastern Estonia facilitated the dispersal of generalist plant species more than forest specialist species, (Liira and Paal, 2013).

Regardless of whether they are beneficial to specialists and generalists equally, the presence and structure of edges can have implications for species movement and survival in certain contexts.

1.2 Forest edges

The edges of forests are important for understanding the population dynamics of forest-dwelling species. Edges can serve as beneficial habitat to generalist species because it represents an area of low quality or inhospitable forest that effectively reduces the habitat available to forest interior specialists, or as a unique habitat that is required for certain edge specialist organisms to flourish (Lövei et al., 2006; Ruete et al., 2017; Taylor et al., 2008). On the other hand, interior specialists have a competitive edge over generalist species that can survive both in the forest 'islands' and the 'sea' of non-forest habitat in large patches because larger patches have more interior habitat where interior specialists are favoured; species richness of generalist ground beetles is lower in larger areas of forest than smaller ones (Lövei et al., 2006). In addition to the effect of patch size, the forest patch edges themselves can be detrimental to forest specialists; in black spruce forests in eastern Canada, the effects of edges on ground dwelling spiders extended 30-50m into the patch. This meant that the theoretical minimum size for a forest patch to harbour interior specialist spiders was 100m wide (Larrivée et al., 2008). Overall, small patches are detrimental to forest dwellers and, having a higher edge:area ratio, more permeable to non-forest specialists, while patches larger than 100m wide would have the capacity to support interior specialist ground dwelling spiders and, at its edges, also supporting generalists and edge specialists.

The huge amount of anthropogenic change in natural forests, and creation of large areas of plantation forests, mean that human activities determine the present distribution and fragmentation of most forests. This makes the study of how fragmentation and edge habitats impact species dispersal important for conserving species in increasingly anthropogenic habitats. The structure of forest fragments and distribution of edges is especially important in the context of anthropogenic forests because the history of the edges themselves can cause differential effects on different species and their movement. Anthropogenic edges, which are maintained by recent human disturbance, are less permeable to forest specialist carabids (Magura *et al.*, 2017) and fungi (Ruete *et al.*, 2017) than edges maintained by natural processes. In the context of plantation forest or any kind of managed woodland, this highlights the degree of influence that management of edges in forests can have of on all species including edge specialists.

Plantation forests represent a significant portion of forested area in the UK (Defra, 2021) and the management of these forests for timber necessitates canopy gaps to provide access for forestry machinery and timber planting or harvesting, in addition to firebreaks, geographical features and land ownership boundaries that constrain where can be planted. Many of the resulting canopy gaps will be linear. These gaps can harbour a distinct fauna (Oxbrough *et al.,* 2006) and flora (Smith *et al.,* 2007) from the interior of stands, providing refuges for species that might otherwise be unable to tolerate the planation environment. Some spider species found in rides greater than 15m wide in plantations forests in Ireland are absent from the forest interiors (Oxbrough *et al.,* 2006). Sunlight would seem to be an important factor in the differences in species richness and composition between canopy gaps and the interior of stands; the species richness of vascular plants is lower in more shaded rides (Sparks *et al.,* 1996), while shaded areas are richer in bryophyte species (Smith *et al.,* 2007). The presence of different species compositions in rides indicates that these features play an important role in maintaining biodiversity in the plantation environment.

The ability of the rides to harbour distinct communities is dependent on characteristics of the rides that are dependent on management practices, such as width. Rides narrower than 15m do not support a distinct spider fauna, as rides greater than 15m do (Oxbrough *et al.*, 2006), while similar results have been found for vascular plants (Smith *et al.*, 2007). Ride orientation also influences the suitability on rides for certain species; in southern England ground spiders (Lycosidae) are more abundant on south facing edges, while ground beetle (Carabidae) abundance is unaffected by ride orientation (Carter *et al.*, 1991), while no effect of edge orientation was found on any invertebrate group studied in northern Finland (Jokimäki *et al.*, 1998). These studies have focused on taxonomic groups, while some individual species may be edge specialists and may respond differently to the characteristics of rides.

1.3 Edge specialists

1.3.1 Why are some organisms edge specialists?

Some species are more abundant in edge and transitional habitats between forest and open area because edges also allow species to benefit from two habitats at once. In Australia, the noisy miner (*Manorina melanocephala*) is considered an ‘aggressive edge specialist’, strongly favouring the edges of forests (Major *et al*., 2001; Taylor *et al*., 2008) because it allows them better visibility to defend their territory and exclude other birds (Loyn, 1987). White-tailed deer (*Odocoileus virginianus*) are thought to spend more time foraging at forest edges because it allows them to benefit from the greater food resources in open habitats whilst remaining close to cover and a potential refuge from predator (Williamson and Hirth, 1985). Similarly, plants may benefit from improved seed dispersal or pollination opportunities provided by the edge habitat (Lamb and Mallik, 2003) while maintaining the benefits of shelter and nutrient availability (Weathers *et al*., 2001) from the forest.

The preference of some species for edge and transitional habitats may be because they are merely 'edge-tolerant' generalists that can thrive where specialists of the bordering habitats cannot and encounter less competition as a result (Ries and Sisk, 2010), rather than having any particular adaptive preference for edges. However, this criticism of the edge-specialist concept is primarily a problem for highly mobile species, such as butterflies (Ries and Sisk, 2010), as edge specialists; if a poor disperser or a sessile species is more abundant in edge habitats than anywhere else it would undergo serious decline were the edges removed (its main habitat is the edge habitat), while a mobile species can utilise edges when available and survive in bordering habitats when they are not.

1.3.2 How can edge characteristics affect edge specialists

Because of the importance of edges to some species, some study has been directed at the question of which qualities of edges are important for determining the population dynamics. The geometry of the edge can be a consideration; the presence of complexities in the forests edge, such as corners, projections, and peninsulas of vegetation, are good predictors of noisy miner (*M. melanocephala*) occupation (Taylor *et al*., 2008). Both edge geographical orientation (henceforth: bearing) and corridor width affect the diversity and composition of butterfly communities, with a greater diversity of forest dwelling butterflies found on shadier south-facing edges (southern hemisphere). Additionally, transient butterflies were less strongly affected by edge bearing than less mobile ones (van Schalkwyk *et al.*, 2022). On the other hand, communities of leaf miners, parasitoids and plants seen to be relatively unaffected by differences in light availability due to bearing (Bernaschini *et al*., 2020). All of these studies show effects of edges on population distributions, and it is therefore likely, though much less studied, that the characteristics of edges and corridors, especially bearing and width, could affect the dispersal of organisms.

1.3.3 *Formica lugubris* as an edge specialist

Formica lugubris is one of three species of wood ant in the *Formica rufa* group found in the UK and the only one that is common on the North York Moors. The UK populations of *F. lugubris* establish new nests exclusively by budding: a mated queen and some workers leave the maternal nest on foot to establish new nests (Maeder *et al.*, 2016). As a result, they are very poor dispersers and previous data suggest that the North York Moors *F. lugubris* population margins grow by less than 50m per year, despite suitable habitat for colonisation (Procter, 2016). In this population, 78.5% of *F. lugubris* nests are found within 10m of canopy gaps (Procter *et al.*, 2015) and they are more likely to be encountered on the north side of gaps (Sudd et al., 1977). The preference for canopy gaps (especially those facing south) corresponds well with what we know about the habitat requirements of *Formica lugubris*: whilst they require honeydew from arboreal aphids as the ants' main source of carbohydrate, they also require sunlight to regulate the temperature of their nest (Domisch *et al*., 2016). Because these wood ants require direct sunlight from canopy gaps, their potential for dispersal and population expansion will be to some extent dependant on the distribution of shade. In managed forestry land where canopy gaps in the form of fire breaks, access roads, footpaths and felled areas are abundant, the distribution of shade will be determined by management decisions made during planting and ongoing management practices, and this raises the question of how characteristics of rides affect the population dynamics of *F. lugubris*?

1.4 Hypotheses and questions

The orientation of linear canopy openings has the potential to affect both the abundance and dispersal ability of wood ants. In plantation forests, such as the sites on the North York Moors, the majority of canopy gaps are anthropogenic: the results of roads, footpaths, firebreak, non-selective row thinning (henceforth: rides) and the transition from one stand age/species to another. As a result, these canopy gaps are often long (sometimes several kilometres) and usually straight. Along canopy gaps that run approximately east-west, the shadier (south) side of the ride will receive little insolation, so we would predict that wood ants would be less able to utilise nesting sites on the south side of these rides, and we would almost exclusively find nests on the north side. Both sides of canopy gaps that run north-south will receive sunlight for part of the day, so we would expect that both sides of these rides would be suitable for wood ants to build nests. However, because neither side of an N-S ride would receive as much sunlight as the north side of an E-W ride, we might expect to find larger or fewer nests than on a similar E-W ride. Finally, we would predict that the width of a ride could affect wood ant abundance: narrow rides with tall trees on the south side will experience partial shade on the north side as well, so we would expect fewer, larger nests on narrow rides and more, smaller nests on wider rides. The width-volume/abundance relationship will be non-linear; for rides wide enough that trees on the south side cast no shade on the north side of the ride, we would not expect to see differences in nest abundance or volume because insolation is already maximal. Because of the importance of direct sunlight for *F. lugubris*, we expect that differences in the duration and pattern of light availability in linear canopy gaps caused by these two factors, orientation, and width, will affect success of the wood ant populations in different locations within plantation forest.

Because *F. lugubris* establish new colonies by budding, the suitability of potential nest sites and the health and size of the parent colony will be determining factors in the rate of new nest founding (Ellis and Robinson, 2014). We predict that, because the orientation and width of rides will affect the abundance of ants and ant nests, the rate of new nest establishment will also be affected, and this will correspond to a faster rate of population margin expansion on rides where the orientation and width favour greater abundance. We conducted a survey of canopy gaps and edge characteristics in plantation forest of the North York Moors, and combined pre-existing long-term monitoring data with new data on wood ant populations at the study sites to answer the question how do characteristics of rides affect the population dynamics of *F. lugubris*? We tested the following hypotheses:

H1 - The orientation of anthropogenic canopy gaps (degrees from N; 0-90°) affects wood ant nest a) abundance and b) total volume along those canopy gaps.

H2 - The orientation of anthropogenic canopy gaps (degrees from N; 0-90°) affects wood ant dispersal rate along those canopy gaps.

2. Methods

2.1 Ride selection: abundance and volume measures

Rides suitable for testing the hypothesis that canopy gap orientation will affect wood ant nest abundance and volume (H1) were identified prior to the field survey using pre-existing long-term data on wood ant population in the North York Moors (Procter *et al.*, 2015) to conduct a desk survey. A ride was defined as a linear feature causing a break in the canopy at least 5m wide, starting and ending where they intersected other rides or reached the end of the forest. Examples of rides included linear canopy gaps due to roads and footpaths, as well as gaps caused by forest management such as areas of row thinning (strips of trees harvested at intervals, leaving most of the crop standing) or fire breaks. We measured the length of the wood ant-occupied portion of the ride from the oldest nest on it to the nest furthest from the source population. The population margins and the source identified using long-term data on the wood ant populations in the North York Moors (Procter, 2016; Holgate, 2021; Chapters 3&4). For rides with nests along their entire length, this measurement equalled the total length of the ride. When mapping the margins, the survey attempt was stopped if no nest was encountered for 200m, as this is far greater than typical dispersal distance for this species, consistent with the long-term data on these populations that we used (Procter *et al.*, 2015). Rides were considered to have ended if the ride entered a stand of different tree species, age/tree height, or rounded a corner (ride bearing changes by more than 15 degrees). We measured the length and bearing of the ride using the *Measure tool* in ArcGIS Pro version 2.3.3, connecting the first and last nest on the ride.

2.2 Selecting rides for calculating rate of expansion

In order to determine whether ride bearing affects wood ant dispersal, we required a subset of rides at the population margins, where population margin expansion could have occurred during our study period, allowing us to use long-term wood ant monitoring on the North York Moors (since 2011) to calculate the average yearly population margins expansion along rides. In addition to the selection criteria in the previous section, margin rides were also required to meet the following criteria:

1. Have had potential for population expansion between 2011 and 2022 i.e., must have uncolonized length that does not extend into unsuitable habitat like open farmland.
2. Expansion has been unidirectional, from a single point of origin to exclude situations where sections of the ride has been colonised from two origins (due to intersecting two rides with ant presence), as this might inflate the measures of margins expansion on this ride.
3. Expansion has not been interrupted by factors such as areas of forest on the ride being harvested during the period for which we have data, causing the ride to become unsuitable for wood ants. In cases where the expansion had been interrupted, we used the data up to the interruption. For example, a ride that was surveyed from 2011-21, but that was clear-felled in 2019, can provide us with an eight-year average expansion rate rather than ten.

An initial 13 suitable rides were identified from long-term data at Cropton and Broxa (Procter *et al.*, 2015) to assess the feasibility of this study. A power analysis on these data (power = 0.8, alpha = 0.05) suggested that a final sample size of 37 rides would be suitable to test H1 and 16 would be adequate for H2. Based on our desk survey using the long-term data for Cropton and Broxa (Procter *et al.*, 2015), this exceeded the number of rides suitable for each hypothesis at these sites. As a result, additional rides from East Moor Wood in the North York Moors were included. The final number of rides selected for the study was 50, including all 29 of margins rides that were suitable for H2 (site = number of rides/number of rides on the margin; Cropton = 11/11; Broxa = 14/9; East Moor Wood = 25/9). The 21 non-margins rides were selected randomly from Broxa and East Moor Wood.

2.3 Nest abundance and volume measurements

For each ride, the surveyor walked down one side of the ride and up the other, recording nest presence and volume. Nests more than 5m from the edge were excluded to ensure all surveyed nests were directly utilising the ride canopy gap. In practice, light from a gap may penetrate deeper than 5m, but this is highly tree species dependant. For example, many pines have very little light-blocking foliage low down on the trunk, whereas spruce can present a dense wall of needles that lets very little light through at any height. As a result, dominant tree species on each side of the ride was also recorded. In areas where the understory is relatively open, spotting nests up to 5m from the edge does not present a challenge but in areas where the understory is denser, some nests were difficult to spot. At each ride, a judgement of the condition of the understory was made, and if the understory was too thick to confidently spot nests up to 5m from the edge, a second transect was walked parallel to the first 2.5m from the edge (behind obscuring vegetation) to minimise the risk of missing nests. At each nest, we recorded the location (latitude and longitude) and on which side of the ride (east or west/north or south) the nest was, giving each nest a unique ID code to prevent recounting.

Additionally, nest width, length and height were measured to calculate nest volume as a proxy for number of ants (Chen and Robinson, 2013).

Ride details were also be recorded: ride width (between opposite points where the canopy is directly overhead), canopy height (measured using *Toolbox* android app calibrated against a gun clinometer) of both sides of the ride and ride bearing (expressed as degrees east or west of north). We measured each of these ride variables at the beginning, midpoint and end of each ride and averaged them across the three to provide the ride characteristics. Latitude and longitude were recorded at the start and end of each ride so that the length of the ride could be measured retrospectively using ArcGIS Pro version 2.3.3.

2.4 Calculating rate of margins expansion along rides

From the long-term data, we calculated two measures of margins change a) distance change and b) number of nests. The distance the margin changed along a ride was the distance in metres between the location of the last nest along a ride recorded in the oldest long-term data and the location of the last nest on the same ride surveyed in 2022. The change in the number of nests was defined as the number of nests between the last nest at the date of the earliest survey in the long-term data and the last nest along the ride in the 2022 survey. Although both rate of distance changed and the rate of nest abundance change can be calculated from this data, rate of nest abundance change is a less reliable measure of expansion than the rate of distance change for two reasons. Firstly, there is a five-year gap in the long-term data and the entire population was not revisited on each survey (Procter *et al.*, 2015). This means that, in many cases, we have no evidence of continuous occupation, nor of the number of nests that may have been established and subsequently abandoned in the intervening period. Secondly, in areas where the wood ants have recently colonised, a period of consolidation may follow later in the year. Some small nests may be abandoned, and the occupying ants absorbed into neighbouring nests in the polydomous network (Burns *et al.*, 2020) and the numbers of nests may fluctuate. On the other hand, the predicted rate of distance change was low, owing to the slow dispersal of this species (Procter *et al.*, 2015) whereas we anticipated that the change in the number of nests would be large and more easily detectable. As a result, we collected both distance change and nest number change of wood ant margins change to afford us the benefits of both measures.

2.5 Statistical methods

2.5.2 Modelling the relationship between ride characteristics and population measures

The resulting data set included 50 rides, of which 29 were on the margins, each with record of the bearing of the ride, length, mean width, the number of nests on each side of the ride. For the 29 rides on the margins, we also had two measures of the rate of margin change calculated from long-term population data: abundance change (nests/year) and distance change (m/year). To test H1 (i.e., the effect of ride characteristics (bearing, width, and side) on the abundance and relative volume of nests) we fitted generalised additive models using the mgcv package version 1.8-41 (Wood, 2011) in R (version 4.2.1). Because our orientation data were circular and we could not make assumptions about the shape of the relationship between orientation and our wood ant population measures, the additional flexibility of a GAM was preferred over a GLM. We fitted models including all combinations of the three ride characteristics above, as well as site and ride ID as random effects and used the minimum AIC to select the most parsimonious model for each response variable. Because of the circular nature of ride bearing (-90° and 90° relative to north are equivalent), we included ride bearing smoothing term as a cyclic p-spline, whereas mean width was included as a p-spline only. We plotted response vs. fitted values, fitted vs. observed and histograms of the residuals to inspect the model fit and predicted from the models for visualisation. The GAMs provided estimations of degrees of freedom.

2.5.2 Pooling bearing into categories for margins growth analysis

Our initial power analysis used data gathered from the known locations of nests along rides undergoing wood ant population margins expansion that were at either extreme of bearing (close to E-W or N-S) and indicated that 30 rides would be adequate for an alpha of 0.1. However, this power analysis cut the data such that:

1. Bearing was categorical.
2. The difference between N-S and E-W rides was tested.

The data that we finally collected gave us sufficient resolution to treat bearing as continuous, and this was used to fit the GAM model for margins growth as described above. Inspection of the data, however, suggested a bigger difference between rides bearing near the cardinal points (N, S, E, W) and rides bearing near the intercardinals (NE, SW etc.; Figure 4.1) than between N-S and E-W rides. This suggests that, to test pooled bearing, bins should be E-W +/- 22.5°, N-S +/- 22.5°, and intercardinal +/- 22.5°, in order to appropriately capture the variability in the data. This variability has sound ecological justification: assuming that there is a minimum threshold of daily sunlight exposure for nesting sites to be viable for the wood ant nests to persist, we can be sure that this threshold lies some below 50% of summer day lengths, as both sides of N-S rides are often utilised by ants (Figure 4.2). This threshold is also greater than 0% of the daily hours of sunlight because wood ants were often entirely absent from the south side of E-W rides. As such, going around the compass from north, the hours of available light on the north side will gradually increase from 50% up to c100% after 90°. Meanwhile, the south side will decrease from 50% to nearly 0%, passing below the threshold for wood ants to utilise potential nesting sites somewhere between. This reduction in potential nesting sites and the total availability of sunlight on the ride will have negative effects on wood ant populations and result in slower population growth leading to slower margins expansion.

As a result, the power analysis predictions cannot be relied upon; they were not based on testing the two extreme groups and may have overestimated the sample size required for the desired alpha. Alternatively, pooling the bearings in the power analysis, as opposed to treating bearing as a continuous variable, may have entirely counteracted this and our sample size estimates are too small to achieve the desired alpha with bearing as a continuous variable. Although our inspection of the raw data indicated a relationship between bearing and our two metrics of population margins growth (distance and nest abundance), the low R^2 of our GAMs and the non-significance of bearing as a smoothing term in the models suggest that the latter is true. Regardless, the data did allow us to test the hypothesis that the rides running in approximately intercardinal directions experience slower wood ant population margins growth than rides running in approximately cardinal directions. In our final models of nest abundance, the number of nests on a ride was offset by log(length of ride occupied by *F. lugubris*) to account for the effect of effort in the point count model because count data is zero inflated requiring a negative binomial model.

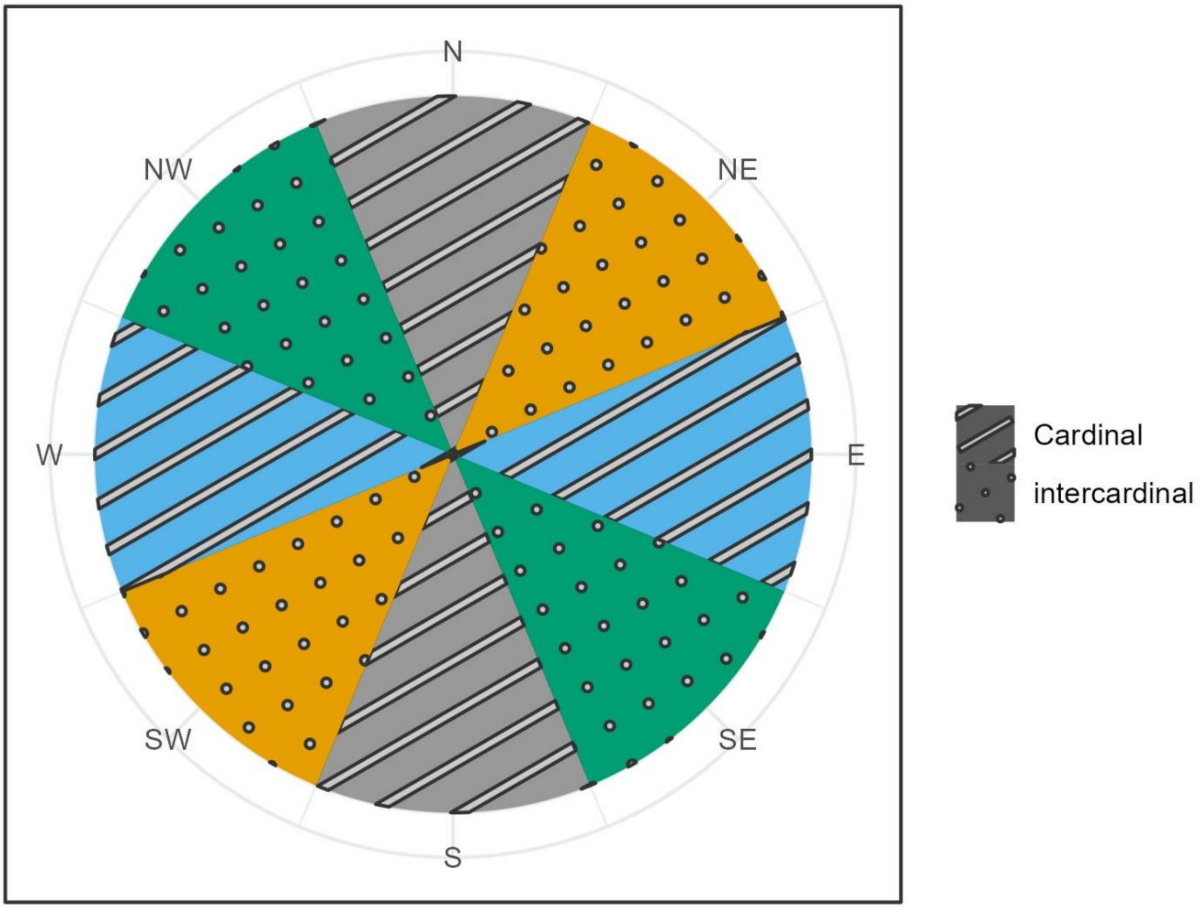


Figure 4.1. We pooled the data for margins change for rides of different bearing into categories, in two ways: four categories of N-S, E-W, NW-SE, NE-SW (+/- 22.50 in each case) and two categories for rides running along cardinal and intercardinal directions (+/- 22.50) so that we could test the differences between more or less exclusive groups respectively.

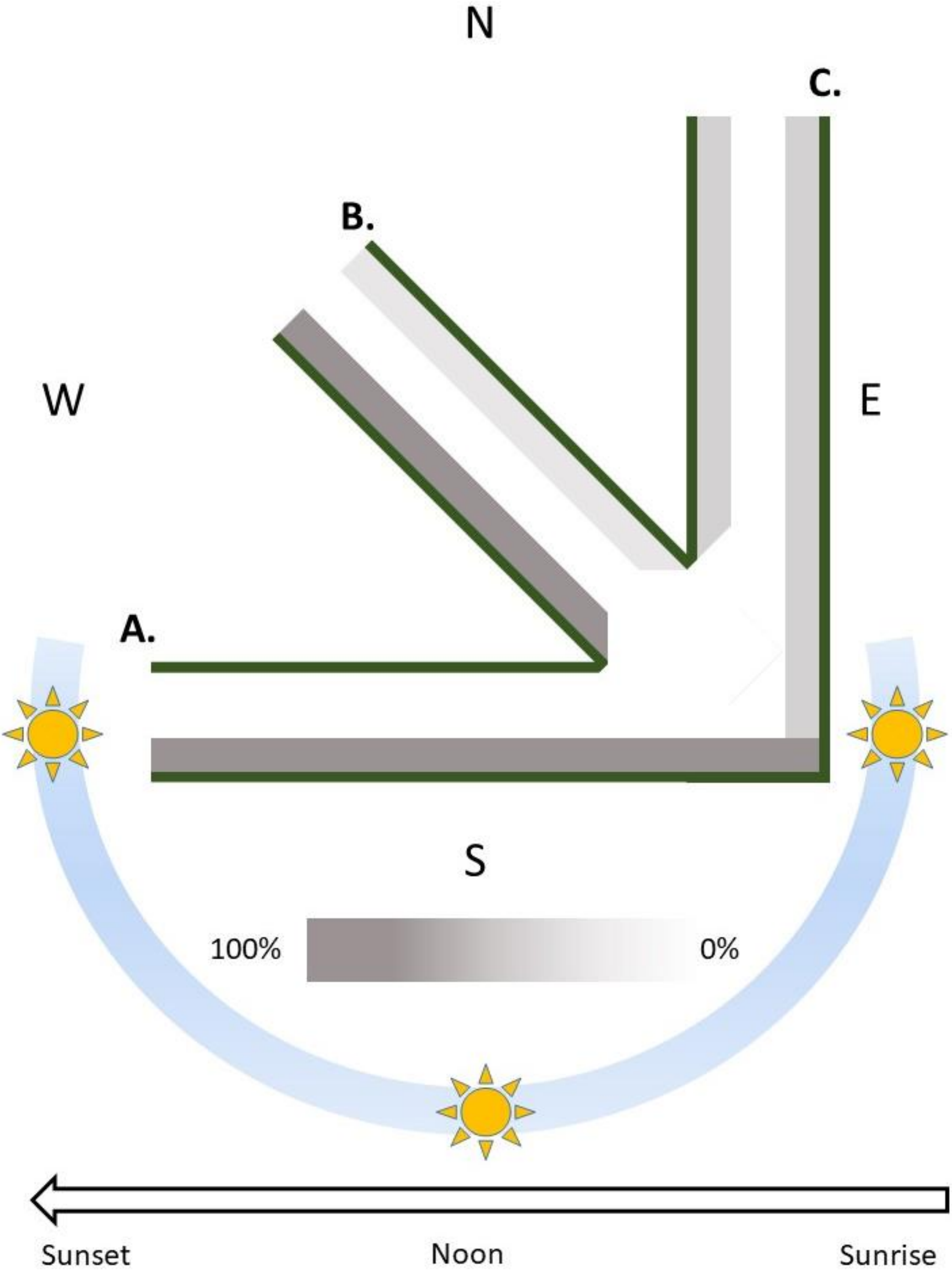

N
C.
B.
W
E
A.
S
100%
0%
Sunset
Noon
Sunrise

Figure 4.2. An E-W ride (A) receives a full day of sun on the north side, whereas a N-S ride (C) receives half of a day of sunlight on each side (in the morning on the west side, in the afternoon on the east). Rides in intercardinal directions (e.g., B) will receive fewer hours of sunlight on the north side than and E-W ride, but still receive little or no direct sunlight on the south side. The hours of sunlight available on each side will approach 50% as the ride bearing approaches 0°, while hours of sunlight available will reach maximum asymmetry for rides bearing 90/270° (E-W). Only the north side of the ride A will be suitable for wood ants to nest, and the south will remain unsuitable for all potential bearings until the hours of sunlight reaches a threshold (between B and C) at which both sides can be utilised by the ants but are both sub-optimal compared to the north side of an E-W ride.

3. Results

3.1 Ride bearing distribution

A total of 371 nests were recorded along 50 rides, including 29 rides on the population margins. One of the rides on the margins was also at the true edge of a forest stand and therefore had no measurable width and only one side on which nests could occur. This ride was dropped from analyses that incorporated side or ride width as variables. The distribution of the rides we were able to collect data for represented bearings at most points of the compass and no orientation was much underrepresented. Regardless, there are orientations that we have more data for: rides approximately 15-30^o west of north and 70-80^o east of north were more abundant than other orientations (Figure 4.3A).

3.2 Aspect distribution

The aspect (direction of the long face/lower edge) of nests was overwhelmingly south facing (Figure 4.3B) with a circular mean of 191.47^o (circular mean, $r = 197.47$, $var = 0.46$, $p < 0.0001$). This is in line with expectations, based on the assumption that the nests are constructed to present a large surface area to the sun and maximise insolation.

3.3 Does the orientation of canopy gaps affect wood ant nest abundance and volume?

3.3.1 Nest abundance GAMs

The most parsimonious model, based on the comparison of AIC values for different combinations of explanatory variables in the model, included only side, bearing and width (Figure 4.4; Table 4.1). The model explained 31% of deviance and ride bearing was a significant smoothing term for both sides. Deviance explained is favoured over R^2 for non-Gaussian models as a more robust measure of explanatory power (Wood, 2006). The smooths for each side of the ride are also significantly different from one another (Table 4.1) and plots of the model predictions for values of ride bearing show that the number of nests per side is compensated by the other (Figure 4.4). When the east side has few nests (at bearings that cause the east side to be shaded), the west side has more: overall, the total sum of nests on each side varies little with bearing. Generally, nest density is lower on a given side at ride bearings where that side

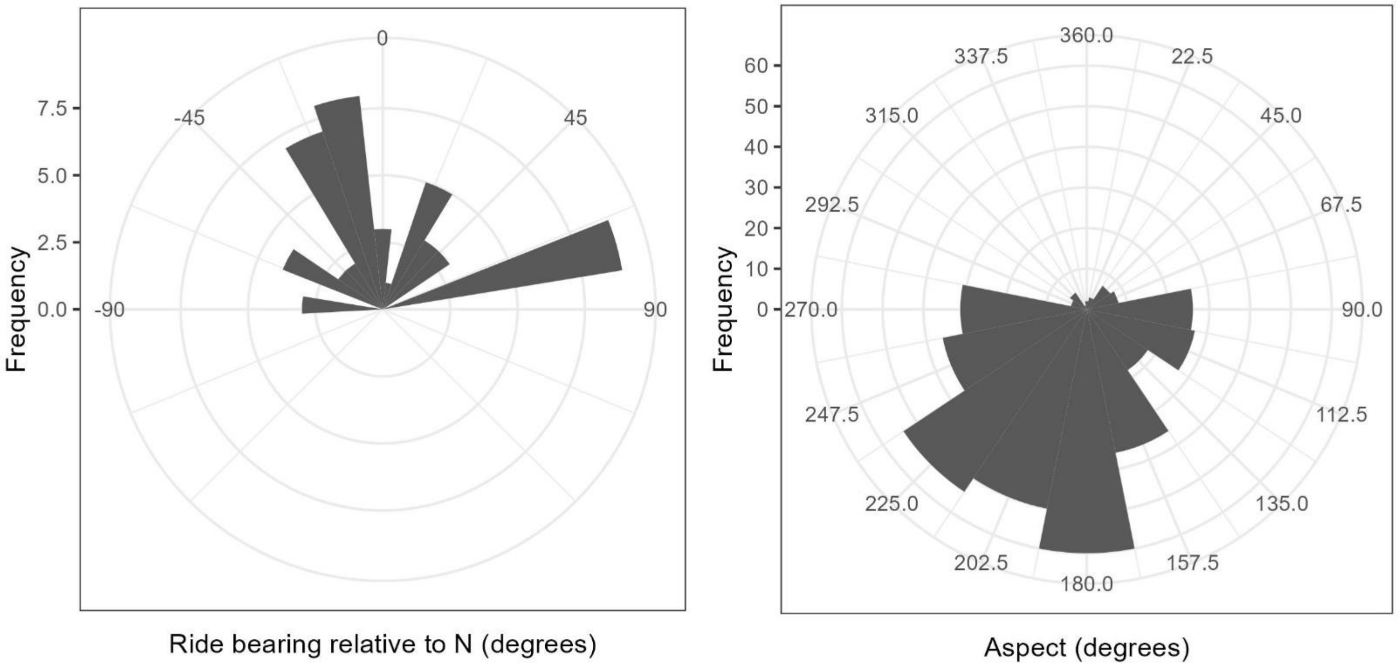


Figure 4.3. A. The frequency of rides at different bearings was determined by the availability of suitable rides at the field sites. Despite this, the data contains rides bearing along most possible directions without excessively favouring one direction. B. The aspect (direction of lower slope) of nests was far more often SSW, with a circular mean of 191.04 (r = 197.47, var = 0.46, p < 0.0001).

Table 4.1. We fit generalised additive models to predict several wood ant population measures using ride characteristics. Models 1-3 included the side of the ride that nests were on as a 'by' term (effectively fitting the two sides as separate splines) so that we can test the significance of each side (East and West) smooths (difference from line with gradient of 0) and test the smooths against on another (East:West).

Model	Dependant variable	'By' interaction	Smoothing term		Effective degrees of freedom	Test statistic (F unless specified)	P-Value	N	R^2 (Deviance explained)	Notes
1	Nest abundance	Side	Ride Bearing:	East	4	17.741 (X^2)	**0.001**	98	0.054 (31%)	Nest abundance offset by ride length (Figure 4.4)
				West	4	16.883 (X^2)	**0.002**			
				East:West	4	17.75 (X^2)	**0.001**			
			Ride Width		1.142	0.407 (X^2)	0.557			
2	Mean nest volume	Side	Ride Bearing:	East	5	3.476	**0.008**	69	0.267 (40.5%)	AIC = 82.64 (Figure 4.6)
				West	5	1.059	0.393			
				East:West	5	0.877	0.502			
			Ride Width		1.823	5.487	**0.006**			
3	Mean nest volume	Side	Ride Bearing:	East	5	3.775	**0.005**	69	0.299 (44.2%)	AIC = 80.36 (Figure 4.5)
				West	5	1.157	0.342			
				East:West	5	0.877	0.502			
			Ride Width		1.921	6.258	**0.003**			
			Site		0.98	1.11	0.107			
4	Mean nest volume	None	Ride Bearing		4	1.187	0.332	46	0.18 (28.7%)	(Figure 4.7)
			Ride Width		2.164	5.053	**0.009**			
5	Margins nest change per year	None	Ride Bearing		4	4.443	0.082	28	0.163 (41.1%)	(Figure 4.8)
			Ride Width		4	2.061	0.126			
6	Margins distance change per year	None	Ride Bearing		4	1.934	0.148	28	0.256 (50.8%)	
			Ride Width		4	1.011	0.428			
			Site		1.154	1.53	0.098			

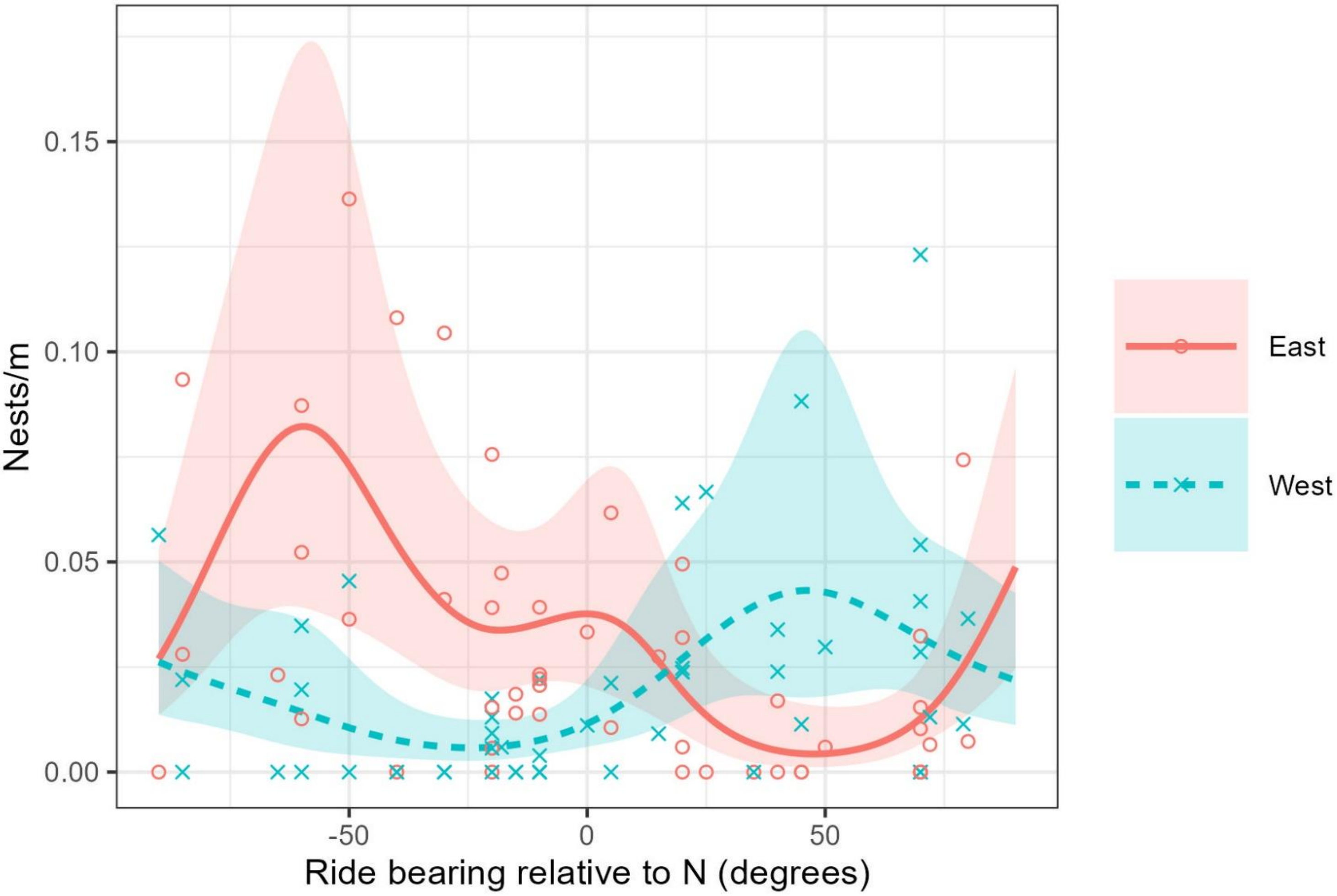


Figure 4.4. The number of nests per side of a ride (E or W) for rides of different bearings. Lines (by side) fitted from predicted values for ride bearing of a point count generalised additive model offset by ride length with the formula nest abundance ≈ side + s(bearing) + s(width) of the negative binomial family; Link function = log, offset = log(length), $R^2 = 0.0538$, deviance explained = 31%. Though the offset was included in the model for statistical testing, the offset is ignored when predicting. The points represent the real data, the lines are predicted values and the shaded areas are 95%CIs. Both east and west smooths were significant ($p < 0.005$) and significantly different from each other, width was not significant as a smoothing term in this model. Note that deviance explained is favoured for non-Gaussian models rather than variance based R^2 (Wood, 2006).

would be shaded, i.e., lower at west of north bearings for the east side of the ride and the reverse for the west side of the ride. Ride width was not significant as a smoothing term in this model.

3.3.2 Nest volume GAMs

Additional GAMs were fit for the mean nest volume per ride by side with the explanatory variables of site, ride bearing and ride width. Based on AIC values, the most parsimonious model included site, bearing and width as smoothing terms (Figure 4.5; Table 4.1), however the ΔAIC between models with and without site (Figure 4.6; Table 4.1) as a term is 2.278 and only just outside of the widely used cut-off 2 for supporting a more complex model. Furthermore, site was not significant as a (random effect) smoothing term and, despite the slight difference in the mean nest volume of the three sites; its inclusion is unhelpful to the interpretation of the overall pattern and results in a very small increase in R^2 (0.267 without site; 0.299 with). In both models, the ride bearing was significant only for the east side smooth and the smooths of the two sides were not significantly different from one another. The asymmetry of this result, and the lack of difference between the two sides, suggests that ride bearing is a poor predictor of mean nest volume for these data. Additionally, the bearings where a horizontal line could not sit entirely within the 95% confidence intervals of the east smooth (i.e., the bearings that are responsible for the significance of the smooth) correspond to two extreme values for mean nest volume.

Mean ride width was significant as a smoothing term in both models ($p < 0.01$; Table 4.1) and a plot of model predictions (Figure 4.7) shows that the mean volume of nests is lower on wider rides but does not continue to change for rides wider than 8m. It is important to note, however, that a relatively small number of large nests on rides narrower 6m may be major contributors to this effect. This small number of nests (6 with volume above upper 95% confidence interval and ride width less than 6m) were, however, distributed across all three sites.

3.4 Does the orientation canopy gaps affect wood ant dispersal rate?

3.4.1 Nest number change

We used two measures of population margins growth: the change in the number of nests at the margin and the distance that the margins moved per year over the study period. The GAM that best explained (lowest AIC) the change in nest number per year included ride bearing and width (Figure 4.8; Table 4.1). Neither term was below our chosen significance threshold of 0.05 (ride bearing $p = 0.082$, width $p = 0.126$) and the model explained only approximately 15% of the variation. A plot of the model predictions for values of ride bearing, and ride width fixed at the mean (7.118m), suggested a similar shaped pattern

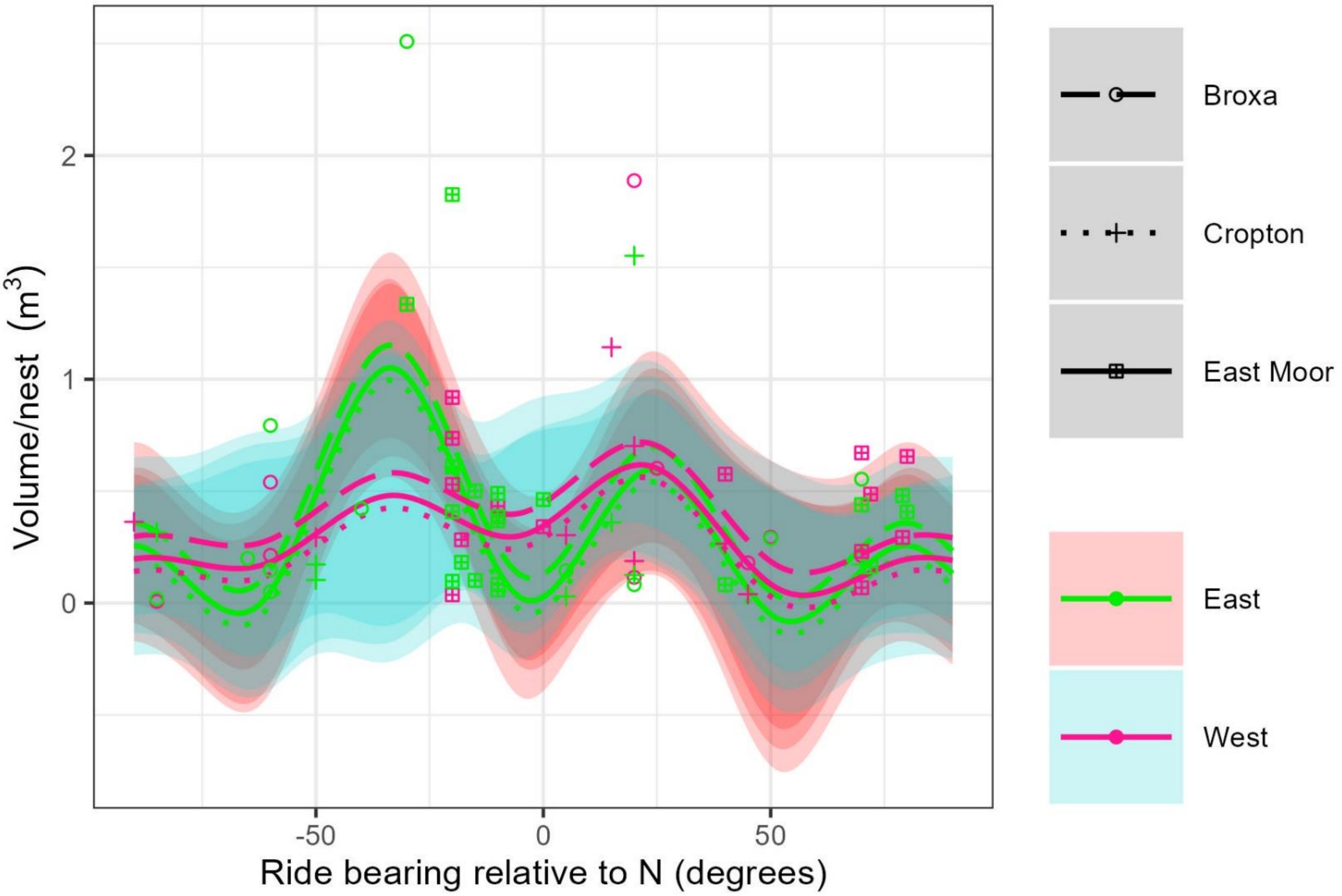


Figure 4.5. Predicted values from a generalised additive model (GAM) with the formula volume per nest ≈ side + s(bearing) + s(width) + s(site) $R^2 = 0.299$, deviance explained = 44.2% were plotted for values of ride bearing (lines) alongside the original data (points) and 95%CIs (shaded areas). Although the east side and mean width smooths were significantly different from a line at the intercept of gradient = 0 ($p < 0.01$), there was no significant difference between the east and west smooths and no clear pattern is discernible from the plot. Based on AIC values, this was more parsimonious than the model excluding site as a smoothing term (Figure 4.6), however the ΔAIC = 2.278, only just outside of the widely used cut-off for supporting a more complex model. As a result, both models have been presented here.

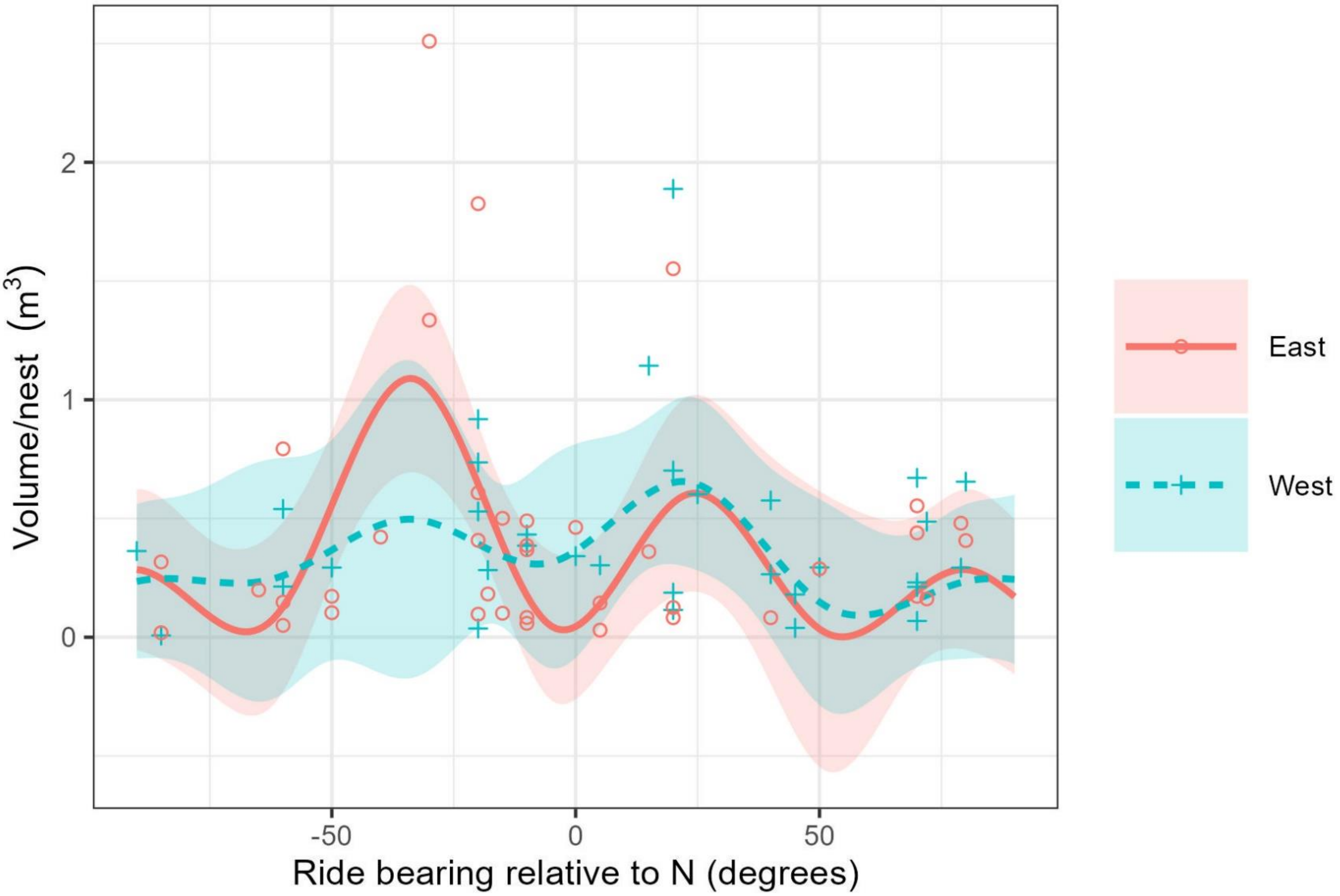


Figure 4.6. The total volume of all nests on each side of rides of different bearings. The lines are predicted values from a generalised additive model (GAM) with the formula volume per nest ≈ side + s(bearing) + s(width), $R^2 = 0.267$, deviance explained = 40.5% were plotted for values of ride bearing (lines) alongside the original data (points) and 95%CIs (shaded areas). Although the east side smooth was significantly different from a line at the intercept of gradient = 0 ($p < 0.01$), there was no significant difference between the east and west smooths and no clear pattern is discernible from the plot. Mean width was also significant as a smoothing term (Figure 4.7; Table 4.1, models 2-4).

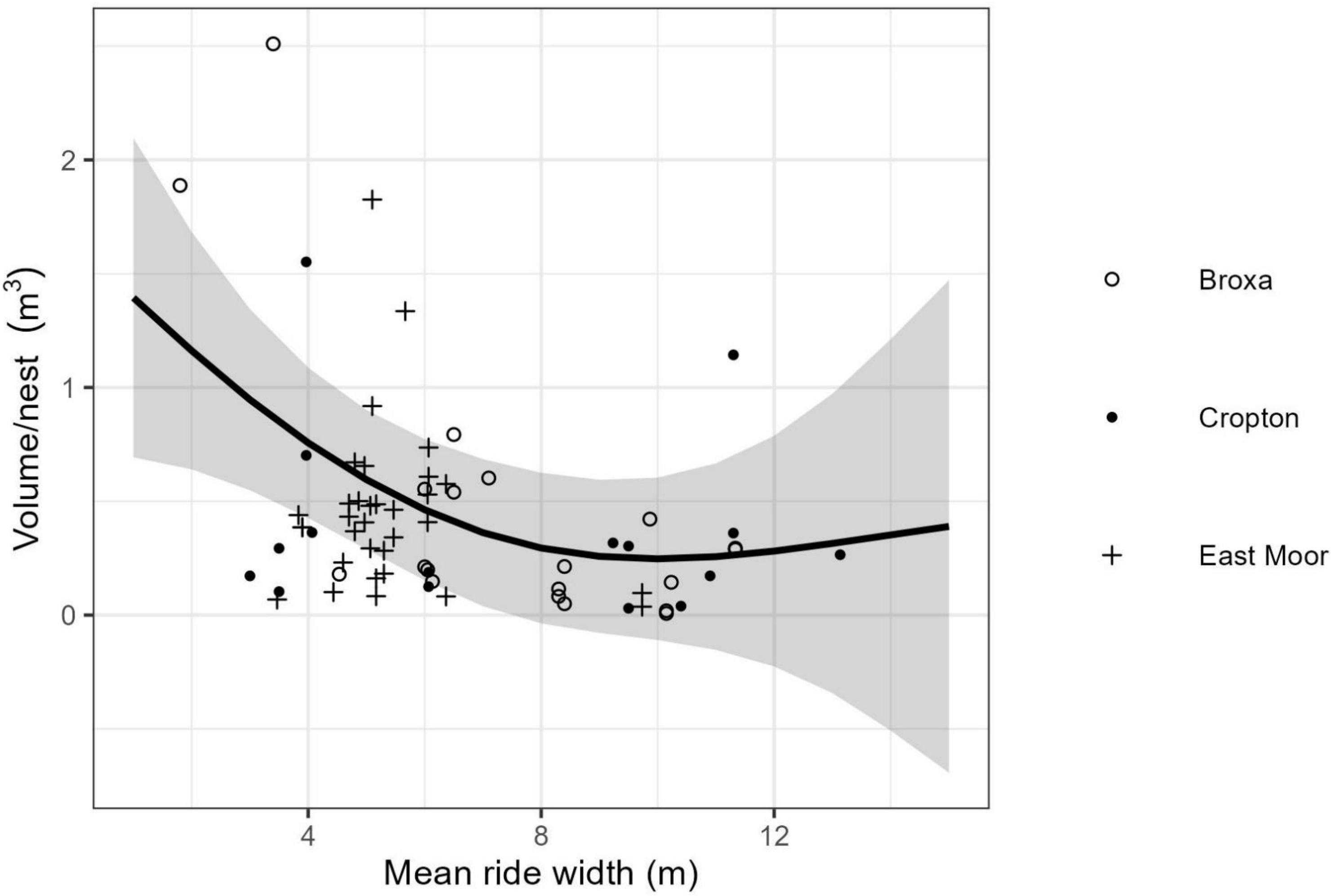


Figure 4.7. Predicted values from a generalised additive model (GAM) with the formula volume per nest ≈ s(bearing) + s(width), $R^2 = 0.18$, deviance explained = 28.7% were plotted for values of width (line) alongside the original data (points) and 95%CIs (shaded area). The smooth of mean width was significantly different from the intercept ($p < 0.01$), whereas ride bearing alone (i.e. not split by side) was not.

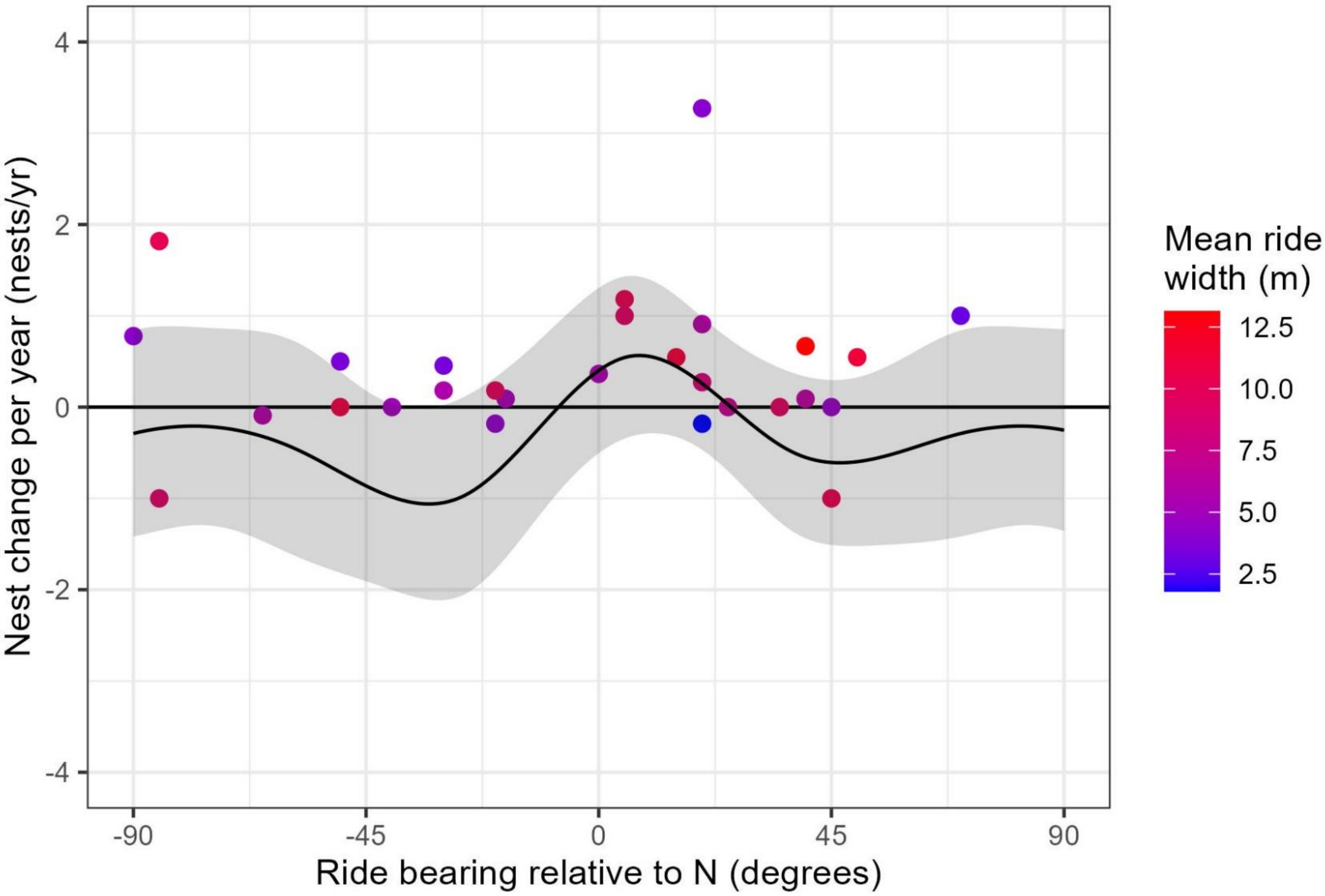


Figure 4.8. A generalised additive model (GAM) was fit for the change in the number of nests on rides on the margin with the formula nest change per year ≈ s(bearing) + s(width), $R^2 = 0.163$, deviance explained = 41.1% and the predictions for values of ride bearing were plotted (solid line) with 95%CIs (shaded areas). Ride bearing was significant as a smoothing term only to an alpha of 0.1, and the model has little explanatory power. Ride width is not correlated with bearing.

in the rate of nest number change as we saw for total nest abundance, with minima for rides bearing approximately NW-SE and NE-SW (intercardinal), though without statistical significance. The inclusion of width as a smoothing term results in the predictions being consistently lower than the observed values (Figure 4.8) due to the fixing of ride width at the mean value, which may predict lower than observed values if ride with is highly skewed or non-Gaussian. The ride width distribution appears similar to a bimodal distribution, lending weight to this, but the high antimode relative to the maximum frequencies means that interpreting it as a Gaussian distribution is equally plausible. Regardless, this model has poor predictive power, but does suggest that bearing may play some role in the rate of change in nest number.

When the data were pooled into four groups of rides (those oriented N-S, E-W, NW-SE, NE-SW +/- 22.5^{o}; Figure 4.2) the low rate of nest number change on intercardinal rides is still apparent (Figure 4.9) but non-significant (one-way ANOVA, F = 1.123, df = 3, p = 0.359; Table 4.2). The median rate of nest change was greater on cardinal rides than intercardinal ones (approximately 0.5 nests/year; Figure 4.10), but we found that the difference between groups was just above our threshold for statistical significance (Welch's *t*-test, *t* = 2.021, df = 21.368, p = 0.056).

3.4.2 Distance of population margins change

The distance that the margins moved per year over the study period was also included as a response variable in a GAM and the best model based on minimum AIC includes site, ride bearing and ride as smoothing terms (Figure 4.11; Table 4.1). This model performs better than the nest number change model (R^2 = 0.256) and the overall pattern was the same (minima on rides near intercardinal directions), but none of the smoothing terms were significant except for the random effect 'site', and that only to an alpha of 0.1 (p = 0.098; Table 4.1). Model predictions showed that rides in Cropton Forest experienced more wood ant population growth than either of the other two sites.

Pooling the data revealed the same pattern for ride bearing that we have seen for other variables and in the GAMs; that the rides running in intercardinal directions are less favourable to wood ants and result in lower population margins growth (Figure 4.12). Reducing the number of bins to two and testing only cardinal and intercardinal rides against each other, we found that the rides that bear in cardinal directions experience significantly more margins expansion than intercardinal ones (Welch's *t*-test, *t* = 2.122, df = 22.497, p = 0.045; Figure 4.13) and the effect size was medium, based on the recommended interpretation of Cohen's *d* (0.74).

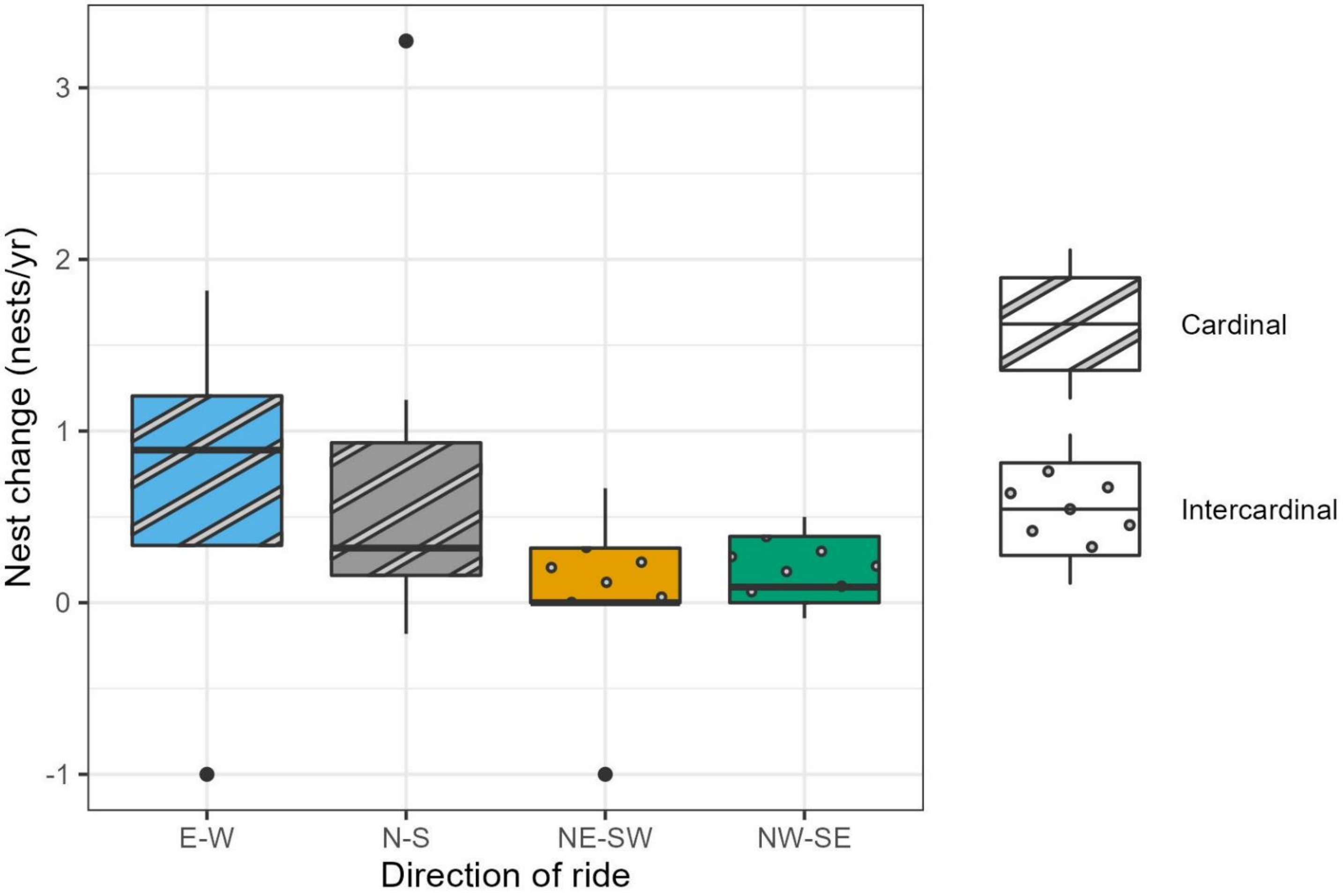


Figure 4.9. The ride data were pooled by bearing so that the categories consisted of rides bearing +/- 22.5° of the cardinal and intercardinal points. E-W and N-S rides appear to have undergone slightly more (positive) change in nest number than NE-SW and NW-SE rides.

Table 4.2. We tested the difference in the rate of change in the margins along rides from 2011 to 2022 between rides of varied orientation relative to north, with orientation binned into four and two groups separately (Figure 4.2). The four bins were for rides running N-S, E-W, NW-SE, NE-SW (+/- 22.5^0 in each case); the two bins were for rides running along cardinal and intercardinal directions (+/- 22.5^0).

Measure	Bins	Tests	Degrees of freedom	Test statistic	P-value
Rate of change in nest number at margins	4	One-way ANOVA	3	F = 1.123	0.359
	2	Welch's *t*-test	21.368	t = 2.021	0.056
Rate of distance change at margins	4	One-way ANOVA	3	F = 2.154	0.119
	2	Welch's *t*-test	22.497	t = 2.122	**0.045**

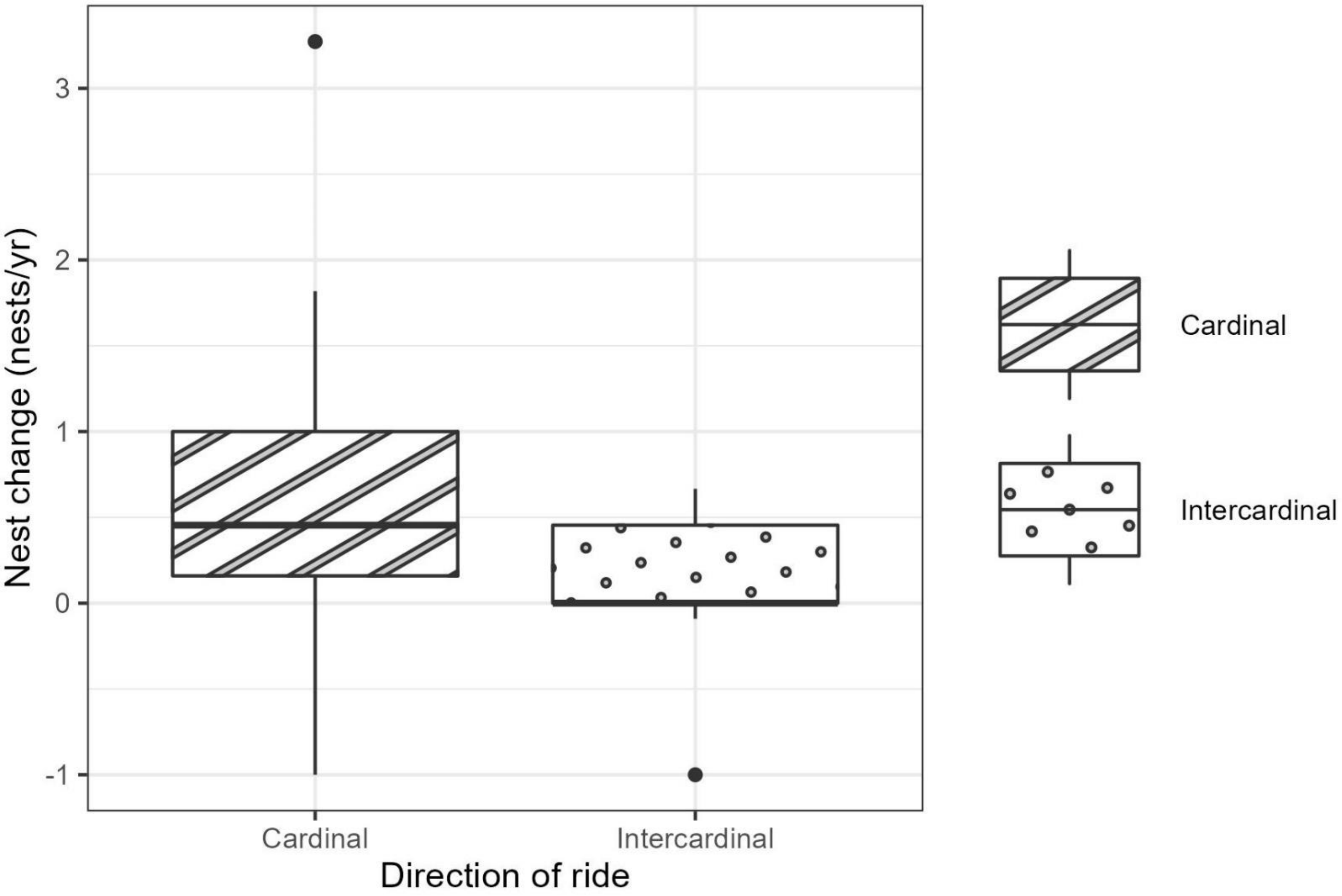


Figure 4.10. We pooled ride data for change in nest number into two categories: cardinal (22.5° +/- N, S, E or W) and intercardinal (22.5° +/- NE, NW, SE or SW).

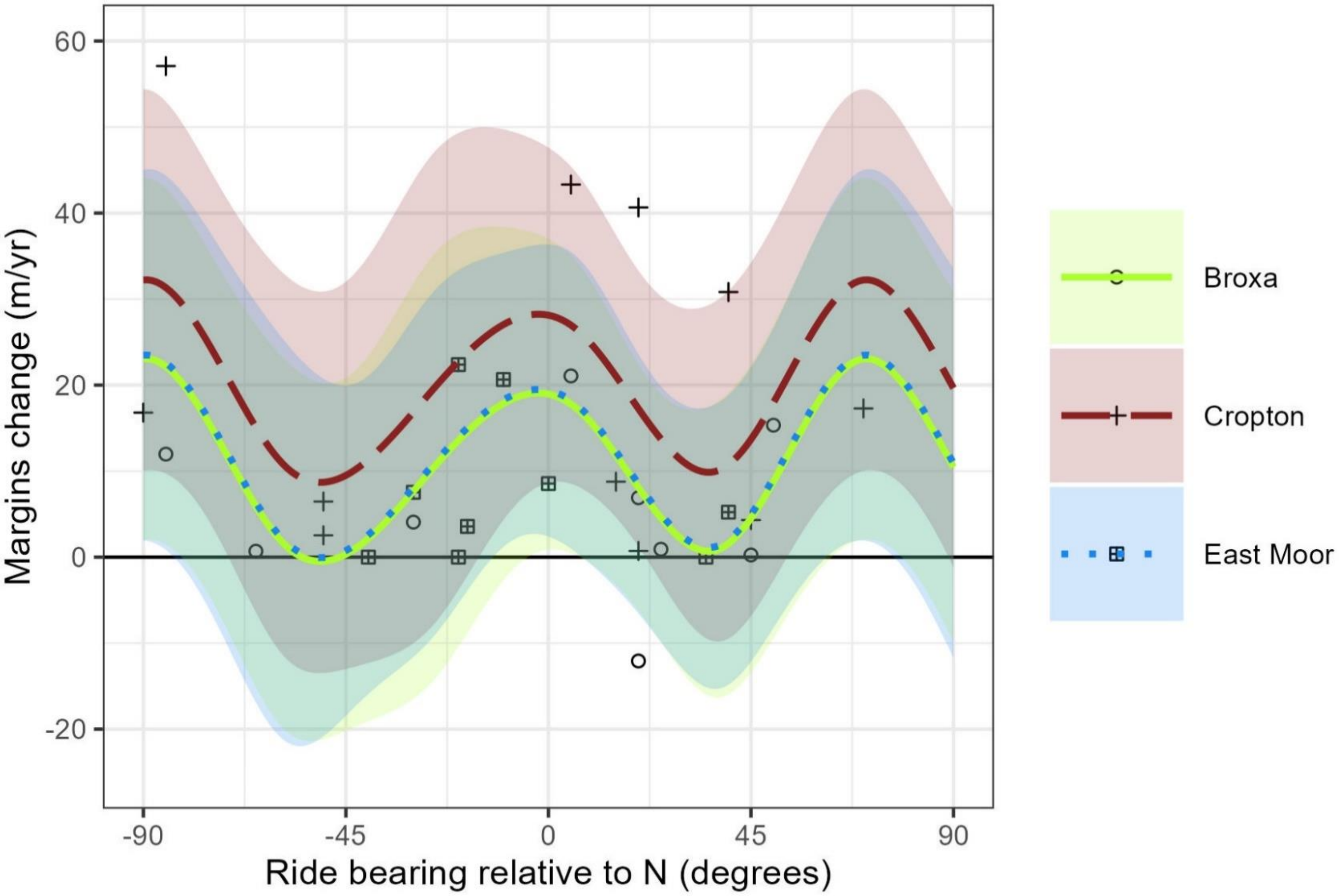


Figure 4.11. A generalised additive model was fit to predict the distance change along rides on wood ant population margins on the North York Moors with the formula margins change ≈ s(bearing) + s(width) + s(site), $R^2 = 0.256$, deviance explained = 50.8%. Empirical data (points), model predictions (lines) and 95%CIs (shaded areas) are shown. None of the smoothing terms were significant to an alpha of 0.05, but site was a significant random effect and its inclusion resulted in the most parsimonious model (ΔAIC < 2).

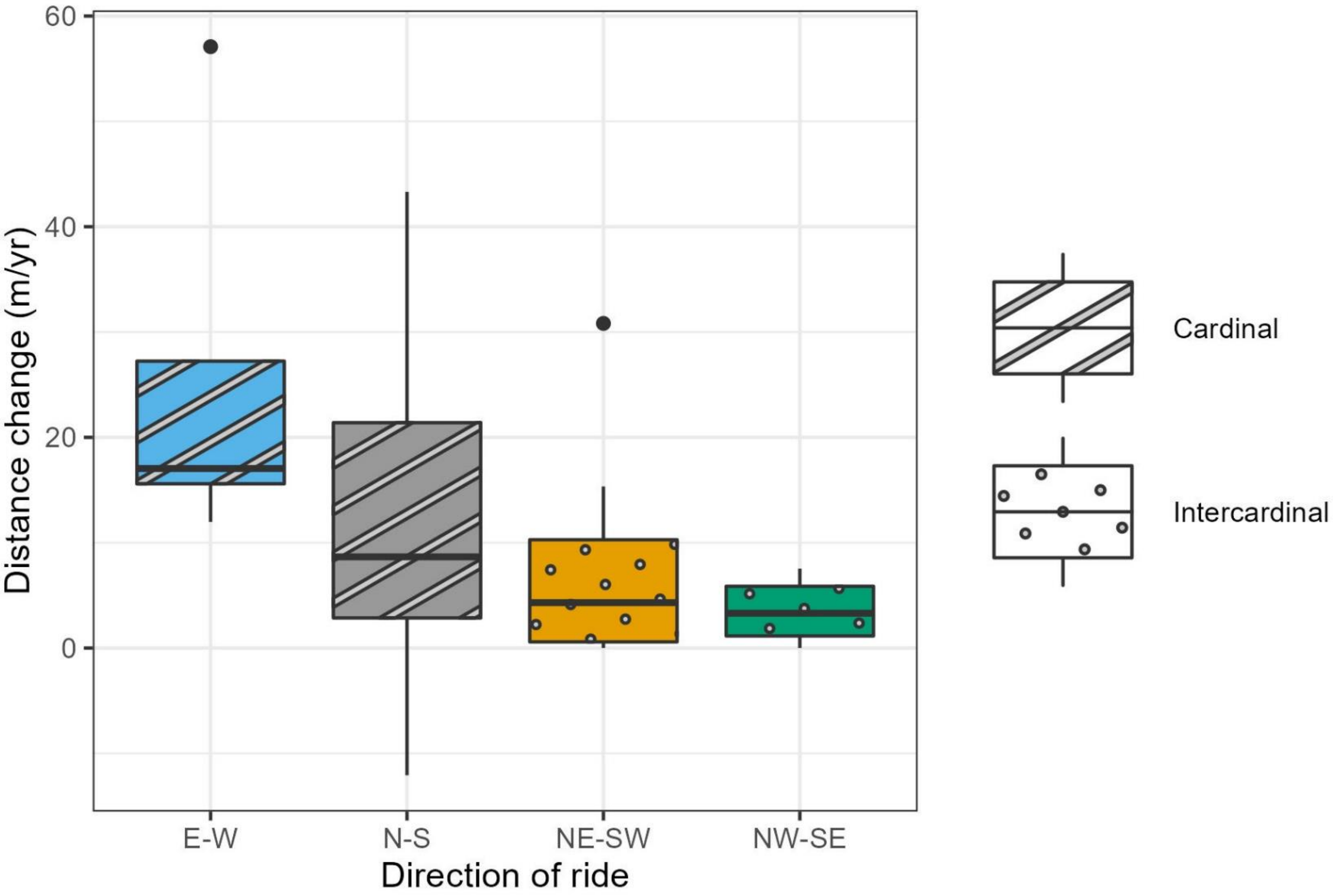


Figure 4.12. We pooled the data by bearing so that the categories consisted of rides bearing +/- 22.5° of the cardinal and intercardinal points. Although the differences in distance change between category were not significant (ANOVA, $p > 0.05$), E-W and N-S rides appear to have undergone slightly more (positive) change in margins position than NE-SW and NW-SE rides.

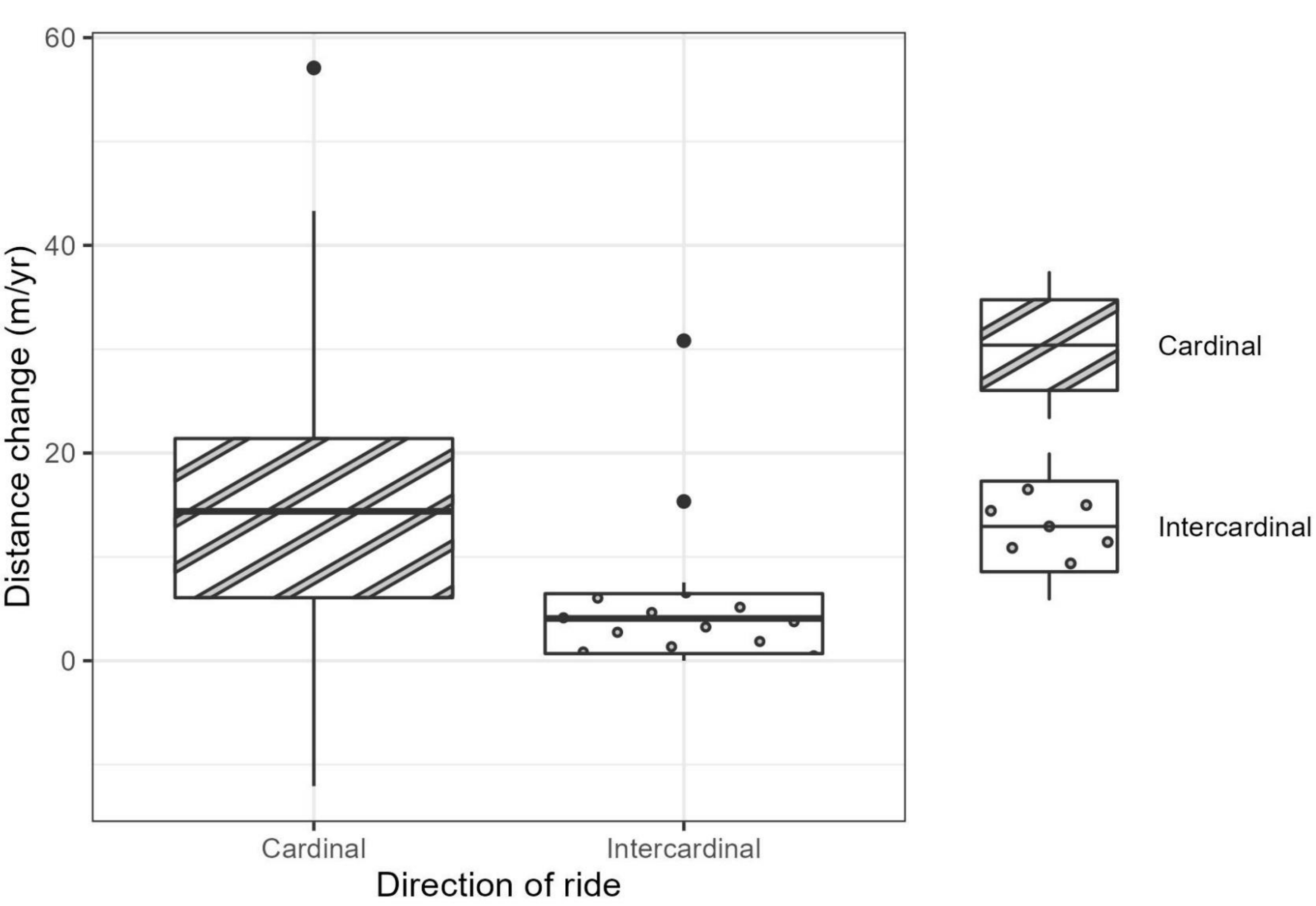


Figure 4.13. We pooled ride data for distance margin change into two categories: cardinal (22.5° +/- N, S, E or W) and intercardinal (22.5° +/- NE, NW, SE or SW). This was based on initial observations of the data and ecological reasons we may expect differences between these groups (see methods).

4. Discussion

4.1. Summary of results

We set out to determine the effect of anthropogenic canopy gap characteristics on populations of an edge specialist, the northern hairy wood ant *Formica lugubris*. Our results clearly show that the orientation and width of linear canopy gaps can affect *F. lugubris* populations. Nests were more abundant on the northern side of rides at in any orientation, as predicted, but orientation did not affect nest size in a consistent way; despite the statistical significance of east smooth there is little ecologically significance to the effect of bearing on nest volume on the east side of rides, as it is largely the result of two extreme values from atypical nests. In general, Narrow rides have larger nests on them, while wider rides were populated by smaller nests. This is consistent with predictions; mean ride width will be a major determining factor in the amount of shade a nest will receive, and the relationship between canopy cover (and thus insolation) and nest volume is established (Chen and Robinson, 2014).The greater nest abundance on the north side of rides of different orientations led to compensation of nest abundance between the sides that reached parity on rides that ran roughly north-south. Finally, we found that, as predicted, the orientation of rides affected *F. lugubris* dispersal. Populations of *F. lugubris* have dispersed more quickly along rides that run in cardinal directions (N, E, S, W) than ones that run in intercardinal directions (NE, SE, SW, NW).

4.2. The importance of edge characteristics

We have shown that the orientation of edge habitats relative to north is an important factor in edge quality for *Formica lugubris*,and is sufficient to have measurable effect on nest abundance and populations margins expansion. Width is also a factor in edge quality for these wood ants; larger nests in narrower rides, in line with previous work that has shown that larger nests are found in shadier areas because they are better able to thermoregulate (Chen and Robinson, 2014). The strong south-facing bias in nest aspect we found confirms that our other results are likely to driven by insolation, as sunlight is important for many aspects of wood ant biology; The relative scarcity of direct sunlight may result in later initiation of foraging, at least in small colonies (Rosengren *et al.*, 1987), slower brood maturation (Kadochová and Frouz, 2013) and slower colony growth.

4.3. Dispersal along rides

Not only did we find that the abundance of wood ants (nest volume and numbers of nests) responded (and respond differently) to ride characteristics such as ride bearing and width, but the ability of the wood ants to disperse through these plantation forests is also affected by ride bearing, with most rapid dispersal along rides oriented along the cardinal bearings (N-S or E-W). We hypothesise that the slower population margins expansion observed for rides bearing in intercardinal directions is due to a minimum threshold of insolation for nests of *F. lugubris* to be viable. Above this threshold, a wood ant nest's outcomes continue to improve. We suggest that the south side of a ride with an intercardinal bearing receives insolation below this minimum threshold, due to being shaded for most of the day by the trees on the southern side, while the north side will receive less insolation than the north side of a ride running east-west. This means nests on these bearings are in a 'worst of both worlds' environment. Due to the negative effects that shade can have on the onset of foraging (Rosengren *et al.*, 1987) and brood maturation (Kadochová and Frouz, 2013), this would result in fewer individuals and a reduced ability to form new nests in the polydomous network. Polydomy allows for food and labour sharing between nests that can help a new nest that may be non-foraging initially (Ellis and Robinson, 2015). Due to the small size of newly founded nests and the negative effects that low light availability has on small colonies (Rosengren *et al.*, 1987), newly founded nests in shadier areas may require more support from neighbouring nests, so being further from the centre of this network may leave new nests more vulnerable to abandonment. The combination of lower rates of nest foundation and a higher failure rate for nests that have been established further from the parental nests, could explain the reduced margins growth that we measured in shadier, intercardinal rides. Due to the slow dispersal of *F. lugubris*, the difference of 15m/year is equivalent to three times the rate of dispersal in cardinal rides compared to intercardinal rides.

4.4. Practical implications

Given that wood ants may be a beneficial presence in plantation forests under certain circumstances (Laine and Niemela, 1980; Karhu and Neuvonen 1998; Zingg *et al.*, 2018), the results that we have presented here may be useful in plantations adjacent to existing populations of wood ants, or in areas where translocation of wood ants' nests is being considered (Nielsen *et al.*, 2018). Wood ants can reduce defoliating pest burden (Karhu and Neuvonen 1998), increase aphid abundance (Frouz *et al.*, 2008), compete with other insectivores (Haemig, 1992), and change the spatial distribution of soil resources (Chapter 3), the effects of ride characteristics on dispersal have major implications for conservation and forest management. When planning new areas of forestry, or selectively felling existing stands, we would recommend cutting fire breaks, access tracks etc. in cardinal directions to maximise the ability of wood ants to disperse, if increased wood ant occupancy is desired. This could also benefit other edge-specialist woodland species that rely on insolation, e.g., herbaceous plants.

On the other hand, the width of the ride should also be considered when managing forest to promote species richness or dispersal. Previous work has suggested that canopy gaps should be at least 15m wide in order to harbour species that would be shaded out in the forest interior (Oxbrough *et al.,* 2006; Smith *et al.,* 2007), and our data seem to suggest that wood ants similarly have a minimum threshold of insolation (also impacted by ride width) that allows them to thrive and disperse.

4.5. Wider ecological implications

The work presented here adds to a body of research showing that linear canopy gaps in plantation forests have important implications forest dwelling species. The characteristics of rides, such as width, affect the diversity or abundance of butterflies (Greatorex-Davies *et al.*, 1993), spiders (Oxbrough *et al.,* 2006; Carter *et al.,* 1991), ground beetles (Carter *et al.,* 1991), vascular plants (Sparks *et al.,* 1996; Smith *et al.,* 2007), and bryophytes (Smith *et al.,* 2007). Meanwhile, the ecological effects of ride orientation on other organisms in similar habitats to the one studied here have been minimal (Jokimäki *et al.*, 1998). We have shown that, in addition to the effects that ride characteristics can have on the diversity and abundance of forest species in plantation, the orientation of rides can influence the dispersal ability of an edge specialist, opening up the question of whether other species with similar habitat requirements might be similarly affected.

Managing plantations in a manner favourable to wood ant dispersal (by cutting fire breaks and other necessary linear gaps along cardinal directions) could be beneficial to other species and biodiversity in economically productive forests in two ways. Firstly, the presence of wood ants themselves can be beneficial to other species. The nests of wood ants are home to many myrmecophilous species, with over 100 myrmecophiles currently identified in wood ants' nests (Robinson *et al*., 2016), including *Formicoxenus nitidulus* (the shining guest ant) that can only be found in nests of mound building wood ants and is a British Action Plan species (JNCC, 2007). Additionally, wood ants can play an important role in the dispersal of seed, including some declining and charismatic wildflowers like the endangered *Melampyrum cristatum* (crested cow-wheat) which is dispersed by wood ants and is probably range-limited by the availability of dispersers (Stachnowicz, 2013). Secondly, other species with similar habitat requirements and dispersal ability to the wood ants would benefit from the same rides as dispersal corridors as the wood ants. Due to their poor dispersal and sunlight requirement, species that might benefit from the same corridor design as wood ants are likely to be wildflowers that likewise require direct sunlight but benefit from other conditions provided by the forest edge such as protection from wind, acidic soil or edge related nutrient influx (Weathers *et al*., 2001).

On the other hand, edge specialists with the potential to benefit from improved dispersal due to edge orientation may also be pests, for example, the larvae of *Gilpinia virens,* a pine sawfly and common pest of *Pinus sylvestris*, are found in higher numbers in stands with relatively open canopies (Gawęda and Grodzki, 2020). As a result, pests such as *G. virens* may also benefit from the presence of canopy gaps cut in favourable, cardinal directions, although it should be noted that it does not necessarily follow that a preference for canopy gaps will result in the same response to different gap characteristics as we see in wood ants.

4.6. Conclusions

The potential to promote dispersal of both rare and desirable species as well as pests of canopy gaps in plantation forests makes forest edges and linear canopy gaps worthy of more detailed study. Very little work has been done on the effects of gap orientation on the dispersal ability of plants or animals that might utilise plantation forests (but see van Schalkwyk *et al*., 2022) despite the necessity of gaps in plantations forests as fire breaks or for access for logging machinery, and the control that forestry planners have over the placement of fire breaks and other linear canopy gaps. The increase in demand for timber products and forested areas to reach carbon offset goals will likely lead to an increase in the area and intensity of plantation forests in the future (McEwan et al., 2020). If these economic and environmental goals are not to come at the detriment of biodiversity or resilience, care must be taken to ensure the development of forestry practices that allow wildlife to proliferate in plantation forests, for the ecosystem services they can provide and for the biodiversity that they represent.

Chapter 5 – General discussion and advice to forest managers

1. Overview

In the previous chapters, we have explored some of the bidirectional interactions between *Formica lugubris* and plantation forests. In Chapter 2, we conducted an extensive meta-analysis of literature on the effects that ants have on the soils in their nests and integrated the ants feeding and nesting traits to better understand the role that these aspects of ant biology play in determining the magnitude and direction of ant effects on soil. We did so with the intention of determining if wood ants, and ants that share their nesting and feeding biology, have a greater, lesser, or fairly typical role in soil modification compared to other ants. We found that ants that build thatching mounds, as wood ants do, were separate from species with other nesting strategies, often having a larger effect on soil properties than other species. This justifies continued interest in the species group and its effects on soil. In Chapter 3, we expanded our knowledge of wood ant effects on soil beyond the nest, and used field data to measure the effects that *Formica lugubris* has on biologically important soil properties in non-nest soils. We developed a model that allowed us to simulate the effects of *F. lugubris* on nest and non-nest soils and determine their role in changing the spatial variability of these soil properties. We showed that some soil properties, such as those we might associated with nitrogen poor organic matter (e.g., the litter that wood ants use to thatch their mounds), were more variable in areas occupied by the *F. lugubris*, while others were less variable. Importantly, we showed that the 'hotspot' effect of the nest was not the main driver of wood ant mediated spatial heterogeneity at the larger (circa. 1km^2) scales, and this ant mediated spatial heterogeneity is found in the soils surrounding the nests. Finally, in Chapter 4, we investigated how *F. lugubris* in plantations respond to differences in the structure of forest stands. By combining long-term data on populations of *F. lugubris* in plantation forests of the North York Moors with data on the orientation and width of linear canopy gaps in those plantations, we demonstrated the importance of insolation to the establishment of new nests in *F. lugubris* and how the orientation of linear canopy gaps can have substantial effects on the rate of population margins growth for such a slow disperser.

2. *Formica lugubris* in plantation forests

2.1 Soil modification by wood ants

Our work here has contributed to the understanding of the role that wood ants, and potentially other ants that have documented effects on the soil, have in modulating the availability of resources in soil: wood ant presence in forests increases the spatial heterogeneity of carbon and nitrogen pools while decreasing the spatial heterogeneity of phosphate and nitrate nutrients, and the mechanism is unrelated to reported hotspot effects of nests (Lenoir et al., 2001). Carbon and nitrogen are correlated with organic matter content, and it is therefore likely that the mechanism is the removal of leaf litter from some areas of the forest floor by the ants for nest building. Organic matter content of soils can affect soil physical properties like compaction (Soane, 1990) and water retention potential (Yang *et al.*, 2014), so the introduction of areas of higher and lower organic matter content on a small scale could be important for making microhabitats for organisms that are sensitive to differences in these soil properties. Equally, some plants are sensitive to high concentrations of nutrients like nitrate and phosphates and other species of plant may tolerate or require higher concentrations (Ozinga et al., 1997; Krahulec et al., 2001). By reducing the spatial variability of these nutrients, the wood ants may reduce the likelihood of plant species with very specific nutrient tolerances establishing in the forests where the ants are abundant. In this section, we will discuss the significance of the effects of wood ants on the spatial heterogeneity of soil beyond the nest in the context of the nest effects observed here and elsewhere, and explore some of the groups of organisms that may be affected by the changes that wood ants bring about in the soil, both positively and negatively.

The thatching of nest mounds by ants of the *Formica rufa* group is almost exclusive to this group and, as we demonstrated in Chapter 2, may be major reason why the effects that wood ants have on soil in the nests is often greater than in ants that do not thatch their nest structures. In Chapter 3, we found that the presence of wood ants increases the spatial variability of carbon and nitrogen pools and concluded that this is because they remove organic material for nest building in an uneven way. As such, their effects on organic matter heterogeneity go beyond then nest. The nests of many ant species can be very different from surrounding soil (Farji-Brener and Werenkraut, 2017; Chapter 2), including wood ants (Lenoir et al., 2001; Kilpeläinen et al., 2007; Ohashi et al., 2007) and it has been argued that this is a contribution to the spatial heterogeneity of soil properties (Lenoir et al., 2001; Risch et al., 2005) and it is tempting to assume that heterogeneity of this kind might provide some of the documented benefits of spatial heterogeneity such as increased resilience (Oliver *et al.*, 2015) or coexistence of diverse flora (Ozinga et al., 1997). However, it is doubtful whether any soil resources stored in ant mounds can be utilised by other organisms because ants often remove plants from the mound surface (Laakso and Setälä, 1997) and guard their nest from most other invertebrates very effectively. As such, heterogeneity as a result of the hotspot effect on mounds will be unlikely to have any ecological effects while the nest is still active. On the other hand, spatial heterogeneity in the non-nest soils, as we have demonstrated here, is beyond the area where ants can actively exclude other organisms. The spatial heterogeneity of organic matter in plantation forests is much lower than that of natural or ancient woodland, and this is in part due to the harvesting of timber preventing the accumulation of deadwood or the disruption of the organic layers by uprooting from strong wind (Stone, 1975). By increasing the spatial heterogeneity of the organic matter in the soil of plantation forests in a way that is accessible to other organisms (i.e., not limited to the 'hotspot' effect of the nest) wood ants may mitigate some of the loss of heterogeneity in plantation forests relative to natural ones such that the understory becomes suitable for species typically associated with more mature woodland.

The suppressive effects that ants have on the spatial heterogeneity of the nitrate and phosphate nutrients may well play a role in passive restoration by reducing the suitable habitat for nitrophilous herbs. Nitrophilous plants, plants tolerant of higher concentrations of nitrogenous nutrients such as nitrate, are considered and indicator of degraded habitats (Krahulec *et al.*, 2001; Matthies *et al.*, 2015), while plantations of some non-native trees have been associated with a greater abundance of nitrophilous herbs in the understory (Peterken, 2001). We did not find evidence that wood ant presence decreased the total available pools of nutrients but hypothesised that the reduction in the spatial heterogeneity of these nutrients was due to the removal of hotspots. If this is the case, the ants may be removing areas where nitrophilous species that may outcompete oligotrophic forest specialist (Nicolescu *et al.*, 2020) and preventing the loss of native forest plant species from plantation forest. On the other hand, the spatial heterogeneity of nutrients including nitrate and phosphate could promote coexistence of plant species that would otherwise competitively exclude one another (Ozinga *et al*., 1997), so whether the reduction in heterogeneity results in the exclusion of nitrophilous herbs or oligotrophs will be dependent on whether the soil landscape is already nutrient rich or not. As a result, while the effect will be highly context specific, wood ants may contribute to some form of passive restoration (González *et al*., 2016) in plantation forests when the forests are left unharvested, allowing the understory flora to partially converge with ancient woodland.

Overall, there is some evidence that the presence of wood ants may slightly accelerate changes in availability of soil resources in plantation forests, allowing the soil landscape in these plantations to better resemble mature forest in a few attributes. This may be of some benefit to biodiversity in areas where plantations have been planted adjacent to ancient woodland because it increases the potential suitability of the plantation forest for colonisation by forest specialists. By reducing the contrast between plantation and ancient woodland, they may reduce the negative consequences of high contrast edges for forest specialists (Noreika and Kotze, 2012). On the other hand, this increase in heterogeneity comes at a small cost to the growth of trees due to increased aphid burden in wood ant occupied forests (Frouz *et al.*, 2008), so whether wood ant presence is desirable will be somewhat dependant on the priorities of forest managers.

2.2 Forest structure and species movement

We presented compelling evidence that the availability of sunlight is an important factor in the dispersal of the edge specialist *Formica lugubris*, and that their rate of dispersal is faster along linear canopy gaps that are orientated in cardinal (that is, N, S, E, W) directions than along gaps that lie on intercardinal bearings. This adds to the body of evidence for the edge specialist concept; it has been argued that the concept of edge specialism does not exist, and that 'edge-specialists' are merely edge tolerant opportunists (Ries and Sisk, 2010). The central argument of this critique is that 'edge specialists do not respond to all edges in the same way. While the pigeonholing of species into the category of 'edge-specialist', when they are merely edge tolerant opportunists, would present problems for the definition, this same critique would be equally valid for forest interior specialists; forest specialist will not respond to all forest interiors in the same way (Halme *et al.*, 1993). As a result, we argue that the term 'edge-specialist' still has value, and the work we have presented here provides a clear example of a species can be unambiguously described as an edge specialist. The margins remapping conducted for the long-term data we have used (Procter, 2016; Holgate, 2021) have shown that *F. lugubris* is absent from heavily shaded forest interiors, while in Chapter 4 we showed that properties of edges determine the abundance of *F. lugubris* nests. This indicates that edges can be high-quality and low-quality habitat for *F. lugubris*, and the ants will select the higher quality edge (e.g., south-facing edges) for nesting sites. This runs counter to the notion of them being edge-tolerant opportunists; *F. lugubris* has specific requirements of edge habitat for it to be suitable. We believe that, rather than being an example of the inconsistency of the effect of edges on 'edge-specialists' (Ries and Sisk, 2010), the different response of wood ants to rides of different orientations shows that the quality of the edge matters in plantation forests, as the quality of any other habitat or feature would change a species ability to utilise it.

By showing that edge properties such as orientation can affect the dispersal of *F. lugubris* as an edge-specialist, we have provided some grounds to suppose that other edge-specialist forest organisms with similar edge requirements (resources from the forest, insolation from the canopy gap) may be similarly affected by the orientation of linear canopy gaps. Due to the slow dispersal of *F. lugubris*, its reliance on a static nest, and its need for sunlight, there are clear comparisons with herbaceous plants, and we hypothesise that edge-specialist forest herbs may also spread more rapidly along cardinally oriented linear canopy gaps than intercardinal canopy gaps, though these observations may also apply to some other invertebrates that share habitat preferences with *F. lugubris*. The herbs that might benefit from this improved dispersal are unlikely to be forest interior specialists, however (Hofmeister *et al.*, 2022), and the benefits to edge-specialists may come at the cost of forest specialists. In plantation forests, that are generally depauperate in forest interior specialists (Rédei *et al.*, 2020), this may still represent a net gain for local biodiversity; with the areas of plantation forest in the UK set to continue increasing (Defra, 2021), areas of open habitat will be replaced with plantation forest, and these linear canopy gaps may provide refuges for species of the open habitat or edge-specialists, reducing the risk of the elimination of small localised populations by afforestation (Peterken, 2001). This means that, in areas where forest specialists are absent and unlikely to be able to colonise it may be desirable to promote the spread of edge-specialists into the plantation forests by ensuring an abundance of cardinally oriented linear canopy gaps, while the opposite might be preferable in plantations adjacent to native woodland, as these may favour forest specialists.

The benefits to species movements of linear canopy gaps may in principle also apply to species that are damaging to plantation forests, or species that it is generally undesirable to spread, such as invasive non-natives. Species that become destructive pests or invasive weeds are often generalists with flexible habitat requirements and are more likely to be found in disturbed areas (e.g., edges) where specialists cannot easily exclude them (Marvier *et al.*, 2004). However, there seems to be little published evidence of pest species utilising linear canopy gaps in the way that we have described here for *F. lugubris* and further work would be required to test if this was a serious risk. The same applies to tree pathogens that used invertebrate pests as vectors (e.g., the fungal pathogen *Ophiostoma novo-ulmi* and the elm bark beetle, *Hylurgopinus rufipes*; McLeod et al., 2005). In the context of forests with wood ant presence, the wood ants may mitigate the effects of the pests (Karhu and Neuvonen 1998), but not necessarily the pathogens that they are vectors for.

2.3 Recommendations

In Britain, *Formca lugubris* is present at many plantation forest sites, and the effects that they have on the environment may be of interest to managers of plantations, as may the effects on edge-specialist movement of linear canopy gaps that we have demonstrated here using *F. lugubris* as a model. We have shown that wood ants affect the spatial heterogeneity of soil resources in a way that might make plantation forests more permeable to other species by providing a greater diversity of microhabitats (Hofmeister *et al.*, 2022). Wood ants have numerous other documented effects in forest ecosystems: they may have disruptive competitive effects on insectivorous birds (Jäntti *et al.*, 2001), and they can affect the populations of invertebrates directly by predation (Zingg *et al.*, 2018) or by competitive exclusion (Hawes *et al.*, 2013). This predatory behaviour can be an economic benefit to forestry by reducing defoliation by invertebrate pests (Laine and Niemela, 1980) resulting in ‘green islands’ of little or no defoliation around wood ant populations during a pest outbreak (Karhu and Neuvonen, 1998). Soil amelioration by wood ants leads to increased tree growth (Frouz et al., 2008), but only in the immediate vicinity of the nest, while the mutualistic relationship that wood ants have with sap-sucking aphids could result in increased aphid densities, and this results in reduced rates of tree growth away from the localised effects of soil amelioration (Frouz *et al.*, 2008), which may be undesirable in forestry contexts. Ultimately, this represents the kind of productivity-resilience trade off that is a common consideration in the production of many resources (Karakoc and Konar, 2021); the presence of wood ants may increase the prevalence of sapsucking aphids with a high probability of slightly slower growth but offer considerable protection from defoliating pests that have a lower probability of destroying the whole crop. As we have shown that their spread can be influenced by plantation design, forest managers in areas where *F. lugubris* is present may wish to consider the effects that wood ants have on biodiversity, productivity, and resilience at the planning stage.

At sites where large areas are devoted to a single crop species that may be vulnerable to defoliating pests, and the woodland is being managed exclusively for timber production, it will be desirable to design plantations in a way that promotes the dispersal of wood ants, so that the added resistance to pest outbreaks can be distributed through the crop. Outbreaks of defoliating pests can result in reductions in income per rotation of up to 7.5% due to damage to the crop (Straw *et al*., 2002), so the small reduction in tree growth may be acceptable in some cases. On the other hand, in plantations where there is a high diversity of tree species and therefore greater redundancy and innate resistance to pest outbreaks (Jactel *et al.*, 2002), or in regions where pest outbreaks are rare, the added resilience to defoliating pests provided by wood ants may be less desirable in the short term. However, due to the difficulty of translocating wood ants (Trigos-Peral *et al.*, 2021), managing the forests in a way that continues to support wood ant populations in areas where they are already found will not only prevent the loss of the species, but also retain a reservoir of agents of pest control, should the needs of the plantation forest change in the long term. Finally, any forest that is being managed with biodiversity or recreation as a high priority should consider managing the woodland in a way that promotes *F. lugubris* spread. Not only do they have potential to increase spatial heterogeneity and promote diversity (e.g., by providing habitat for *Formicoxenus nitidulus*, a UK Biodiversity Action Plan priority species; JNCC, 2007), but they may suppress tick populations (Zingg *et al.*, 2018), and provide a valuable and highly conspicuous opportunity for members of the public to witness a charismatic invertebrate species when using the forests for recreation.

3. Limitations and further questions

While we were able to provide compelling evidence of the effect that wood ants have on the spatial heterogeneity of soil resources, our analysis of spatial heterogeneity was not a perfect measure of spatial heterogeneity because this was a secondary use of data that had been collected to test other hypotheses. As a result, a study specifically designed to measure spatial heterogeneity would potentially provide a deeper insight into the affects that ants can have on soil heterogeneity, especially as we have now shown that there are grounds to predict an effect of ants on spatial heterogeneity in the wider environment.

Though we have attempted to address the effects that wood ants have on plantation forest ecosystems, the scope of our empirical research is necessarily limited, and we have presented data only on their role in modifying the soil. In order to understand the full scope of the effects that the arrival of wood ants in forest could have, further research is needed into the interactions that wood ants have with other organisms in plantation forests. Previous studies have investigated their effects on pest species (Karhu and Neuvonen 1998), arthropod predators (Hawes *et al*., 2002), ticks (Zingg *et al.*, 2018) and even insectivorous birds (Jäntti *et al.*, 2001), However, our understanding of the effects of wood ants on the diversity and abundance of organisms in plantation forests is incomplete and would benefit from a comprehensive study of invertebrate diversity in areas with and without wood ants.

Whilst we have demonstrated that the orientation of linear canopy gaps can have an effect on the movement of one species, *Formica lugubris*, our results are not yet generalisable to other species of edge specialists. Despite the ubiquity of linear canopy gaps in anthropogenic forests and the importance of sunlight to many organisms, there have been few controlled experiments examining the effects of the orientation of linear canopy gaps on species movement, while the data presented in Chapter 4 is specific to *F. lugubris*. In the absence of appropriate long-term data on species movement in other study systems, opportunistic studies of pest outbreaks and rapid biological invasion by suspected edge specialists will help to develop our understanding of these dynamics.

4. Conclusions

Here, we have presented two original field studies and one meta-analysis that have developed our understanding of the interactions between wood ants and their habitat. By demonstrating the effects that wood ants have on the soil environment, we have provided information that will be useful to forest managers in areas of wood ant presence, and bettered our understanding of the contribution that ants can have to the complexity of the soil environment, whilst also demonstrating how management practices can modulate the dispersal of edge specialists through forest ecosystems. This thesis demonstrates the important bidirectional interactions that can take place between organisms and even very heavily modified landscapes and highlights the importance of understanding organism-ecosystem interactions to better manage biodiversity and natural resources.

Appendices

Appendix 1

Data papers reference list (Chapter 2)

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Whitford, W. G. (1978). STRUCTURE AND SEASONAL ACTIVITY OF CHIHUAHUA DESERT ANT COMMUNITIES. In *Insectes Sociaux* (Vol. 25, Issue 1).

Wiescher, P. T. (2010). *ANT COEXISTENCE IN A SPATIALLY HETEROGENEOUS REGION IN CENTRAL FLORIDA*.

Wilson, E. O. (2003). *Pheidole in the New World: A dominant, hyperdiverse ant genus*. Harvard University Press.

Appendix 3

Sources used to generate search terms used to gather data for meta-analysis (Chapter 2)

Table S1. Search terms identified from the key words lists of published papers on the topic.

Paper	Key words	Key words selected
(Frouz and Jilková, 2008)	Ants, soil, nutrient cycling, porosity, organic matter, moisture, microbial activity, review	Ants, Soil, nutrient cycling
(Jurgensen *et al.*, 2008)	*Formica rufa*, *Formica obscuripes*, ant-tended aphids, CO2, red wood ants	Ant-tended aphids
(Jouquet *et al.*, 2006)	Termites, ants, earthworms, ecosystem engineers, soil ecology	Ants, ecosystem engineers, soil ecology
(Farji-Brener and Werenkraut, 2017)	ants, ecological engineers, soil disturbance	Ants, ecological engineers
(Kilpeläinen *et al.*, 2007)	Boreal forest, *Formica rufa* group, carbon, nitrogen, phosphorous, bulk density	Carbon, Nitrogen, Phosphorous
	Final search terms	
List of search terms from literature	Ants, soil, nutrient cycling, ecosystem engineers, soil ecology, ecological engineers, carbon, nitrogen, phosphorous	
Additional terms	Nests, ant nests, nutrients, soil nutrients	

Appendix 4

Search string used for each database, and the number of papers each search yielded (Chapter2)

Table S2. Refined search terms for the three databases to be used in this meta-analysis and the number of results returned.

Database	Search string	Number of papers returned
Scopus	TITLE-ABS-KEY ((ant OR ants) AND soil* AND ("nutrient cycl*" OR "ecosystem engineer*" OR "soil ecology" OR "ecological engineer*" OR carbon OR nitr* OR phosph* OR nutrients OR "soil nutrients") AND (nest* OR "ant nests" OR mound* or hill*))	305 (27/01/21 UK)
Web of Science	ALL=(((ant OR ants) AND soil* AND ("nutrient cycl*" OR "ecosystem engineer*" OR "soil ecology" OR "ecological engineer*" OR carbon OR nitr* OR phosph* OR nutrients OR "soil nutrients") AND (nest* OR "ant nests" OR mound* or hill*)))	357 (27/01/21 UK)
PubMed	(all fields): (ant OR ants) AND soil* AND ("nutrient cycl*" OR "ecosystem engineer*" OR "soil ecology" OR "ecological engineer*" OR carbon OR nitr* OR phosph* OR nutrients OR "soil nutrients") AND (nest* OR "ant nests" OR mound* or hill*)	54 (27/01/21 UK)

Appendix 5

Additional pairwise comparisons (Chapter 2)

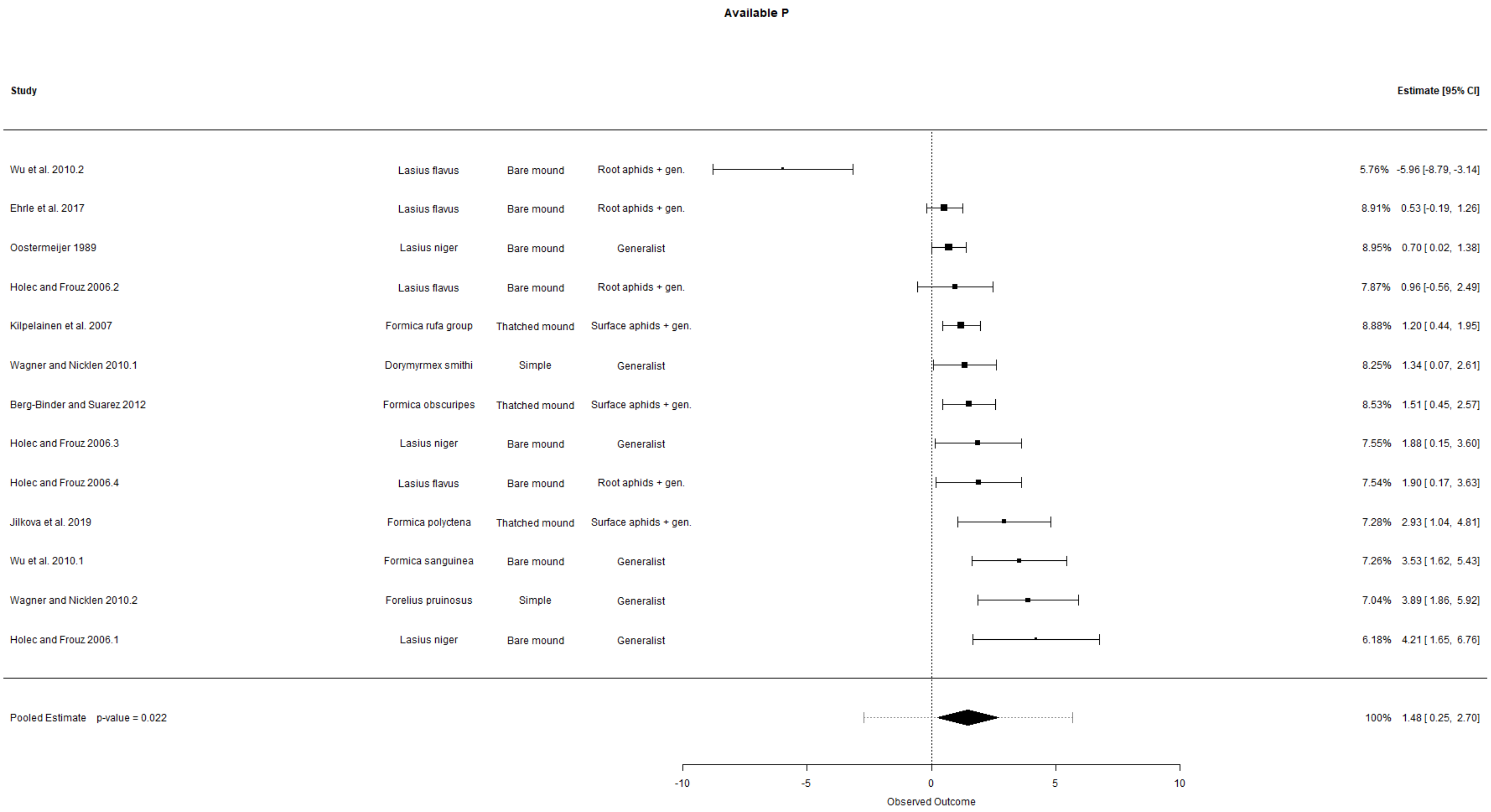
Table S3. Additional pairwise comparison, omitted from Table 5 because comparisons between a feeding strategy and a nesting strategy are not meaningful, as they belong to different categories.

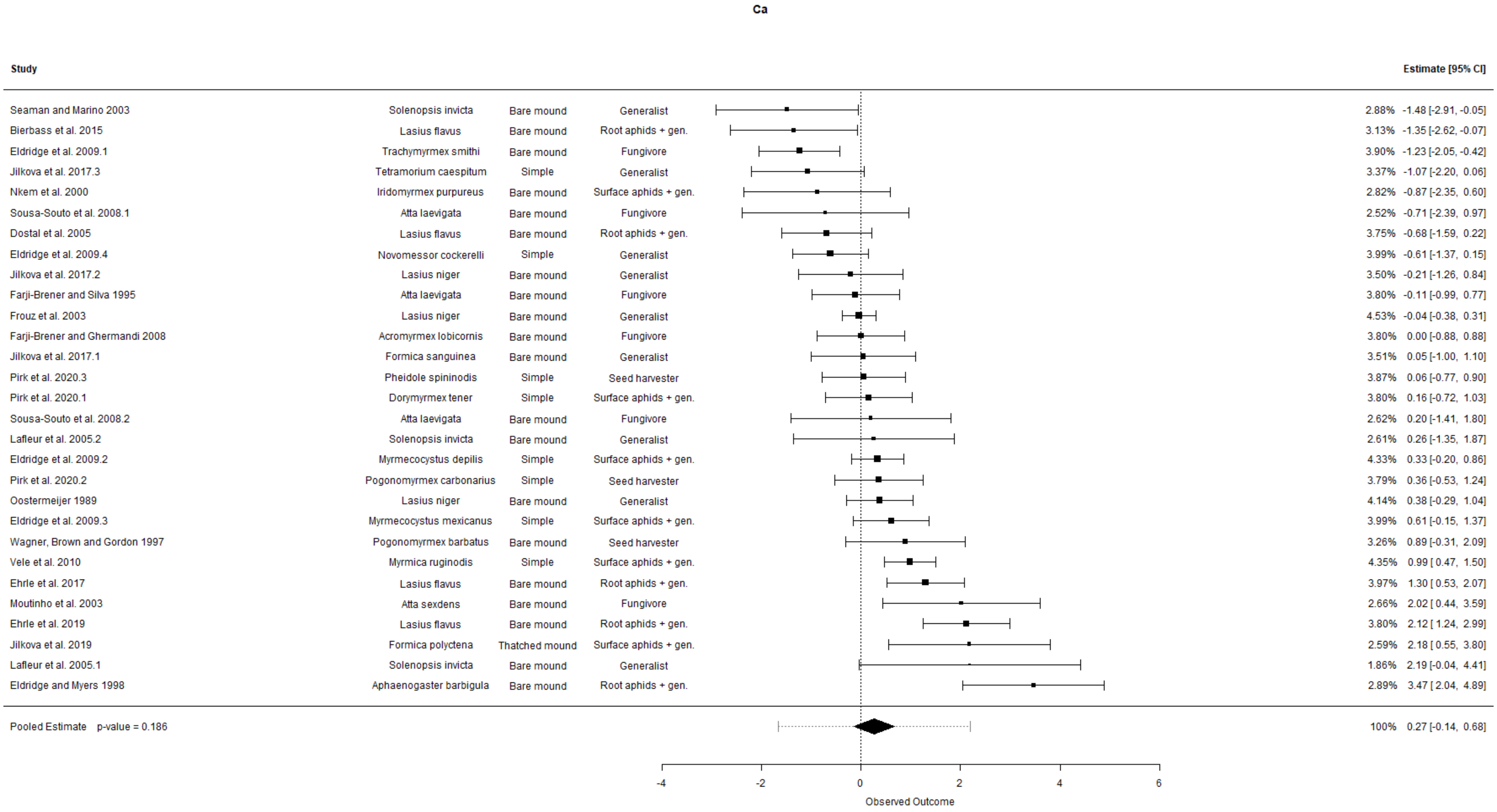
Significant pairwise comparisons		**Variable**	**Estimate**	**Z value**	***p*-value**
Root aphid + generalist	Simple/no mound	pH	2.245	2.997	0.039 *

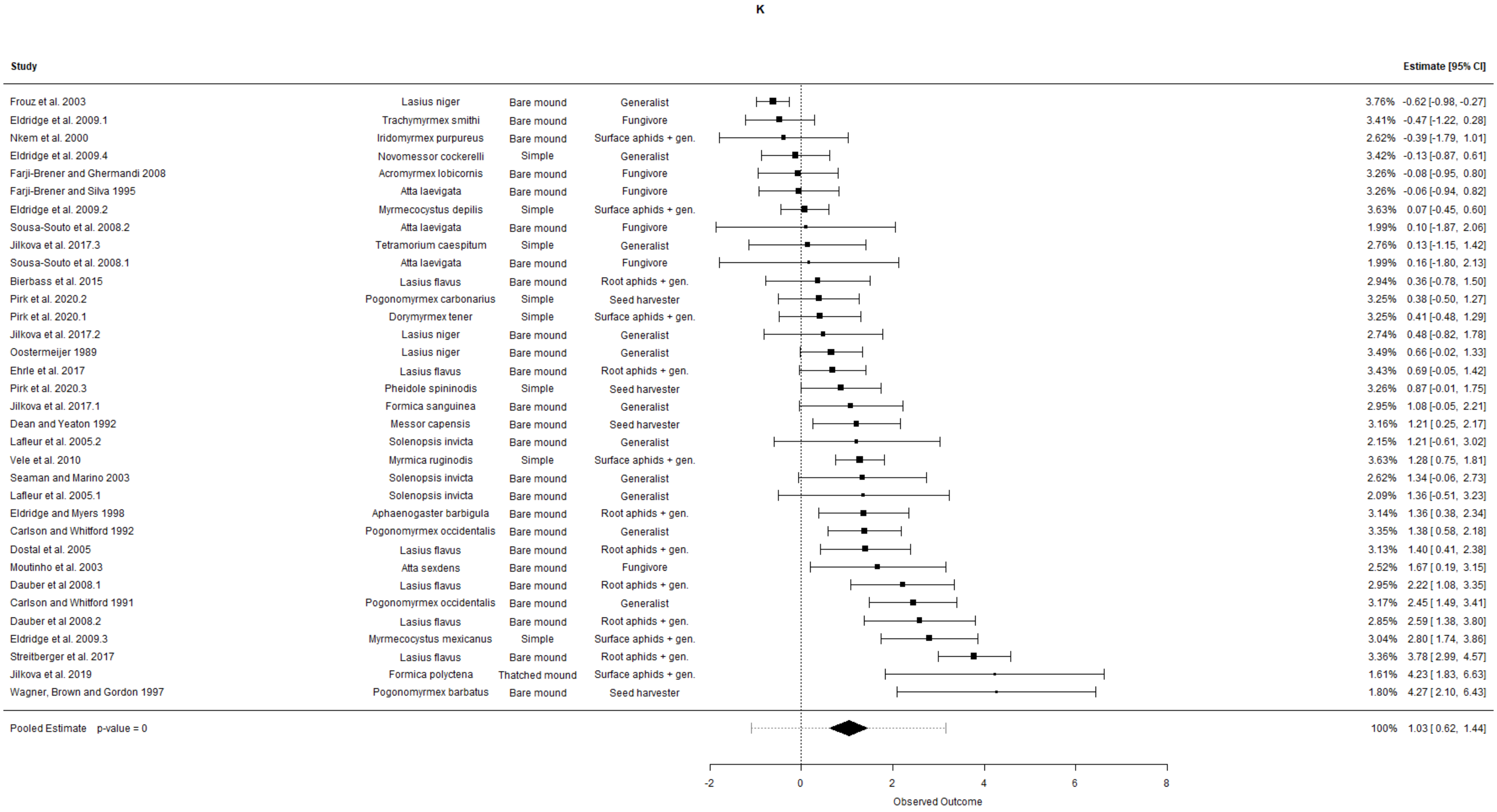
Appendix 6

Forest plots for pooled effect sizes obtained in meta-analysis (Chapter 2)

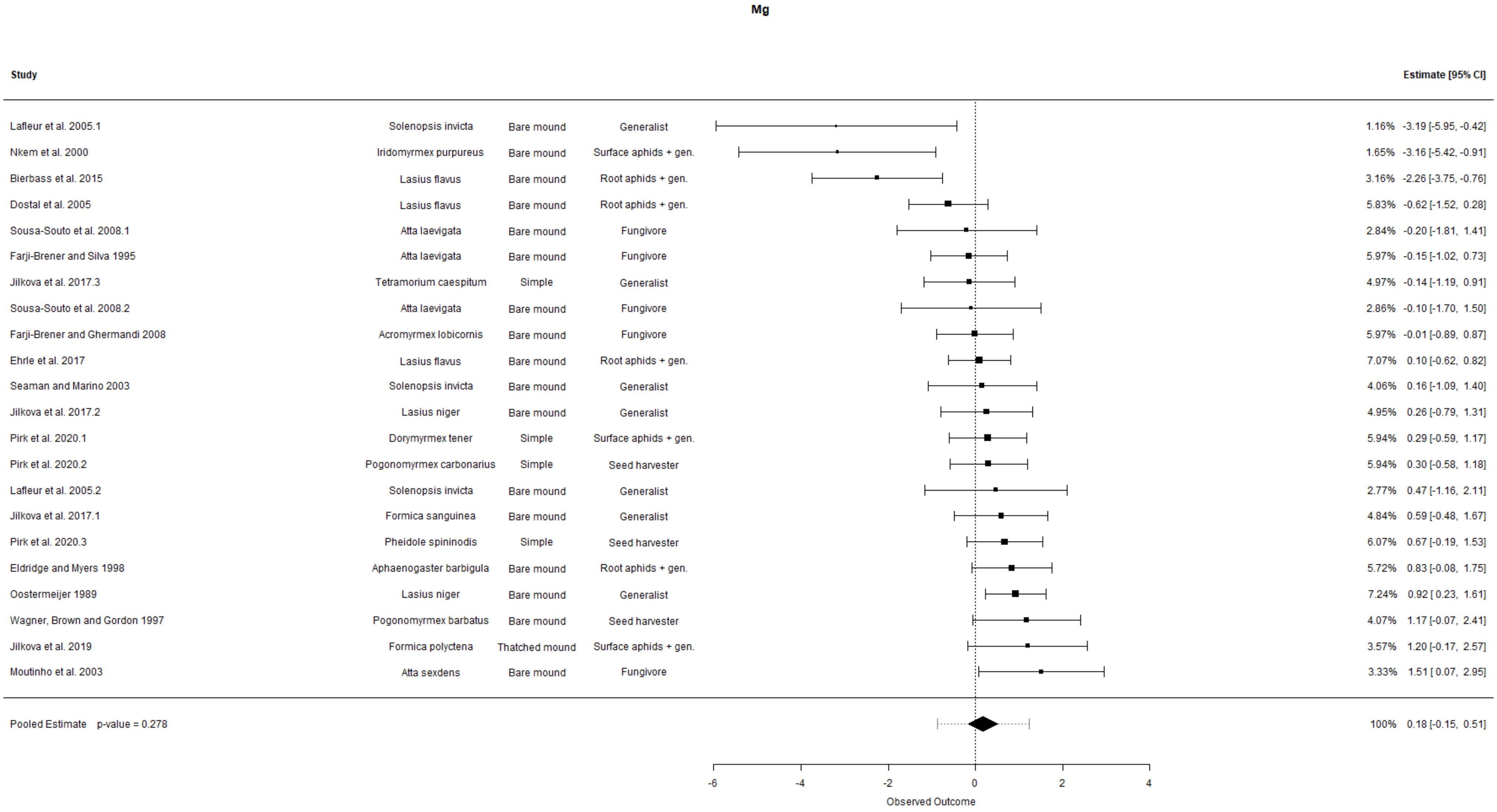
Figures S1-S11. Effect sizes of Total C (Hedge's g) were calculated for each study and overall pooled effect sizes calculated for each variable. Effect sizes (SMD; Hedge's g), confidence intervals and weightings are presented on the right, and the effect sizes and confidence intervals for each study are represented graphically in the centre of the plot. The overall pooled estimate and 95% CI displayed at the bottom of the plot as the summary diamond, while the dotted lines either side of the summary diamond are the prediction intervals (the estimated intervals 95% of the true outcomes should fall between).

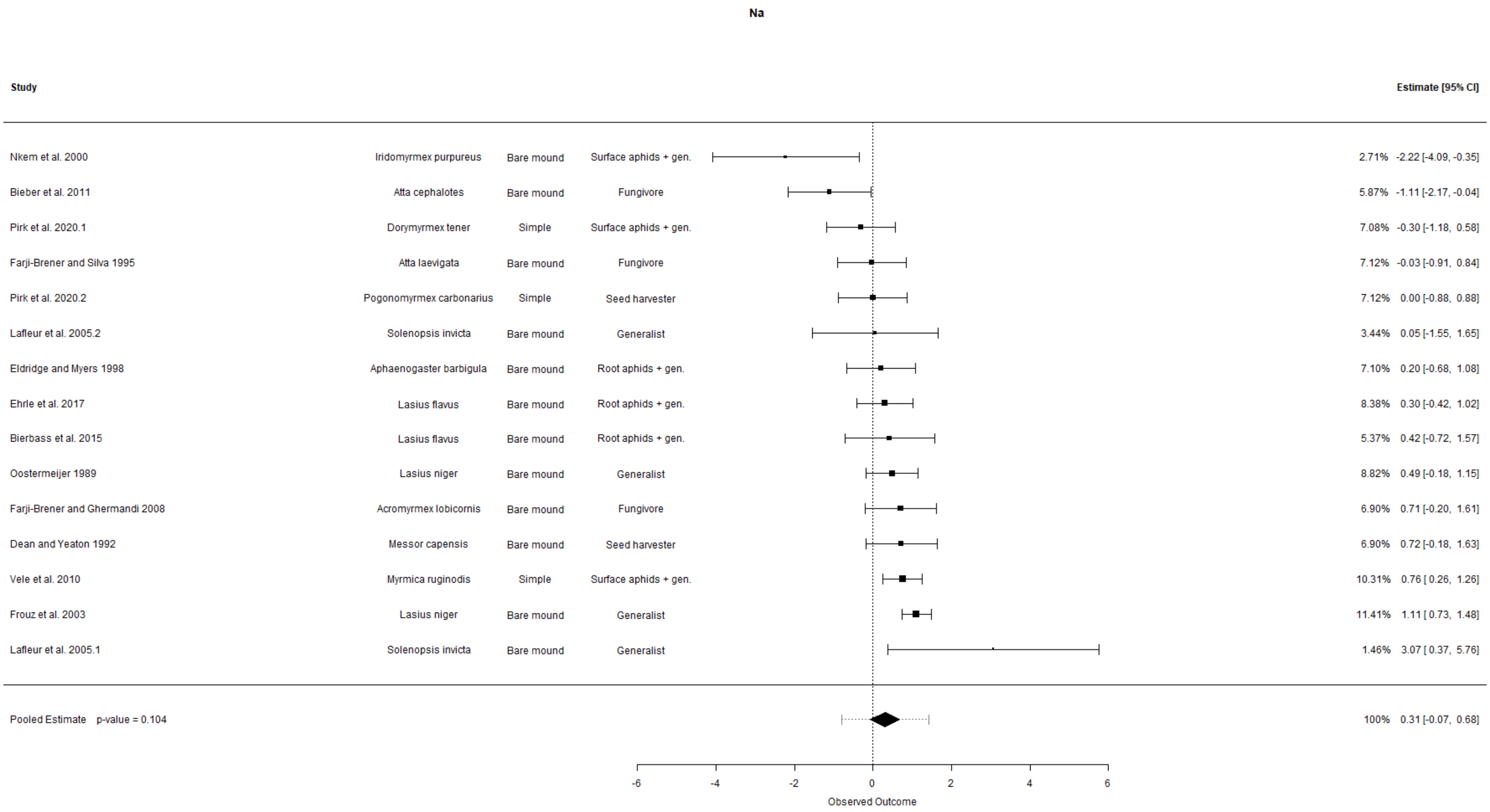

Available P
Study
Estimate [95% CI]
Wu et al. 2010.2 Lasius flavus Bare mound Root aphids + gen. 5.76% -5.96 [-8.79, -3.14]
Ehrle et al. 2017 Lasius flavus Bare mound Root aphids + gen. 8.91% 0.53 [-0.19, 1.26]
Oostermeijer 1989 Lasius niger Bare mound Generalist 8.95% 0.70 [0.02, 1.38]
Holec and Frouz 2006.2 Lasius flavus Bare mound Root aphids + gen. 7.87% 0.96 [-0.56, 2.49]
Kilpelainen et al. 2007 Formica rufa group Thatched mound Surface aphids + gen. 8.88% 1.20 [0.44, 1.95]
Wagner and Nicklen 2010.1 Dorymyrmex smithi Simple Generalist 8.25% 1.34 [0.07, 2.61]
Berg-Binder and Suarez 2012 Formica obscuripes Thatched mound Surface aphids + gen. 8.53% 1.51 [0.45, 2.57]
Holec and Frouz 2006.3 Lasius niger Bare mound Generalist 7.55% 1.88 [0.15, 3.60]
Holec and Frouz 2006.4 Lasius flavus Bare mound Root aphids + gen. 7.54% 1.90 [0.17, 3.63]
Jilkova et al. 2019 Formica polyctena Thatched mound Surface aphids + gen. 7.28% 2.93 [1.04, 4.81]
Wu et al. 2010.1 Formica sanguinea Bare mound Generalist 7.26% 3.53 [1.62, 5.43]
Wagner and Nicklen 2010.2 Forelius pruinosus Simple Generalist 7.04% 3.89 [1.86, 5.92]
Holec and Frouz 2006.1 Lasius niger Bare mound Generalist 6.18% 4.21 [1.65, 6.76]
Pooled Estimate p-value = 0.022 100% 1.48 [0.25, 2.70]
-10
-5
0
5
10
Observed Outcome


Ca
Study
Estimate [95% CI]
Seaman and Marino 2003 Solenopsis invicta Bare mound Generalist 2.88% -1.48 [-2.91, -0.05]
Bierbass et al. 2015 Lasius flavus Bare mound Root aphids + gen. 3.13% -1.35 [-2.62, -0.07]
Eldridge et al. 2009.1 Trachymyrmex smithi Bare mound Fungivore 3.90% -1.23 [-2.05, -0.42]
Jilkova et al. 2017.3 Tetramorium caespitum Simple Generalist 3.37% -1.07 [-2.20, 0.06]
Nkem et al. 2000 Iridomyrmex purpureus Bare mound Surface aphids + gen. 2.82% -0.87 [-2.35, 0.60]
Sousa-Souto et al. 2008.1 Atta laevigata Bare mound Fungivore 2.52% -0.71 [-2.39, 0.97]
Dostal et al. 2005 Lasius flavus Bare mound Root aphids + gen. 3.75% -0.68 [-1.59, 0.22]
Eldridge et al. 2009.4 Novomessor cockerelli Simple Generalist 3.99% -0.61 [-1.37, 0.15]
Jilkova et al. 2017.2 Lasius niger Bare mound Generalist 3.50% -0.21 [-1.26, 0.84]
Farji-Brener and Silva 1995 Atta laevigata Bare mound Fungivore 3.80% -0.11 [-0.99, 0.77]
Frouz et al. 2003 Lasius niger Bare mound Generalist 4.53% -0.04 [-0.38, 0.31]
Farji-Brener and Ghermandi 2008 Acromyrmex lobicornis Bare mound Fungivore 3.80% 0.00 [-0.88, 0.88]
Jilkova et al. 2017.1 Formica sanguinea Bare mound Generalist 3.51% 0.05 [-1.00, 1.10]
Pirk et al. 2020.3 Pheidole spininodis Simple Seed harvester 3.87% 0.06 [-0.77, 0.90]
Pirk et al. 2020.1 Dorymyrmex tener Simple Surface aphids + gen. 3.80% 0.16 [-0.72, 1.03]
Sousa-Souto et al. 2008.2 Atta laevigata Bare mound Fungivore 2.62% 0.20 [-1.41, 1.80]
Lafleur et al. 2005.2 Solenopsis invicta Bare mound Generalist 2.61% 0.26 [-1.35, 1.87]
Eldridge et al. 2009.2 Myrmecocystus depilis Simple Surface aphids + gen. 4.33% 0.33 [-0.20, 0.86]
Pirk et al. 2020.2 Pogonomyrmex carbonarius Simple Seed harvester 3.79% 0.36 [-0.53, 1.24]
Oostermeijer 1989 Lasius niger Bare mound Generalist 4.14% 0.38 [-0.29, 1.04]
Eldridge et al. 2009.3 Myrmecocystus mexicanus Simple Surface aphids + gen. 3.99% 0.61 [-0.15, 1.37]
Wagner, Brown and Gordon 1997 Pogonomyrmex barbatus Bare mound Seed harvester 3.26% 0.89 [-0.31, 2.09]
Vele et al. 2010 Myrmica ruginodis Simple Surface aphids + gen. 4.35% 0.99 [0.47, 1.50]
Ehrle et al. 2017 Lasius flavus Bare mound Root aphids + gen. 3.97% 1.30 [0.53, 2.07]
Moutinho et al. 2003 Atta sexdens Bare mound Fungivore 2.66% 2.02 [0.44, 3.59]
Ehrle et al. 2019 Lasius flavus Bare mound Root aphids + gen. 3.80% 2.12 [1.24, 2.99]
Jilkova et al. 2019 Formica polyctena Thatched mound Surface aphids + gen. 2.59% 2.18 [0.55, 3.80]
Lafleur et al. 2005.1 Solenopsis invicta Bare mound Generalist 1.86% 2.19 [-0.04, 4.41]
Eldridge and Myers 1998 Aphaenogaster barbigula Bare mound Root aphids + gen. 2.89% 3.47 [2.04, 4.89]
Pooled Estimate p-value = 0.186 100% 0.27 [-0.14, 0.68]
-4
-2
0
2
4
6
Observed Outcome



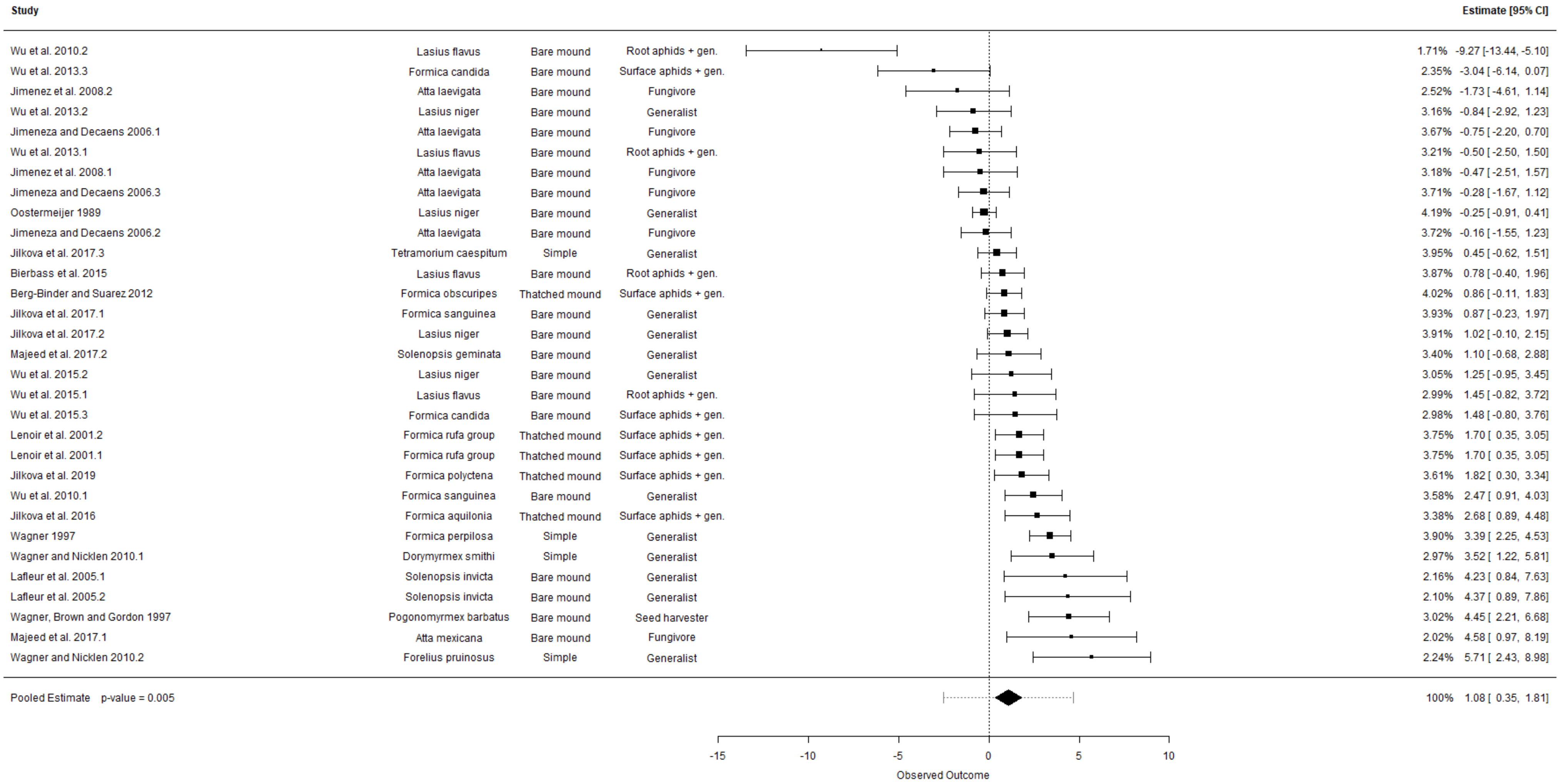
Study					Estimate [95% CI]
Frouz et al. 2003	Lasius niger	Bare mound	Generalist	3.76%	-0.62 [-0.98, -0.27]
Eldridge et al. 2009.1	Trachymyrmex smithi	Bare mound	Fungivore	3.41%	-0.47 [-1.22, 0.28]
Nkem et al. 2000	Iridomyrmex purpureus	Bare mound	Surface aphids + gen.	2.62%	-0.39 [-1.79, 1.01]
Eldridge et al. 2009.4	Novomessor cockerelli	Simple	Generalist	3.42%	-0.13 [-0.87, 0.61]
Farji-Brener and Ghermandi 2008	Acromyrmex lobicornis	Bare mound	Fungivore	3.26%	-0.08 [-0.95, 0.80]
Farji-Brener and Silva 1995	Atta laevigata	Bare mound	Fungivore	3.26%	-0.06 [-0.94, 0.82]
Eldridge et al. 2009.2	Myrmecocystus depilis	Simple	Surface aphids + gen.	3.63%	0.07 [-0.45, 0.60]
Sousa-Souto et al. 2008.2	Atta laevigata	Bare mound	Fungivore	1.99%	0.10 [-1.87, 2.06]
Jilkova et al. 2017.3	Tetramorium caespitum	Simple	Generalist	2.76%	0.13 [-1.15, 1.42]
Sousa-Souto et al. 2008.1	Atta laevigata	Bare mound	Fungivore	1.99%	0.16 [-1.80, 2.13]
Bierbass et al. 2015	Lasius flavus	Bare mound	Root aphids + gen.	2.94%	0.36 [-0.78, 1.50]
Pirk et al. 2020.2	Pogonomyrmex carbonarius	Simple	Seed harvester	3.25%	0.38 [-0.50, 1.27]
Pirk et al. 2020.1	Dorymyrmex tener	Simple	Surface aphids + gen.	3.25%	0.41 [-0.48, 1.29]
Jilkova et al. 2017.2	Lasius niger	Bare mound	Generalist	2.74%	0.48 [-0.82, 1.78]
Oostermeijer 1989	Lasius niger	Bare mound	Generalist	3.49%	0.66 [-0.02, 1.33]
Ehrle et al. 2017	Lasius flavus	Bare mound	Root aphids + gen.	3.43%	0.69 [-0.05, 1.42]
Pirk et al. 2020.3	Pheidole spininodis	Simple	Seed harvester	3.26%	0.87 [-0.01, 1.75]
Jilkova et al. 2017.1	Formica sanguinea	Bare mound	Generalist	2.95%	1.08 [-0.05, 2.21]
Dean and Yeaton 1992	Messor capensis	Bare mound	Seed harvester	3.16%	1.21 [0.25, 2.17]
Lafleur et al. 2005.2	Solenopsis invicta	Bare mound	Generalist	2.15%	1.21 [-0.61, 3.02]
Vele et al. 2010	Myrmica ruginodis	Simple	Surface aphids + gen.	3.63%	1.28 [0.75, 1.81]
Seaman and Marino 2003	Solenopsis invicta	Bare mound	Generalist	2.62%	1.34 [-0.06, 2.73]
Lafleur et al. 2005.1	Solenopsis invicta	Bare mound	Generalist	2.09%	1.36 [-0.51, 3.23]
Eldridge and Myers 1998	Aphaenogaster barbigula	Bare mound	Root aphids + gen.	3.14%	1.36 [0.38, 2.34]
Carlson and Whitford 1992	Pogonomyrmex occidentalis	Bare mound	Generalist	3.35%	1.38 [0.58, 2.18]
Dostal et al. 2005	Lasius flavus	Bare mound	Root aphids + gen.	3.13%	1.40 [0.41, 2.38]
Moutinho et al. 2003	Atta sexdens	Bare mound	Fungivore	2.52%	1.67 [0.19, 3.15]
Dauber et al 2008.1	Lasius flavus	Bare mound	Root aphids + gen.	2.95%	2.22 [1.08, 3.35]
Carlson and Whitford 1991	Pogonomyrmex occidentalis	Bare mound	Generalist	3.17%	2.45 [1.49, 3.41]
Dauber et al 2008.2	Lasius flavus	Bare mound	Root aphids + gen.	2.85%	2.59 [1.38, 3.80]
Eldridge et al. 2009.3	Myrmecocystus mexicanus	Simple	Surface aphids + gen.	3.04%	2.80 [1.74, 3.86]
Streitberger et al. 2017	Lasius flavus	Bare mound	Root aphids + gen.	3.36%	3.78 [2.99, 4.57]
Jilkova et al. 2019	Formica polyctena	Thatched mound	Surface aphids + gen.	1.61%	4.23 [1.83, 6.63]
Wagner, Brown and Gordon 1997	Pogonomyrmex barbatus	Bare mound	Seed harvester	1.80%	4.27 [2.10, 6.43]
Pooled Estimate p-value = 0				100%	1.03 [0.62, 1.44]


Mg
Study
Estimate [95% CI]
Lafleur et al. 2005.1 Solenopsis invicta Bare mound Generalist 1.16% -3.19 [-5.95, -0.42]
Nkem et al. 2000 Iridomyrmex purpureus Bare mound Surface aphids + gen. 1.65% -3.16 [-5.42, -0.91]
Bierbass et al. 2015 Lasius flavus Bare mound Root aphids + gen. 3.16% -2.26 [-3.75, -0.76]
Dostal et al. 2005 Lasius flavus Bare mound Root aphids + gen. 5.83% -0.62 [-1.52, 0.28]
Sousa-Souto et al. 2008.1 Atta laevigata Bare mound Fungivore 2.84% -0.20 [-1.81, 1.41]
Farji-Brener and Silva 1995 Atta laevigata Bare mound Fungivore 5.97% -0.15 [-1.02, 0.73]
Jilkova et al. 2017.3 Tetramorium caespitum Simple Generalist 4.97% -0.14 [-1.19, 0.91]
Sousa-Souto et al. 2008.2 Atta laevigata Bare mound Fungivore 2.86% -0.10 [-1.70, 1.50]
Farji-Brener and Ghermandi 2008 Acromyrmex lobicornis Bare mound Fungivore 5.97% -0.01 [-0.89, 0.87]
Ehrle et al. 2017 Lasius flavus Bare mound Root aphids + gen. 7.07% 0.10 [-0.62, 0.82]
Seaman and Marino 2003 Solenopsis invicta Bare mound Generalist 4.06% 0.16 [-1.09, 1.40]
Jilkova et al. 2017.2 Lasius niger Bare mound Generalist 4.95% 0.26 [-0.79, 1.31]
Pirk et al. 2020.1 Dorymyrmex tener Simple Surface aphids + gen. 5.94% 0.29 [-0.59, 1.17]
Pirk et al. 2020.2 Pogonomyrmex carbonarius Simple Seed harvester 5.94% 0.30 [-0.58, 1.18]
Lafleur et al. 2005.2 Solenopsis invicta Bare mound Generalist 2.77% 0.47 [-1.16, 2.11]
Jilkova et al. 2017.1 Formica sanguinea Bare mound Generalist 4.84% 0.59 [-0.48, 1.67]
Pirk et al. 2020.3 Pheidole spininodis Simple Seed harvester 6.07% 0.67 [-0.19, 1.53]
Eldridge and Myers 1998 Aphaenogaster barbigula Bare mound Root aphids + gen. 5.72% 0.83 [-0.08, 1.75]
Oostermeijer 1989 Lasius niger Bare mound Generalist 7.24% 0.92 [0.23, 1.61]
Wagner, Brown and Gordon 1997 Pogonomyrmex barbatus Bare mound Seed harvester 4.07% 1.17 [-0.07, 2.41]
Jilkova et al. 2019 Formica polyctena Thatched mound Surface aphids + gen. 3.57% 1.20 [-0.17, 2.57]
Moutinho et al. 2003 Atta sexdens Bare mound Fungivore 3.33% 1.51 [0.07, 2.95]
Pooled Estimate p-value = 0.278 100% 0.18 [-0.15, 0.51]
-6
-4
-2
0
2
4
Observed Outcome

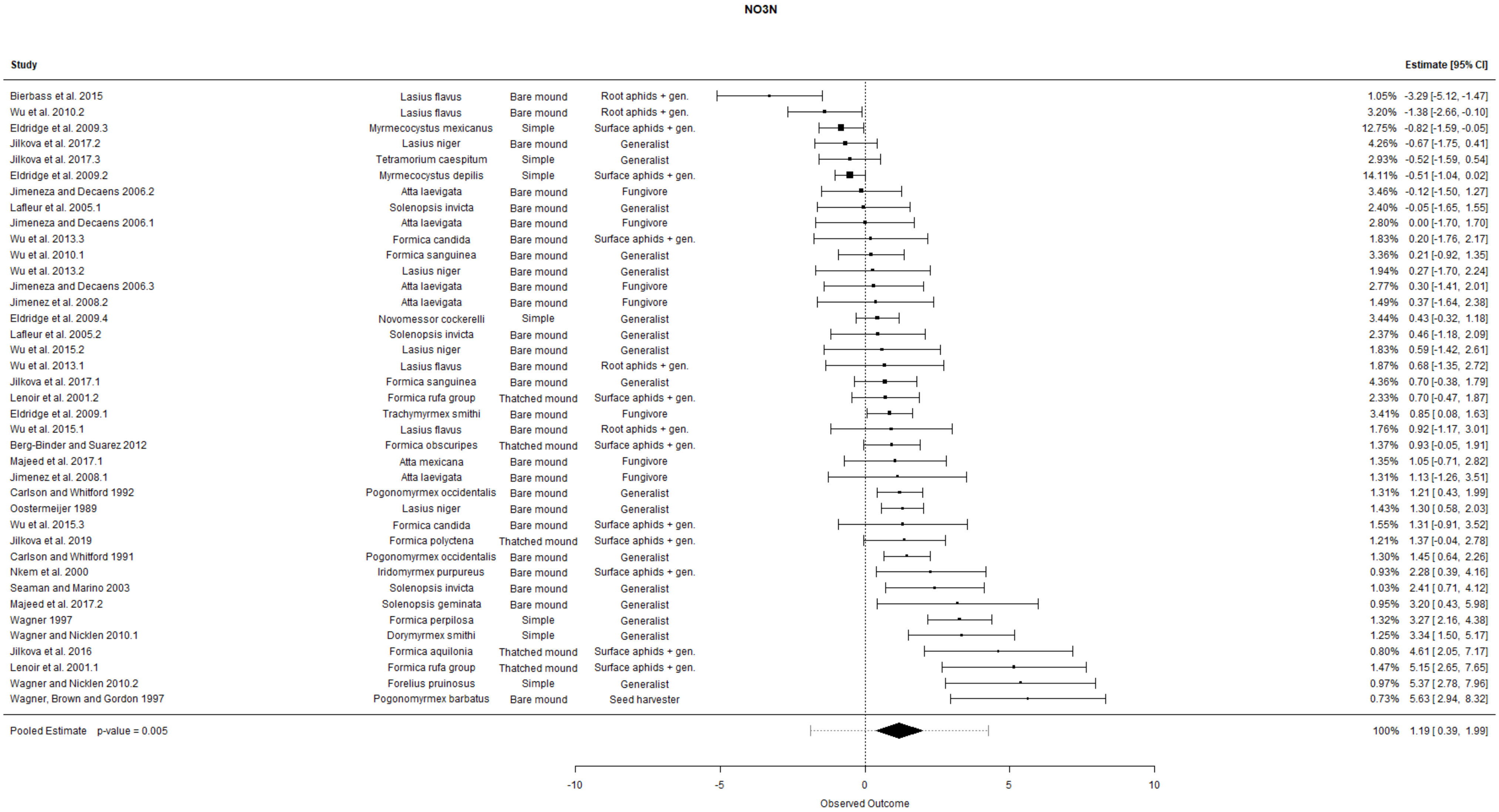


Study					Estimate [95% CI]
Nkem et al. 2000	Iridomyrmex purpureus	Bare mound	Surface aphids + gen.	2.71%	-2.22 [-4.09, -0.35]
Bieber et al. 2011	Atta cephalotes	Bare mound	Fungivore	5.87%	-1.11 [-2.17, -0.04]
Pirk et al. 2020.1	Dorymyrmex tener	Simple	Surface aphids + gen.	7.08%	-0.30 [-1.18, 0.58]
Farji-Brener and Silva 1995	Atta laevigata	Bare mound	Fungivore	7.12%	-0.03 [-0.91, 0.84]
Pirk et al. 2020.2	Pogonomyrmex carbonarius	Simple	Seed harvester	7.12%	0.00 [-0.88, 0.88]
Lafleur et al. 2005.2	Solenopsis invicta	Bare mound	Generalist	3.44%	0.05 [-1.55, 1.65]
Eldridge and Myers 1998	Aphaenogaster barbigula	Bare mound	Root aphids + gen.	7.10%	0.20 [-0.68, 1.08]
Ehrle et al. 2017	Lasius flavus	Bare mound	Root aphids + gen.	8.38%	0.30 [-0.42, 1.02]
Bierbass et al. 2015	Lasius flavus	Bare mound	Root aphids + gen.	5.37%	0.42 [-0.72, 1.57]
Oostermeijer 1989	Lasius niger	Bare mound	Generalist	8.82%	0.49 [-0.18, 1.15]
Farji-Brener and Ghermandi 2008	Acromyrmex lobicornis	Bare mound	Fungivore	6.90%	0.71 [-0.20, 1.61]
Dean and Yeaton 1992	Messor capensis	Bare mound	Seed harvester	6.90%	0.72 [-0.18, 1.63]
Vele et al. 2010	Myrmica ruginodis	Simple	Surface aphids + gen.	10.31%	0.76 [0.26, 1.26]
Frouz et al. 2003	Lasius niger	Bare mound	Generalist	11.41%	1.11 [0.73, 1.48]
Lafleur et al. 2005.1	Solenopsis invicta	Bare mound	Generalist	1.46%	3.07 [0.37, 5.76]
Pooled Estimate p-value = 0.104				100%	0.31 [-0.07, 0.68]

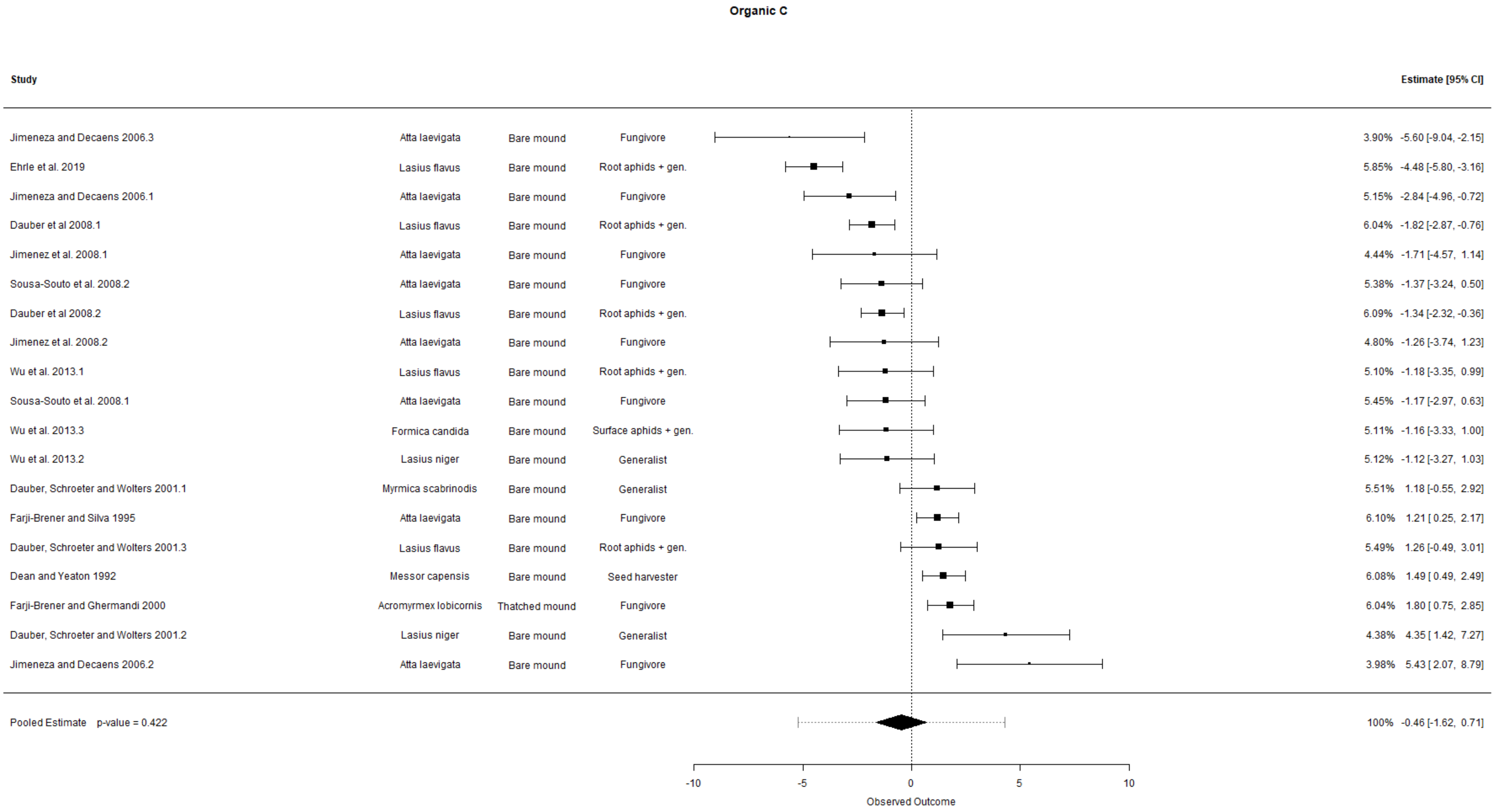
NH4N



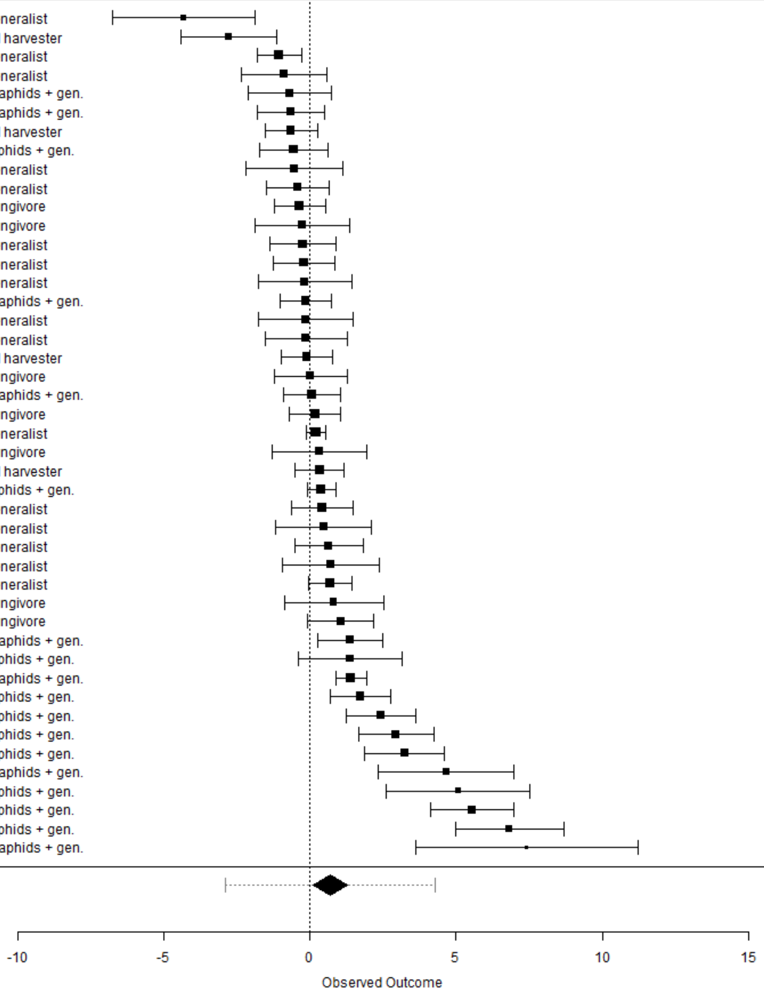
Study					Estimate [95% CI]
Wu et al. 2010.2	Lasius flavus	Bare mound	Root aphids + gen.	1.71%	-9.27 [-13.44, -5.10]
Wu et al. 2013.3	Formica candida	Bare mound	Surface aphids + gen.	2.35%	-3.04 [-6.14, 0.07]
Jimenez et al. 2008.2	Atta laevigata	Bare mound	Fungivore	2.52%	-1.73 [-4.61, 1.14]
Wu et al. 2013.2	Lasius niger	Bare mound	Generalist	3.16%	-0.84 [-2.92, 1.23]
Jimeneza and Decaens 2006.1	Atta laevigata	Bare mound	Fungivore	3.67%	-0.75 [-2.20, 0.70]
Wu et al. 2013.1	Lasius flavus	Bare mound	Root aphids + gen.	3.21%	-0.50 [-2.50, 1.50]
Jimenez et al. 2008.1	Atta laevigata	Bare mound	Fungivore	3.18%	-0.47 [-2.51, 1.57]
Jimeneza and Decaens 2006.3	Atta laevigata	Bare mound	Fungivore	3.71%	-0.28 [-1.67, 1.12]
Oostermeijer 1989	Lasius niger	Bare mound	Generalist	4.19%	-0.25 [-0.91, 0.41]
Jimeneza and Decaens 2006.2	Atta laevigata	Bare mound	Fungivore	3.72%	-0.16 [-1.55, 1.23]
Jilkova et al. 2017.3	Tetramorium caespitum	Simple	Generalist	3.95%	0.45 [-0.62, 1.51]
Bierbass et al. 2015	Lasius flavus	Bare mound	Root aphids + gen.	3.87%	0.78 [-0.40, 1.96]
Berg-Binder and Suarez 2012	Formica obscuripes	Thatched mound	Surface aphids + gen.	4.02%	0.86 [-0.11, 1.83]
Jilkova et al. 2017.1	Formica sanguinea	Bare mound	Generalist	3.93%	0.87 [-0.23, 1.97]
Jilkova et al. 2017.2	Lasius niger	Bare mound	Generalist	3.91%	1.02 [-0.10, 2.15]
Majeed et al. 2017.2	Solenopsis geminata	Bare mound	Generalist	3.40%	1.10 [-0.68, 2.88]
Wu et al. 2015.2	Lasius niger	Bare mound	Generalist	3.05%	1.25 [-0.95, 3.45]
Wu et al. 2015.1	Lasius flavus	Bare mound	Root aphids + gen.	2.99%	1.45 [-0.82, 3.72]
Wu et al. 2015.3	Formica candida	Bare mound	Surface aphids + gen.	2.98%	1.48 [-0.80, 3.76]
Lenoir et al. 2001.2	Formica rufa group	Thatched mound	Surface aphids + gen.	3.75%	1.70 [0.35, 3.05]
Lenoir et al. 2001.1	Formica rufa group	Thatched mound	Surface aphids + gen.	3.75%	1.70 [0.35, 3.05]
Jilkova et al. 2019	Formica polyctena	Thatched mound	Surface aphids + gen.	3.61%	1.82 [0.30, 3.34]
Wu et al. 2010.1	Formica sanguinea	Bare mound	Generalist	3.58%	2.47 [0.91, 4.03]
Jilkova et al. 2016	Formica aquilonia	Thatched mound	Surface aphids + gen.	3.38%	2.68 [0.89, 4.48]
Wagner 1997	Formica perpilosa	Simple	Generalist	3.90%	3.39 [2.25, 4.53]
Wagner and Nicklen 2010.1	Dorymyrmex smithi	Simple	Generalist	2.97%	3.52 [1.22, 5.81]
Lafleur et al. 2005.1	Solenopsis invicta	Bare mound	Generalist	2.16%	4.23 [0.84, 7.63]
Lafleur et al. 2005.2	Solenopsis invicta	Bare mound	Generalist	2.10%	4.37 [0.89, 7.86]
Wagner, Brown and Gordon 1997	Pogonomyrmex barbatus	Bare mound	Seed harvester	3.02%	4.45 [2.21, 6.68]
Majeed et al. 2017.1	Atta mexicana	Bare mound	Fungivore	2.02%	4.58 [0.97, 8.19]
Wagner and Nicklen 2010.2	Forelius pruinosus	Simple	Generalist	2.24%	5.71 [2.43, 8.98]
Pooled Estimate p-value = 0.005				100%	1.08 [0.35, 1.81]



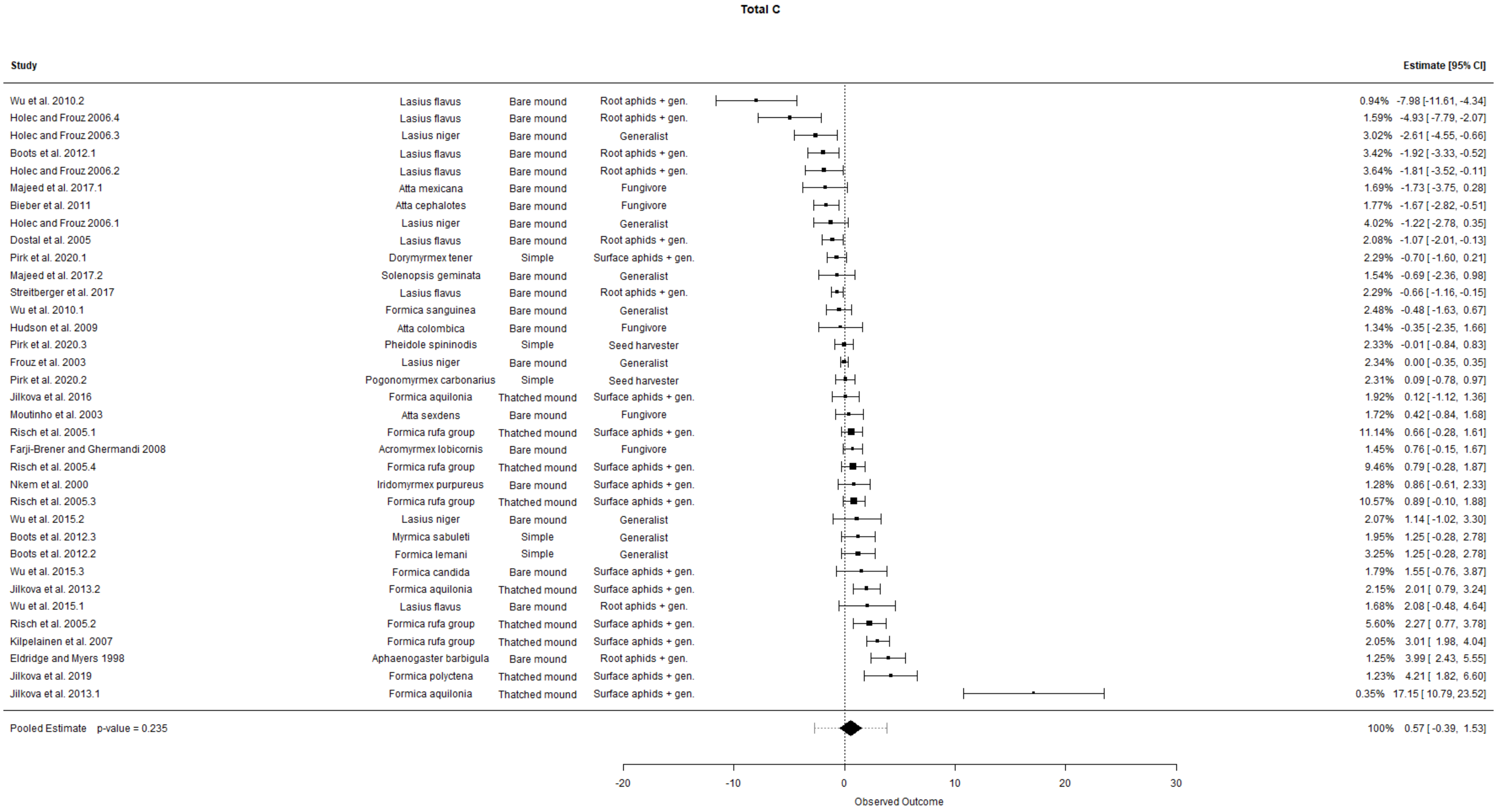
Study					Estimate [95% CI]
Bierbass et al. 2015	Lasius flavus	Bare mound	Root aphids + gen.	1.05%	-3.29 [-5.12, -1.47]
Wu et al. 2010.2	Lasius flavus	Bare mound	Root aphids + gen.	3.20%	-1.38 [-2.66, -0.10]
Eldridge et al. 2009.3	Myrmecocystus mexicanus	Simple	Surface aphids + gen.	12.75%	-0.82 [-1.59, -0.05]
Jilkova et al. 2017.2	Lasius niger	Bare mound	Generalist	4.26%	-0.67 [-1.75, 0.41]
Jilkova et al. 2017.3	Tetramorium caespitum	Simple	Generalist	2.93%	-0.52 [-1.59, 0.54]
Eldridge et al. 2009.2	Myrmecocystus depilis	Simple	Surface aphids + gen.	14.11%	-0.51 [-1.04, 0.02]
Jimeneza and Decaens 2006.2	Atta laevigata	Bare mound	Fungivore	3.46%	-0.12 [-1.50, 1.27]
Lafleur et al. 2005.1	Solenopsis invicta	Bare mound	Generalist	2.40%	-0.05 [-1.65, 1.55]
Jimeneza and Decaens 2006.1	Atta laevigata	Bare mound	Fungivore	2.80%	0.00 [-1.70, 1.70]
Wu et al. 2013.3	Formica candida	Bare mound	Surface aphids + gen.	1.83%	0.20 [-1.76, 2.17]
Wu et al. 2010.1	Formica sanguinea	Bare mound	Generalist	3.36%	0.21 [-0.92, 1.35]
Wu et al. 2013.2	Lasius niger	Bare mound	Generalist	1.94%	0.27 [-1.70, 2.24]
Jimeneza and Decaens 2006.3	Atta laevigata	Bare mound	Fungivore	2.77%	0.30 [-1.41, 2.01]
Jimenez et al. 2008.2	Atta laevigata	Bare mound	Fungivore	1.49%	0.37 [-1.64, 2.38]
Eldridge et al. 2009.4	Novomessor cockerelli	Simple	Generalist	3.44%	0.43 [-0.32, 1.18]
Lafleur et al. 2005.2	Solenopsis invicta	Bare mound	Generalist	2.37%	0.46 [-1.18, 2.09]
Wu et al. 2015.2	Lasius niger	Bare mound	Generalist	1.83%	0.59 [-1.42, 2.61]
Wu et al. 2013.1	Lasius flavus	Bare mound	Root aphids + gen.	1.87%	0.68 [-1.35, 2.72]
Jilkova et al. 2017.1	Formica sanguinea	Bare mound	Generalist	4.36%	0.70 [-0.38, 1.79]
Lenoir et al. 2001.2	Formica rufa group	Thatched mound	Surface aphids + gen.	2.33%	0.70 [-0.47, 1.87]
Eldridge et al. 2009.1	Trachymyrmex smithi	Bare mound	Fungivore	3.41%	0.85 [0.08, 1.63]
Wu et al. 2015.1	Lasius flavus	Bare mound	Root aphids + gen.	1.76%	0.92 [-1.17, 3.01]
Berg-Binder and Suarez 2012	Formica obscuripes	Thatched mound	Surface aphids + gen.	1.37%	0.93 [-0.05, 1.91]
Majeed et al. 2017.1	Atta mexicana	Bare mound	Fungivore	1.35%	1.05 [-0.71, 2.82]
Jimenez et al. 2008.1	Atta laevigata	Bare mound	Fungivore	1.31%	1.13 [-1.26, 3.51]
Carlson and Whitford 1992	Pogonomyrmex occidentalis	Bare mound	Generalist	1.31%	1.21 [0.43, 1.99]
Oostermeijer 1989	Lasius niger	Bare mound	Generalist	1.43%	1.30 [0.58, 2.03]
Wu et al. 2015.3	Formica candida	Bare mound	Surface aphids + gen.	1.55%	1.31 [-0.91, 3.52]
Jilkova et al. 2019	Formica polyctena	Thatched mound	Surface aphids + gen.	1.21%	1.37 [-0.04, 2.78]
Carlson and Whitford 1991	Pogonomyrmex occidentalis	Bare mound	Generalist	1.30%	1.45 [0.64, 2.26]
Nkem et al. 2000	Iridomyrmex purpureus	Bare mound	Surface aphids + gen.	0.93%	2.28 [0.39, 4.16]
Seaman and Marino 2003	Solenopsis invicta	Bare mound	Generalist	1.03%	2.41 [0.71, 4.12]
Majeed et al. 2017.2	Solenopsis geminata	Bare mound	Generalist	0.95%	3.20 [0.43, 5.98]
Wagner 1997	Formica perpilosa	Simple	Generalist	1.32%	3.27 [2.16, 4.38]
Wagner and Nicklen 2010.1	Dorymyrmex smithi	Simple	Generalist	1.25%	3.34 [1.50, 5.17]
Jilkova et al. 2016	Formica aquilonia	Thatched mound	Surface aphids + gen.	0.80%	4.61 [2.05, 7.17]
Lenoir et al. 2001.1	Formica rufa group	Thatched mound	Surface aphids + gen.	1.47%	5.15 [2.65, 7.65]
Wagner and Nicklen 2010.2	Forelius pruinosus	Simple	Generalist	0.97%	5.37 [2.78, 7.96]
Wagner, Brown and Gordon 1997	Pogonomyrmex barbatus	Bare mound	Seed harvester	0.73%	5.63 [2.94, 8.32]
Pooled Estimate p-value = 0.005				100%	1.19 [0.39, 1.99]


Organic C
Study
Estimate [95% CI]
Jimeneza and Decaens 2006.3 | Atta laevigata | Bare mound | Fungivore | 3.90% -5.60 [-9.04, -2.15]
Ehrle et al. 2019 | Lasius flavus | Bare mound | Root aphids + gen. | 5.85% -4.48 [-5.80, -3.16]
Jimeneza and Decaens 2006.1 | Atta laevigata | Bare mound | Fungivore | 5.15% -2.84 [-4.96, -0.72]
Dauber et al 2008.1 | Lasius flavus | Bare mound | Root aphids + gen. | 6.04% -1.82 [-2.87, -0.76]
Jimenez et al. 2008.1 | Atta laevigata | Bare mound | Fungivore | 4.44% -1.71 [-4.57, 1.14]
Sousa-Souto et al. 2008.2 | Atta laevigata | Bare mound | Fungivore | 5.38% -1.37 [-3.24, 0.50]
Dauber et al 2008.2 | Lasius flavus | Bare mound | Root aphids + gen. | 6.09% -1.34 [-2.32, -0.36]
Jimenez et al. 2008.2 | Atta laevigata | Bare mound | Fungivore | 4.80% -1.26 [-3.74, 1.23]
Wu et al. 2013.1 | Lasius flavus | Bare mound | Root aphids + gen. | 5.10% -1.18 [-3.35, 0.99]
Sousa-Souto et al. 2008.1 | Atta laevigata | Bare mound | Fungivore | 5.45% -1.17 [-2.97, 0.63]
Wu et al. 2013.3 | Formica candida | Bare mound | Surface aphids + gen. | 5.11% -1.16 [-3.33, 1.00]
Wu et al. 2013.2 | Lasius niger | Bare mound | Generalist | 5.12% -1.12 [-3.27, 1.03]
Dauber, Schroeter and Wolters 2001.1 | Myrmica scabrinodis | Bare mound | Generalist | 5.51% 1.18 [-0.55, 2.92]
Farji-Brener and Silva 1995 | Atta laevigata | Bare mound | Fungivore | 6.10% 1.21 [0.25, 2.17]
Dauber, Schroeter and Wolters 2001.3 | Lasius flavus | Bare mound | Root aphids + gen. | 5.49% 1.26 [-0.49, 3.01]
Dean and Yeaton 1992 | Messor capensis | Bare mound | Seed harvester | 6.08% 1.49 [0.49, 2.49]
Farji-Brener and Ghermandi 2000 | Acromyrmex lobicornis | Thatched mound | Fungivore | 6.04% 1.80 [0.75, 2.85]
Dauber, Schroeter and Wolters 2001.2 | Lasius niger | Bare mound | Generalist | 4.38% 4.35 [1.42, 7.27]
Jimeneza and Decaens 2006.2 | Atta laevigata | Bare mound | Fungivore | 3.98% 5.43 [2.07, 8.79]
Pooled Estimate p-value = 0.422 | 100% -0.46 [-1.62, 0.71]
-10
-5
0
5
10
Observed Outcome

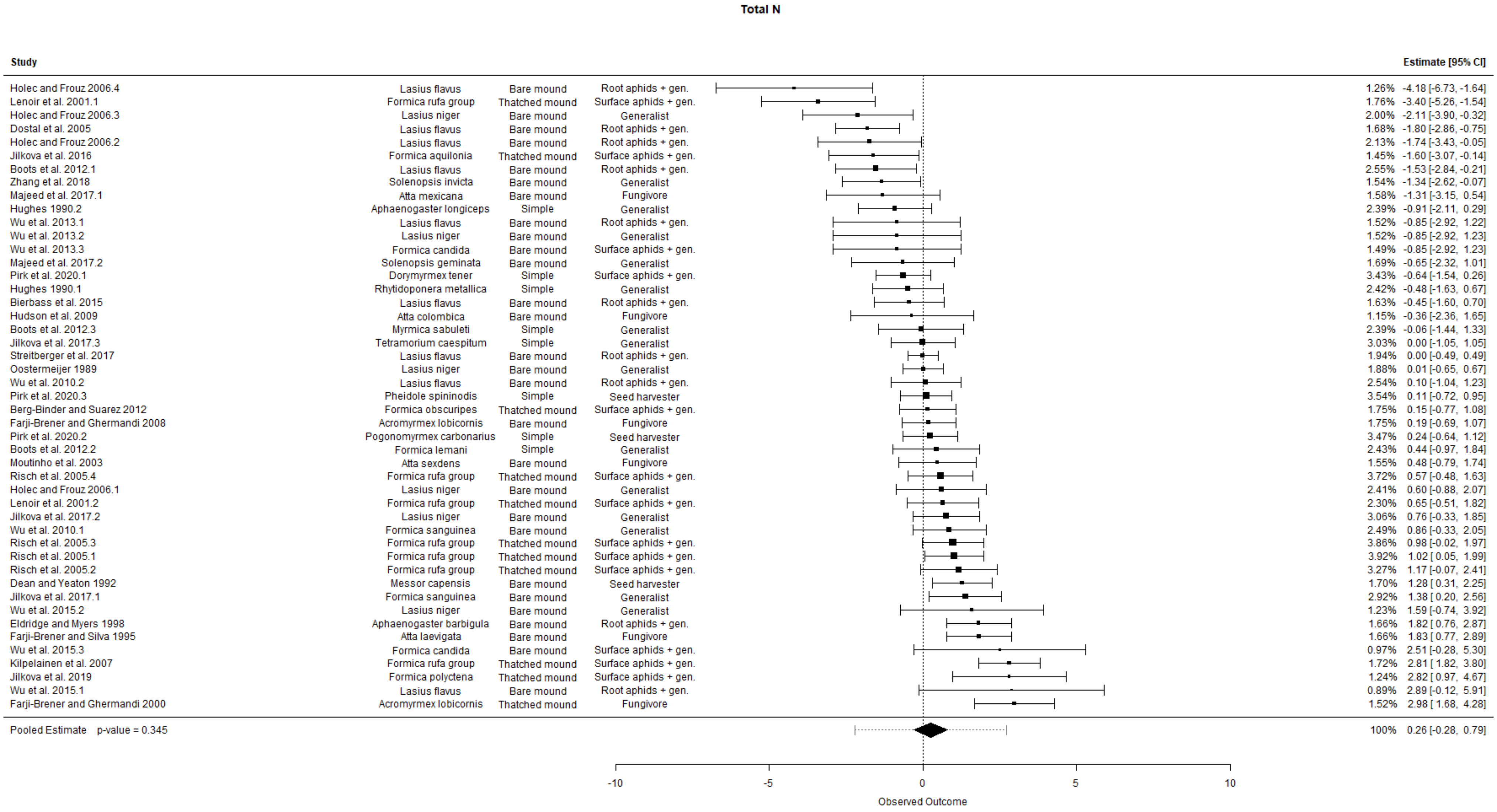
pH



Study					Estimate [95% CI]
Seaman and Marino 2003	Solenopsis invicta	Bare mound	Generalist	1.72%	-4.31 [-6.75, -1.88]
Wagner, Brown and Gordon 1997	Pogonomyrmex barbatus	Bare mound	Seed harvester	2.10%	-2.77 [-4.42, -1.12]
Carlson and Whitford 1992	Pogonomyrmex occidentalis	Bare mound	Generalist	2.46%	-1.04 [-1.81, -0.28]
Boots et al. 2012.3	Myrmica sabuleti	Simple	Generalist	2.18%	-0.89 [-2.35, 0.57]
Nkem et al. 2000	Iridomyrmex purpureus	Bare mound	Surface aphids + gen.	2.19%	-0.69 [-2.12, 0.75]
Lenoir et al. 2001.2	Formica rufa group	Thatched mound	Surface aphids + gen.	2.31%	-0.65 [-1.81, 0.52]
Boulton et al. 2003	Veromessor andrei	Simple	Seed harvester	2.41%	-0.64 [-1.54, 0.26]
Boots et al. 2012.1	Lasius flavus	Bare mound	Root aphids + gen.	2.32%	-0.55 [-1.70, 0.61]
Majeed et al. 2017.2	Solenopsis geminata	Bare mound	Generalist	2.10%	-0.53 [-2.18, 1.11]
Jilkova et al. 2017.1	Formica sanguinea	Bare mound	Generalist	2.36%	-0.42 [-1.48, 0.65]
Farji-Brener and Ghermandi 2008	Acromyrmex lobicornis	Bare mound	Fungivore	2.42%	-0.34 [-1.23, 0.54]
Majeed et al. 2017.1	Atta mexicana	Bare mound	Fungivore	2.12%	-0.25 [-1.86, 1.36]
Hughes 1990.1	Rhytidoponera metallica	Simple	Generalist	2.33%	-0.23 [-1.37, 0.91]
Jilkova et al. 2017.2	Lasius niger	Bare mound	Generalist	2.36%	-0.19 [-1.24, 0.86]
Dauber, Schroeter and Wolters 2001.1	Myrmica scabrinodis	Bare mound	Generalist	2.12%	-0.17 [-1.77, 1.44]
Pirk et al. 2020.1	Dorymyrmex tener	Simple	Surface aphids + gen.	2.42%	-0.13 [-1.01, 0.74]
Lafleur et al. 2005.1	Solenopsis invicta	Bare mound	Generalist	2.12%	-0.13 [-1.74, 1.47]
Boots et al. 2012.2	Formica lemani	Simple	Generalist	2.22%	-0.12 [-1.51, 1.27]
Pirk et al. 2020.2	Pogonomyrmex carbonarius	Simple	Seed harvester	2.42%	-0.10 [-0.98, 0.77]
Moutinho et al. 2003	Atta sexdens	Bare mound	Fungivore	2.28%	0.03 [-1.21, 1.27]
Jilkova et al. 2013.2	Formica aquilonia	Thatched mound	Surface aphids + gen.	2.39%	0.08 [-0.90, 1.06]
Farji-Brener and Ghermandi 2000	Acromyrmex lobicornis	Thatched mound	Fungivore	2.42%	0.19 [-0.69, 1.07]
Frouz et al. 2003	Lasius niger	Bare mound	Generalist	2.55%	0.21 [-0.13, 0.56]
Sousa-Souto et al. 2008.2	Atta laevigata	Bare mound	Fungivore	2.11%	0.33 [-1.29, 1.95]
Pirk et al. 2020.3	Pheidole spininodis	Simple	Seed harvester	2.43%	0.34 [-0.50, 1.18]
Streitberger et al. 2017	Lasius flavus	Bare mound	Root aphids + gen.	2.53%	0.41 [-0.09, 0.90]
Jilkova et al. 2017.3	Tetramorium caespitum	Simple	Generalist	2.36%	0.43 [-0.63, 1.49]
Lafleur et al. 2005.2	Solenopsis invicta	Bare mound	Generalist	2.10%	0.48 [-1.16, 2.12]
Hughes 1990.2	Aphaenogaster longiceps	Simple	Generalist	2.31%	0.65 [-0.52, 1.82]
Dauber, Schroeter and Wolters 2001.2	Lasius niger	Bare mound	Generalist	2.10%	0.71 [-0.94, 2.36]
Carlson and Whitford 1991	Pogonomyrmex occidentalis	Bare mound	Generalist	2.47%	0.71 [-0.03, 1.45]
Sousa-Souto et al. 2008.1	Atta laevigata	Bare mound	Fungivore	2.07%	0.82 [-0.88, 2.53]
Madureira et al. 2013	Atta robusta	Simple	Fungivore	2.33%	1.06 [-0.07, 2.19]
Jilkova et al. 2013.1	Formica aquilonia	Thatched mound	Surface aphids + gen.	2.34%	1.38 [0.27, 2.48]
Dauber, Schroeter and Wolters 2001.3	Lasius flavus	Bare mound	Root aphids + gen.	2.03%	1.38 [-0.40, 3.16]
Vele et al. 2010	Myrmica ruginodis	Simple	Surface aphids + gen.	2.52%	1.42 [0.88, 1.96]
Dostal et al. 2005	Lasius flavus	Bare mound	Root aphids + gen.	2.36%	1.73 [0.69, 2.76]
Dauber et al 2008.1	Lasius flavus	Bare mound	Root aphids + gen.	2.31%	2.44 [1.26, 3.61]
Eldridge and Myers 1998	Aphaenogaster barbigula	Bare mound	Root aphids + gen.	2.26%	2.96 [1.66, 4.25]
Dauber et al 2008.2	Lasius flavus	Bare mound	Root aphids + gen.	2.23%	3.24 [1.87, 4.61]
Lenoir et al. 2001.1	Formica rufa group	Thatched mound	Surface aphids + gen.	1.77%	4.67 [2.35, 6.99]
Bierbass et al. 2015	Lasius flavus	Bare mound	Root aphids + gen.	1.70%	5.07 [2.60, 7.54]
Ehrle et al. 2017	Lasius flavus	Bare mound	Root aphids + gen.	2.20%	5.54 [4.11, 6.98]
Ehrle et al. 2019	Lasius flavus	Bare mound	Root aphids + gen.	2.00%	6.83 [4.98, 8.68]
Jilkova et al. 2016	Formica aquilonia	Thatched mound	Surface aphids + gen.	1.16%	7.43 [3.62, 11.24]
Pooled Estimate p-value = 0.017				100%	0.70 [0.13, 1.26]

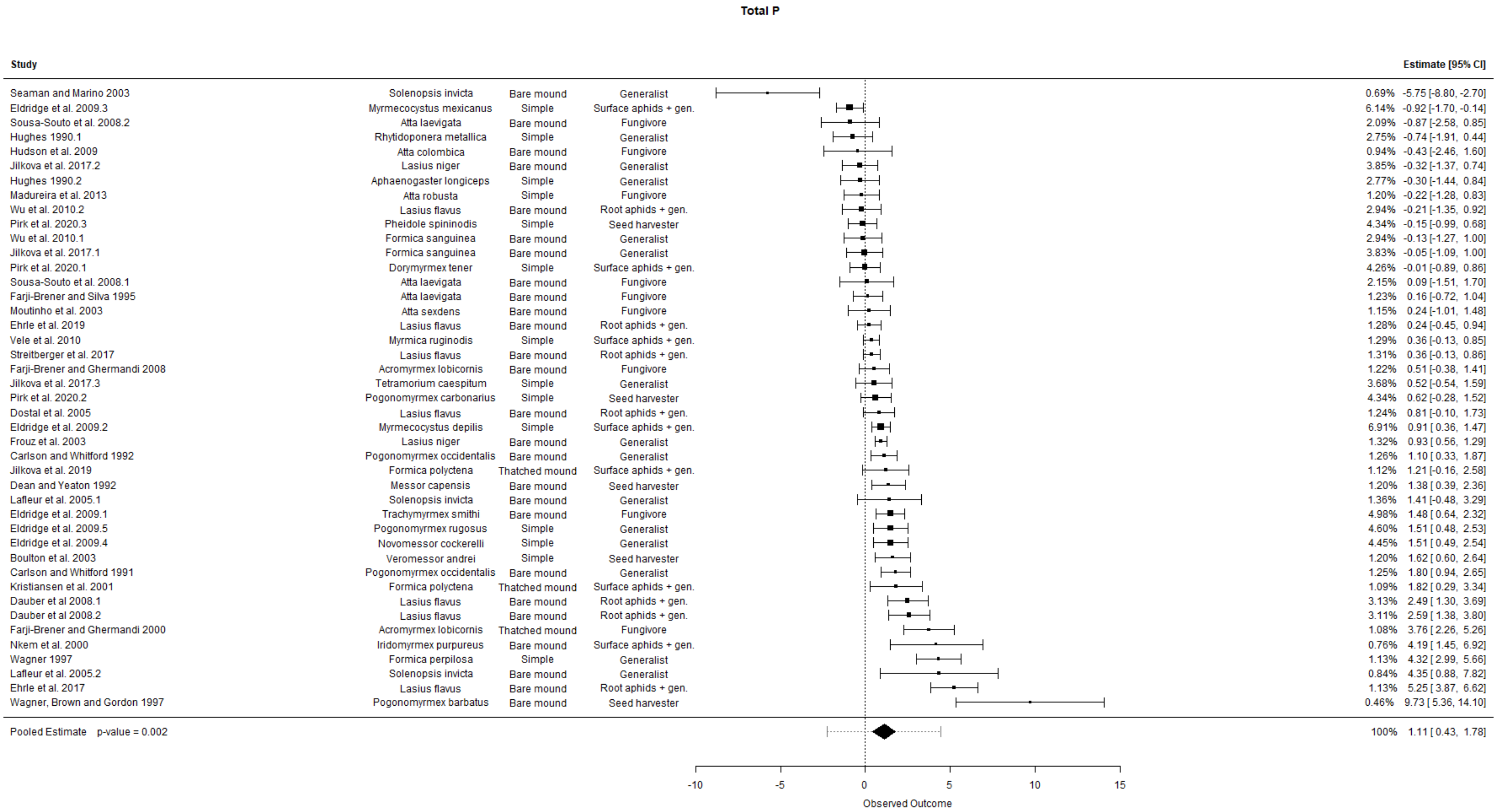


Study					Estimate [95% CI]
Wu et al. 2010.2	Lasius flavus	Bare mound	Root aphids + gen.	0.94%	-7.98 [-11.61, -4.34]
Holec and Frouz 2006.4	Lasius flavus	Bare mound	Root aphids + gen.	1.59%	-4.93 [-7.79, -2.07]
Holec and Frouz 2006.3	Lasius niger	Bare mound	Generalist	3.02%	-2.61 [-4.55, -0.66]
Boots et al. 2012.1	Lasius flavus	Bare mound	Root aphids + gen.	3.42%	-1.92 [-3.33, -0.52]
Holec and Frouz 2006.2	Lasius flavus	Bare mound	Root aphids + gen.	3.64%	-1.81 [-3.52, -0.11]
Majeed et al. 2017.1	Atta mexicana	Bare mound	Fungivore	1.69%	-1.73 [-3.75, 0.28]
Bieber et al. 2011	Atta cephalotes	Bare mound	Fungivore	1.77%	-1.67 [-2.82, -0.51]
Holec and Frouz 2006.1	Lasius niger	Bare mound	Generalist	4.02%	-1.22 [-2.78, 0.35]
Dostal et al. 2005	Lasius flavus	Bare mound	Root aphids + gen.	2.08%	-1.07 [-2.01, -0.13]
Pirk et al. 2020.1	Dorymyrmex tener	Simple	Surface aphids + gen.	2.29%	-0.70 [-1.60, 0.21]
Majeed et al. 2017.2	Solenopsis geminata	Bare mound	Generalist	1.54%	-0.69 [-2.36, 0.98]
Streitberger et al. 2017	Lasius flavus	Bare mound	Root aphids + gen.	2.29%	-0.66 [-1.16, -0.15]
Wu et al. 2010.1	Formica sanguinea	Bare mound	Generalist	2.48%	-0.48 [-1.63, 0.67]
Hudson et al. 2009	Atta colombica	Bare mound	Fungivore	1.34%	-0.35 [-2.35, 1.66]
Pirk et al. 2020.3	Pheidole spininodis	Simple	Seed harvester	2.33%	-0.01 [-0.84, 0.83]
Frouz et al. 2003	Lasius niger	Bare mound	Generalist	2.34%	0.00 [-0.35, 0.35]
Pirk et al. 2020.2	Pogonomyrmex carbonarius	Simple	Seed harvester	2.31%	0.09 [-0.78, 0.97]
Jilkova et al. 2016	Formica aquilonia	Thatched mound	Surface aphids + gen.	1.92%	0.12 [-1.12, 1.36]
Moutinho et al. 2003	Atta sexdens	Bare mound	Fungivore	1.72%	0.42 [-0.84, 1.68]
Risch et al. 2005.1	Formica rufa group	Thatched mound	Surface aphids + gen.	11.14%	0.66 [-0.28, 1.61]
Farji-Brener and Ghermandi 2008	Acromyrmex lobicornis	Bare mound	Fungivore	1.45%	0.76 [-0.15, 1.67]
Risch et al. 2005.4	Formica rufa group	Thatched mound	Surface aphids + gen.	9.46%	0.79 [-0.28, 1.87]
Nkem et al. 2000	Iridomyrmex purpureus	Bare mound	Surface aphids + gen.	1.28%	0.86 [-0.61, 2.33]
Risch et al. 2005.3	Formica rufa group	Thatched mound	Surface aphids + gen.	10.57%	0.89 [-0.10, 1.88]
Wu et al. 2015.2	Lasius niger	Bare mound	Generalist	2.07%	1.14 [-1.02, 3.30]
Boots et al. 2012.3	Myrmica sabuleti	Simple	Generalist	1.95%	1.25 [-0.28, 2.78]
Boots et al. 2012.2	Formica lemani	Simple	Generalist	3.25%	1.25 [-0.28, 2.78]
Wu et al. 2015.3	Formica candida	Bare mound	Surface aphids + gen.	1.79%	1.55 [-0.76, 3.87]
Jilkova et al. 2013.2	Formica aquilonia	Thatched mound	Surface aphids + gen.	2.15%	2.01 [0.79, 3.24]
Wu et al. 2015.1	Lasius flavus	Bare mound	Root aphids + gen.	1.68%	2.08 [-0.48, 4.64]
Risch et al. 2005.2	Formica rufa group	Thatched mound	Surface aphids + gen.	5.60%	2.27 [0.77, 3.78]
Kilpelainen et al. 2007	Formica rufa group	Thatched mound	Surface aphids + gen.	2.05%	3.01 [1.98, 4.04]
Eldridge and Myers 1998	Aphaenogaster barbigula	Bare mound	Root aphids + gen.	1.25%	3.99 [2.43, 5.55]
Jilkova et al. 2019	Formica polyctena	Thatched mound	Surface aphids + gen.	1.23%	4.21 [1.82, 6.60]
Jilkova et al. 2013.1	Formica aquilonia	Thatched mound	Surface aphids + gen.	0.35%	17.15 [10.79, 23.52]
Pooled Estimate p-value = 0.235				100%	0.57 [-0.39, 1.53]



Total N

Study				Weight	Estimate [95% CI]
Holec and Frouz 2006.4	Lasius flavus	Bare mound	Root aphids + gen.	1.26%	-4.18 [-6.73, -1.64]
Lenoir et al. 2001.1	Formica rufa group	Thatched mound	Surface aphids + gen.	1.76%	-3.40 [-5.26, -1.54]
Holec and Frouz 2006.3	Lasius niger	Bare mound	Generalist	2.00%	-2.11 [-3.90, -0.32]
Dostal et al. 2005	Lasius flavus	Bare mound	Root aphids + gen.	1.68%	-1.80 [-2.86, -0.75]
Holec and Frouz 2006.2	Lasius flavus	Bare mound	Root aphids + gen.	2.13%	-1.74 [-3.43, -0.05]
Jilkova et al. 2016	Formica aquilonia	Thatched mound	Surface aphids + gen.	1.45%	-1.60 [-3.07, -0.14]
Boots et al. 2012.1	Lasius flavus	Bare mound	Root aphids + gen.	2.55%	-1.53 [-2.84, -0.21]
Zhang et al. 2018	Solenopsis invicta	Bare mound	Generalist	1.54%	-1.34 [-2.62, -0.07]
Majeed et al. 2017.1	Atta mexicana	Bare mound	Fungivore	1.58%	-1.31 [-3.15, 0.54]
Hughes 1990.2	Aphaenogaster longiceps	Simple	Generalist	2.39%	-0.91 [-2.11, 0.29]
Wu et al. 2013.1	Lasius flavus	Bare mound	Root aphids + gen.	1.52%	-0.85 [-2.92, 1.22]
Wu et al. 2013.2	Lasius niger	Bare mound	Generalist	1.52%	-0.85 [-2.92, 1.23]
Wu et al. 2013.3	Formica candida	Bare mound	Surface aphids + gen.	1.49%	-0.85 [-2.92, 1.23]
Majeed et al. 2017.2	Solenopsis geminata	Bare mound	Generalist	1.69%	-0.65 [-2.32, 1.01]
Pirk et al. 2020.1	Dorymyrmex tener	Simple	Surface aphids + gen.	3.43%	-0.64 [-1.54, 0.26]
Hughes 1990.1	Rhytidoponera metallica	Simple	Generalist	2.42%	-0.48 [-1.63, 0.67]
Bierbass et al. 2015	Lasius flavus	Bare mound	Root aphids + gen.	1.63%	-0.45 [-1.60, 0.70]
Hudson et al. 2009	Atta colombica	Bare mound	Fungivore	1.15%	-0.36 [-2.36, 1.65]
Boots et al. 2012.3	Myrmica sabuleti	Simple	Generalist	2.39%	-0.06 [-1.44, 1.33]
Jilkova et al. 2017.3	Tetramorium caespitum	Simple	Generalist	3.03%	0.00 [-1.05, 1.05]
Streitberger et al. 2017	Lasius flavus	Bare mound	Root aphids + gen.	1.94%	0.00 [-0.49, 0.49]
Oostermeijer 1989	Lasius niger	Bare mound	Generalist	1.88%	0.01 [-0.65, 0.67]
Wu et al. 2010.2	Lasius flavus	Bare mound	Root aphids + gen.	2.54%	0.10 [-1.04, 1.23]
Pirk et al. 2020.3	Pheidole spininodis	Simple	Seed harvester	3.54%	0.11 [-0.72, 0.95]
Berg-Binder and Suarez 2012	Formica obscuripes	Thatched mound	Surface aphids + gen.	1.75%	0.15 [-0.77, 1.08]
Farji-Brener and Ghermandi 2008	Acromyrmex lobicornis	Bare mound	Fungivore	1.75%	0.19 [-0.69, 1.07]
Pirk et al. 2020.2	Pogonomyrmex carbonarius	Simple	Seed harvester	3.47%	0.24 [-0.64, 1.12]
Boots et al. 2012.2	Formica lemani	Simple	Generalist	2.43%	0.44 [-0.97, 1.84]
Moutinho et al. 2003	Atta sexdens	Bare mound	Fungivore	1.55%	0.48 [-0.79, 1.74]
Risch et al. 2005.4	Formica rufa group	Thatched mound	Surface aphids + gen.	3.72%	0.57 [-0.48, 1.63]
Holec and Frouz 2006.1	Lasius niger	Bare mound	Generalist	2.41%	0.60 [-0.88, 2.07]
Lenoir et al. 2001.2	Formica rufa group	Thatched mound	Surface aphids + gen.	2.30%	0.65 [-0.51, 1.82]
Jilkova et al. 2017.2	Lasius niger	Bare mound	Generalist	3.06%	0.76 [-0.33, 1.85]
Wu et al. 2010.1	Formica sanguinea	Bare mound	Generalist	2.49%	0.86 [-0.33, 2.05]
Risch et al. 2005.3	Formica rufa group	Thatched mound	Surface aphids + gen.	3.86%	0.98 [-0.02, 1.97]
Risch et al. 2005.1	Formica rufa group	Thatched mound	Surface aphids + gen.	3.92%	1.02 [0.05, 1.99]
Risch et al. 2005.2	Formica rufa group	Thatched mound	Surface aphids + gen.	3.27%	1.17 [-0.07, 2.41]
Dean and Yeaton 1992	Messor capensis	Bare mound	Seed harvester	1.70%	1.28 [0.31, 2.25]
Jilkova et al. 2017.1	Formica sanguinea	Bare mound	Generalist	2.92%	1.38 [0.20, 2.56]
Wu et al. 2015.2	Lasius niger	Bare mound	Generalist	1.23%	1.59 [-0.74, 3.92]
Eldridge and Myers 1998	Aphaenogaster barbigula	Bare mound	Root aphids + gen.	1.66%	1.82 [0.76, 2.87]
Farji-Brener and Silva 1995	Atta laevigata	Bare mound	Fungivore	1.66%	1.83 [0.77, 2.89]
Wu et al. 2015.3	Formica candida	Bare mound	Surface aphids + gen.	0.97%	2.51 [-0.28, 5.30]
Kilpelainen et al. 2007	Formica rufa group	Thatched mound	Surface aphids + gen.	1.72%	2.81 [1.82, 3.80]
Jilkova et al. 2019	Formica polyctena	Thatched mound	Surface aphids + gen.	1.24%	2.82 [0.97, 4.67]
Wu et al. 2015.1	Lasius flavus	Bare mound	Root aphids + gen.	0.89%	2.89 [-0.12, 5.91]
Farji-Brener and Ghermandi 2000	Acromyrmex lobicornis	Thatched mound	Fungivore	1.52%	2.98 [1.68, 4.28]
Pooled Estimate p-value = 0.345				100%	0.26 [-0.28, 0.79]



Total P

Study					Estimate [95% CI]
Seaman and Marino 2003	Solenopsis invicta	Bare mound	Generalist	0.69%	-5.75 [-8.80, -2.70]
Eldridge et al. 2009.3	Myrmecocystus mexicanus	Simple	Surface aphids + gen.	6.14%	-0.92 [-1.70, -0.14]
Sousa-Souto et al. 2008.2	Atta laevigata	Bare mound	Fungivore	2.09%	-0.87 [-2.58, 0.85]
Hughes 1990.1	Rhytidoponera metallica	Simple	Generalist	2.75%	-0.74 [-1.91, 0.44]
Hudson et al. 2009	Atta colombica	Bare mound	Fungivore	0.94%	-0.43 [-2.46, 1.60]
Jilkova et al. 2017.2	Lasius niger	Bare mound	Generalist	3.85%	-0.32 [-1.37, 0.74]
Hughes 1990.2	Aphaenogaster longiceps	Simple	Generalist	2.77%	-0.30 [-1.44, 0.84]
Madureira et al. 2013	Atta robusta	Simple	Fungivore	1.20%	-0.22 [-1.28, 0.83]
Wu et al. 2010.2	Lasius flavus	Bare mound	Root aphids + gen.	2.94%	-0.21 [-1.35, 0.92]
Pirk et al. 2020.3	Pheidole spininodis	Simple	Seed harvester	4.34%	-0.15 [-0.99, 0.68]
Wu et al. 2010.1	Formica sanguinea	Bare mound	Generalist	2.94%	-0.13 [-1.27, 1.00]
Jilkova et al. 2017.1	Formica sanguinea	Bare mound	Generalist	3.83%	-0.05 [-1.09, 1.00]
Pirk et al. 2020.1	Dorymyrmex tener	Simple	Surface aphids + gen.	4.26%	-0.01 [-0.89, 0.86]
Sousa-Souto et al. 2008.1	Atta laevigata	Bare mound	Fungivore	2.15%	0.09 [-1.51, 1.70]
Farji-Brener and Silva 1995	Atta laevigata	Bare mound	Fungivore	1.23%	0.16 [-0.72, 1.04]
Moutinho et al. 2003	Atta sexdens	Bare mound	Fungivore	1.15%	0.24 [-1.01, 1.48]
Ehrle et al. 2019	Lasius flavus	Bare mound	Root aphids + gen.	1.28%	0.24 [-0.45, 0.94]
Vele et al. 2010	Myrmica ruginodis	Simple	Surface aphids + gen.	1.29%	0.36 [-0.13, 0.85]
Streitberger et al. 2017	Lasius flavus	Bare mound	Root aphids + gen.	1.31%	0.36 [-0.13, 0.86]
Farji-Brener and Ghermandi 2008	Acromyrmex lobicornis	Bare mound	Fungivore	1.22%	0.51 [-0.38, 1.41]
Jilkova et al. 2017.3	Tetramorium caespitum	Simple	Generalist	3.68%	0.52 [-0.54, 1.59]
Pirk et al. 2020.2	Pogonomyrmex carbonarius	Simple	Seed harvester	4.34%	0.62 [-0.28, 1.52]
Dostal et al. 2005	Lasius flavus	Bare mound	Root aphids + gen.	1.24%	0.81 [-0.10, 1.73]
Eldridge et al. 2009.2	Myrmecocystus depilis	Simple	Surface aphids + gen.	6.91%	0.91 [0.36, 1.47]
Frouz et al. 2003	Lasius niger	Bare mound	Generalist	1.32%	0.93 [0.56, 1.29]
Carlson and Whitford 1992	Pogonomyrmex occidentalis	Bare mound	Generalist	1.26%	1.10 [0.33, 1.87]
Jilkova et al. 2019	Formica polyctena	Thatched mound	Surface aphids + gen.	1.12%	1.21 [-0.16, 2.58]
Dean and Yeaton 1992	Messor capensis	Bare mound	Seed harvester	1.20%	1.38 [0.39, 2.36]
Lafleur et al. 2005.1	Solenopsis invicta	Bare mound	Generalist	1.36%	1.41 [-0.48, 3.29]
Eldridge et al. 2009.1	Trachymyrmex smithi	Bare mound	Fungivore	4.98%	1.48 [0.64, 2.32]
Eldridge et al. 2009.5	Pogonomyrmex rugosus	Simple	Generalist	4.60%	1.51 [0.48, 2.53]
Eldridge et al. 2009.4	Novomessor cockerelli	Simple	Generalist	4.45%	1.51 [0.49, 2.54]
Boulton et al. 2003	Veromessor andrei	Simple	Seed harvester	1.20%	1.62 [0.60, 2.64]
Carlson and Whitford 1991	Pogonomyrmex occidentalis	Bare mound	Generalist	1.25%	1.80 [0.94, 2.65]
Kristiansen et al. 2001	Formica polyctena	Thatched mound	Surface aphids + gen.	1.09%	1.82 [0.29, 3.34]
Dauber et al 2008.1	Lasius flavus	Bare mound	Root aphids + gen.	3.13%	2.49 [1.30, 3.69]
Dauber et al 2008.2	Lasius flavus	Bare mound	Root aphids + gen.	3.11%	2.59 [1.38, 3.80]
Farji-Brener and Ghermandi 2000	Acromyrmex lobicornis	Thatched mound	Fungivore	1.08%	3.76 [2.26, 5.26]
Nkem et al. 2000	Iridomyrmex purpureus	Bare mound	Surface aphids + gen.	0.76%	4.19 [1.45, 6.92]
Wagner 1997	Formica perpilosa	Simple	Generalist	1.13%	4.32 [2.99, 5.66]
Lafleur et al. 2005.2	Solenopsis invicta	Bare mound	Generalist	0.84%	4.35 [0.88, 7.82]
Ehrle et al. 2017	Lasius flavus	Bare mound	Root aphids + gen.	1.13%	5.25 [3.87, 6.62]
Wagner, Brown and Gordon 1997	Pogonomyrmex barbatus	Bare mound	Seed harvester	0.46%	9.73 [5.36, 14.10]
Pooled Estimate p-value = 0.002				100%	1.11 [0.43, 1.78]

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