Hill, Jennifer ORCID logoORCID: https://orcid.org/0000-0002-0682-783X, Vater, Amber E, Geary, Andrew P and Matthews, John A (2018) Chronosequences of ant nest mounds from glacier forelands of Jostedalsbreen, southern Norway: Insights into the distribution, succession and geo-ecology of red wood ants (Formica lugubris and F. aquilonia). Holocene, 28 (7). pp. 1113-1130. doi:10.1177/0959683618761551

Official URL: http://dx.doi.org/10.1177/0959683618761551
DOI: http://dx.doi.org/10.1177/0959683618761551
EPrint URI: https://eprints.glos.ac.uk/id/eprint/7878

Chronosequences of ant nest mounds from glacier forelands of Jostedalsbreen, southern Norway: insights into the distribution, succession and geo-ecology of red wood ants (*Formica lugubris* and *F. aquilonia*)

Jennifer L. Hill[a,]*, Amber E. Vater[b], Andrew P. Geary[a] and John A. Matthews[b]

[a] *Department of Geography and Environmental Management, University of the West of England, Coldharbour Lane, Bristol BS16 1QY, UK*

[b] *Department of Geography, College of Science, Swansea University, Singleton Park, Swansea SA2 8PP, Wales, UK*

* Corresponding author.
E-mail address: Jennifer.Hill@uwe.ac.uk

Abstract

Red wood ant nest mounds were investigated on terrain deglaciated since the mid-eighteenth century at three outlet glaciers of the Jostedalsbreen ice cap in southern Norway. Chronosequence methodology was combined with a geo-ecological approach in the context of autecology. Size and composition of 168 mounds, most of which belonged to *Formica lugubris*, were related to terrain age, vegetation characteristics and physical habitat types using non-metric multidimensional scaling (NMDS) linked to segmented bubble plots and inferential statistical techniques. Substantive insights include: (1) colonisation occurs 50–80 years after deglaciation; (2) mounds up to 100 cm high occupy the glacier forelands with a density of 2.5-4.6 mounds/hectare; (3) the positive correlation between mound size and terrain age is weakened by the presence of numerous small mounds attributed to the expansion of polydomous colonies by budding; (4) although mounds are composed mostly of plant remains (litter), they contain up to 17 % mineral material (mostly gravel) on relatively young terrain; (5) mound size and composition are related to the number of trees (*Betula pubescens*) occurring within 5 m of each mound, which reflects the availability of biological resources for mound thatch and ant food, the latter being primarily honeydew from aphids; (6) where aphids are present on trees, the mounds tend to be relatively large, reflecting the presence of ant-aphid mutualism; (7) mounds are larger on moraines and till plains than on outwash deposits, probably reflecting the enhancement of tree growth due to greater moisture availability and soil fertility in the former habitat types; (8) a strong southerly preferred aspect in mound orientation indicates the importance of direct solar radiation in maintaining internal mound temperatures; and (9) glacier-foreland landscapes are not simply time-dependent chronosequences reflecting succession but are the product of spatio-temporal dynamics involving biotic and abiotic interactions, which we summarize in a conceptual geo-ecological model. The main methodological implications are that chronosequences can be used to investigate the autecology of keystone species using a geo-ecological approach and multivariate analysis.

Keywords

red wood ants, *Formica* spp., ant nest mounds, glacier foreland chronosequences, geo-ecological approach, southern Norway

Introduction

Chronosequences are spatial representations in the landscape of temporal sequences, in which differences between terrain ages at one point in time are substituted for changes through time (Cutler et al., 2008; Johnson and Miyanishi, 2008; Lawrence et al., 2010; Stevens and Walker, 1970; Walker et al., 2010). Glacier forelands, the areas of landscape recently deglaciated by retreating glaciers, provide one of the most widely recognised examples of chronosequences. Thus, progressively older landscapes with increasing distance from the glacier margin can be interpreted, by invoking the chronosequence concept, as a ‘natural experiment’, depicting how the landscape has changed and will change through time.

Glacier foreland chronosequences have been widely applied in the context of plant community succession. This, and their use to investigate soil development, was comprehensively reviewed by Matthews (1992, 1999), and research in this field has continued at an accelerating rate (e.g. Darmody et al., 2005; Erschbaumer and Caccianiga, 2016; Garibotti et al., 2011; Jones and del Moral, 2009; Prach and Rachlewicz, 2012; Robbins and Matthews, 2010; Vilmundardóttir et al., 2017). Most recently, invertebrate (e.g. Gobbi et al., 2006; Hågvar, 2012; Hodkinson et al., 2004; Kaufmann, 2001; Vater 2012; Vater and Matthews, 2015) and microbial successions (e.g. Bradley et al., 2014; Doblas-Miranda et al., 2008; Fernández-Martínez et al., 2017; Kaštovská et al., 2005; Schmidt et al., 2015) have been increasingly investigated, while holistic studies of more than one ecosystem component have tended to be neglected - but see Bardgett et al. (2005), Bardgett and Walker (2004), Carlson et al. (2010), Losapio et al. (2015), Matthews and Vater (2015), Matthews et al. (1998), Tampucci et al. (2015) and Tscherko et al. (2005). There have, moreover, been few studies that have used the chronosequence approach to study the autecology of particular plant or animal species, notable exceptions being those of Whittaker (1993) involving selected pioneer herbs and later colonizing shrubs, and Hågvar and Flø (2015) involving the harvestman (*Mitopus morio*) on glacier forelands in southern Norway.

The present investigation is a study of red wood ant autecology in the glacier foreland landscapes of southern Norway. Red wood ants (Hymenoptera: Formicidae) comprise several narrowly related, and hence morphologically and ecologically similar species that belong to the *Formica rufa* group (Goropashnova et al., 2004; Stockan et al., 2016). The species in this group, which occur throughout the temperate boreal regions of the northern Palaearctic, are commonly referred to as true wood ants, thatch ants or mound ants. These names derive from their red and brownish-black colour, habitat and mound-building habit. Vater and Matthews (2013, 2015) demonstrated by pitfall trapping their abundance in invertebrate succession on the glacier forelands of Jostedalsbreen, southern Norway. Two of the most closely related species, *F. lugubris* (the hairy wood ant) and *F. aquilonia* (the northern wood ant) are involved in this study.

There are at least three justifications for this study. First, red wood ants are keystone species within their ecosystems and yet there is limited understanding of their ecology (Robinson and Stockan, 2016; Skinner and Allen, 2015; Stockan and Robinson, 2016; Vandegehuchte et al., 2017). Their nest mounds function as habitats for myrmecophiles (particularly Coleoptera and Araneae) and influence local nutrient cycles (Chen and Robinson, 2014; Jurgensen et al., 2008; Ohashi et al., 2007; Parmentier et al., 2014; Robinson and Robinson, 2013; Robinson et al., 2016). The ants themselves, as dominant predators, can change the insect communities on trees and on the ground, altering the balance between major feeding guilds (Fowler and Macgarvin, 1985; Punttila et al., 2004; Reznikova and Dorosheva, 2004). Wood ant presence can affect the growth of trees negatively, through their herding of sap-feeding aphids, and positively, by increasing predation or harassment of other herbivores (Mahdi and Whittaker, 1993; Styrsky and Eubanks, 2007). Red wood ants defend their territories against other ant species, influencing arthropod biodiversity (Arnan et al., 2009; Koivula and Niemelä, 2003; Mabelis 1984; Savolainen and Vepsäläinen, 1989). Through myrmecochory (seed dispersal by ants), red wood ants can affect the dispersal success of plants (Boulay et al., 2007; Gorb and Gorb, 1995; Manzaneda and Rey, 2009) and enhance plant fitness by nutrient enrichment on and around their nests (Frouz and Jílková, 2008; Jílková et al., 2012; Manzaneda and Rey, 2012).

The second justification for studying this group is that the volume of red wood ant nest mounds, which can be easily calculated from diameter and height measurements, has been shown to provide a close estimate of nest worker population size (Chen and Robinson, 2013, 2014; Freitag et al., 2016). The nest mounds are therefore meaningful ecological entities. Finally, conspicuous nest mounds are particularly conducive to investigation using the chronosequence approach. Nest mounds therefore permit the distribution and relative abundance of ant populations to be studied non-destructively in relation to terrain age and habitat variation without the need for pitfall trapping. Whereas many previous studies have investigated the distribution of the nest mounds of red wood ants in general and of *F.*

lugubris and *F. aquilonia* in particular (e.g. Borkin et al., 2012; Breen, 1979, 2014; Domisch et al. 2005; Hughes, 1999, 2006; Kilpeläinen et al., 2005, 2008; King, 1977; Laine and Niemelä, 1989; Punttila and Kilpeläinen, 2009; Sudd et al., 1977; Vandegehuchte et al., 2017), there have been no specific investigations of the *F. rufa* group on glacier forelands.

The aim of this paper is to make both a substantive contribution to understanding the successional and geo-ecological roles of red wood ants and a methodological contribution to chronosequence studies. There are four specific objectives:

1. To map the distribution, size and density of ant nest mounds on three subalpine glacier forelands of southeastern Jostedalsbreen, southern Norway;
2. To analyse relationships between mound characteristics, terrain age, vegetation and physical habitat (including topography and substrate);
3. To infer possible successional trends and the underlying geo-ecological processes in which red wood ants play a prominent role; and
4. To develop further the chronosequence approach in the context of glacier forelands and the autecology of keystone species.

The glacier forelands and the subalpine environment

The glacier forelands of Nigardsbreen, Bergsetbreen and Fåbergstølsbreen were investigated on the southeastern side of the Jostedalsbreen ice cap (Fig. 1). The glaciers are three of the largest outlet glaciers of Jostedalsbreen (Andreassen and Winsvold, 2012), which have retreated several kilometres from the moraine ridges marking their Little Ice Age maximum extent around AD 1750 (Figs 2-4).

The altitudes of the study sites on the glacier forelands of Nigardsbreen (~260-320 m above sea level), Bergsetbreen (~420-440 m a.s.l.) and Fåbergstølsbreen (~460-560 m a.s.l.) mean they are located within the southern Norwegian boreal zone, where mature vegetation is normally dominated by *Pinus sylvestris* (Moen, 1999). However, on account of local topography, proximity to the ice-cap, and anthropogenic effects (which have historically affected the glacier forelands, particularly through the grazing of domesticated animals and collection of fuel wood), *Betula pubescens* is dominant in mature vegetation beyond the glacier foreland boundary and on the glacier forelands themselves. Consequently, all three forelands may be regarded as subalpine in character.

Climatic data from the closest meteorological station (Bjørkhaug-i-Jostedal; 324 m a.s.l.) indicate a mean annual air temperature of +3.7 °C, with a July mean of +13.4 °C, a January mean of –4.9 °C (Aune, 1993) and a mean annual precipitation of 1380 mm (Førland, 1993). Mean annual maximum snow depth on the glacier forelands is at least 2.0 m and there are >200 days per year on which snow depth is >25 cm (http://www.senorge.no/) with somewhat more snow at Fåbergstølsbreen and somewhat less on the older parts of the glacier forelands of Nigardsbreen and Bergsetbreen.

Parent materials on the glacier forelands are derived from the local granitic gneiss bedrock (Lutro and Tveten, 1996). This yields soils that are initially close to neutral in reaction but rapidly become acidic following deglaciation (Mellor, 1985; Messer, 1988). Many other environmental changes and disturbances affect the glacier foreland landscape especially in the early years after deglaciation, including consolidation and drainage of the sedimentary deposits, cryoturbation, stabilisation of slopes, and the shifting courses of glaciofluvial meltwater streams. These dynamic processes interact with successional change and ecosystem development (cf. Matthews, 1992, 1999; Matthews and Vater, 2015). Typical nest mounds in their glacier foreland habitats are shown in Fig. 5A-C.

Methodology

Field methods

Ant nest mounds were sampled using belt transects 48 m in width extending from the glacier snout in 2015 to beyond the glacier foreland boundary (AD 1750 snout position) at right angles to the isochrones (lines of equal age). At Nigardsbreen (Fig. 2) and Bergsetbreen (Fig. 3), single transects were oriented more-or-less along the axis of the glacier foreland, to the north of the glacier river. At Nigardsbreen the transect was located immediately to the north of the road that crosses the older parts of the foreland and the lake (Nigardsbrevatnet) that occupies much of the younger parts deglaciated since ~AD 1930. At Fåbergstølsbreen (Fig. 4), two similar transects were located to the north and south of the glacier river. Each belt transect was searched systematically for ant nest mounds by three people standing 16 m apart and searching 8 m to their right and left. Thus, for each 250 m length of transect, an area of 12,000 m^2 was searched thoroughly. Each mound (n = 168) was mapped onto enlarged aerial photographs (available at http://www.norgebilder.no/).

Parameters relating to the size and surface composition of ant nest mounds (potential response variables) were defined as follows:

Height = the maximum height of the top of the mound relative to the lowest point of the base (i.e. where the base of the mound intersects with the surrounding terrain);
Width = the maximum diameter of the base of the mound (i.e. the two points farthest apart around the circumference of the base);
Volume = the equivalent mound volume for a spherical cap determined from mound height (h) and basal radius (r), $\pi h^2/3(3r - h)$ (Polyanin and Manzhirov, 2006). This formula has not been used before in the context of ant nest mounds but provides a simple yet effective approximation of mound shape (cf. Porter et al., 1992; Vogt, 2007);
Organic = percentage of the mound surface covered in organic material (including twigs, leaves and humus);
Sand = percentage of the mound surface covered in mineral particles of sand size (>0.063, <0.2 mm);
Gravel = percentage of the mound surface covered in mineral particles of larger than sand size but <10.0 mm.

Parameters relating to terrain age and the environment of ant nest mounds (potential explanatory variables) were defined as follows:

Age = age of the terrain on which the mound is positioned in years before AD 2017 (± 5 years for terrain dating from before AD 1800);
Altitude = altitude of the mound above sea level;
Aspect = orientation of the mound in relation to magnetic north;
Trees = number of trees (tree species growing to a height of >2 m) rooted within 5 m of the mound;
Poles = number of poles (tree species growing to a height of <2 m) rooted within 5 m of the mound;
Ground cover = percentage of the ground covered by shrubs, forbs or

graminoids within 2 m of the mound;

Habitat type = three categories of habitat were recognised – moraine ridge (M), glaciofluvial outwash plain (O), and till-covered surface (T) – with the addition of a road bank habitat (RB) on the Nigardsbreen glacier foreland;

Aphids = presence of aphids or aphid eggs on trees or poles within 5 m of the mound (data collected from Nigardsbreen and Fåbergstølsbreen only).

The positions of the glacier snouts over the last ~267 years, and hence the age of the terrain involved in the glacier foreland chronosequences, is based on annual monitoring of the glacier, documentary evidence and lichenometric dating (Bickerton and Matthews, 1992, 1993). Estimated accuracy varies from ±1 year on the most recently deglaciated terrain to ±5 years before ~AD1900. Beyond the glacier foreland boundary, the terrain was deglaciated in the early Holocene, about 9700 years ago (Dahl et al., 2002; Owen et al., 2007). For computational purposes terrain outside the glacier foreland was assigned an age of 300 years.

Altitude was estimated to ±5 m from topographic maps at a scale of 1:50,000 with a contour interval of 20 m. Aspect was measured with respect to sixteen compass points and refers to the orientation of the longest side of the mound (perfectly symmetrical mounds were rare). Aspect is relevant to the thermal environment of mounds (cf. Chen and Robinson, 2014; Kadochová and Frouz, 2014; Kilpeläinen et al., 2008; Rosengren et al., 1987; Seeley and Heinrich, 1981; Sorvari and Hakkarainen, 2005). Trees, poles and ground cover were used as indices of the biological environment of each mound and especially the resources available to ants during foraging (cf. Blüthgen and Feldhaar, 2010; Chen and Robinson, 2014; Domisch et al., 2016; Ellis et al., 2014). A 5 m radius was used for determining the number of trees in the vicinity of the mounds as it captures the immediate influence of tree canopy on local abiotic conditions and is consistent with previous studies that have shown ants within 5 m of mounds to be two or three times more abundant and carry higher honeydew loads than those at greater distances from the mound (Gibb et al., 2016; Sudd, 1983). The dominant species comprising the ground cover, mostly dwarf shrubs, was recorded as well as the overall percentage ground cover, although only the latter was used in analysis. Each mound was assigned to one of the four physical habitat types according to where it was sited. These habitat types reflect the nature of the substrate, which affects drainage conditions, moisture levels, nutrient availability, mineral cycling and possibly disturbance regimes (cf. Finér et al., 2013; Frouz et al., 2016; Jurgensen et al., 2008; Lenoir et al., 2001; Ohashi et al., 2007; Punttila and Kilpeläinen, 2009). Finally, the presence or absence of aphids was systematically recorded in order to examine ant-aphid mutualism in association with mound development (cf. Domisch et al., 2011, 2016; Gibb and Johansson, 2010; Robinson et al., 2008; Stadler and Dixon, 2005). Typically, aphids and/or their eggs were found on relatively young shoots of *Betula pubescens* trees in this study (Fig. 6).

Analytical techniques

The focal multivariate technique used to explore variation in nest mound characteristics was non-metric multidimensional scaling (NMDS) (Cox and Cox, 2000; Everitt and Hothorn, 2011) using the PRIMER–E Version 7 software package (Clarke and Gorley, 2015; Clarke et al., 2014). This nonparametric ordination technique is well suited to the simultaneous analysis of many response and explanatory variables and the graphical visualisation of their interrelationships in a reduced number of dimensions. Two-dimensional NMDS was carried out on data from the three glacier forelands independently. Six response variables representing mound size (height, width, volume) and surface composition (organic, sand, gravel) were used in each NMDS analysis with Euclidian distance as the resemblance function. In order to limit the distorting effects of outliers and so achieve meaningful distances between samples using Euclidian Distance, selected variables were transformed prior to analysis. Variables were either reflected and natural logarithmic transformed (negative skew) or natural logarithmic transformed (positive skew). All variables were then normalised to a common measurement scale by subtracting the mean and dividing by the standard deviation (Clarke and Gorley, 2015). The stress statistic was used as a measure of distortion (expressed as a percentage) in the resultant NMDS ordination diagram representing the similarities between individual mounds. Segmented bubble plots were added to the ordination diagram to show the relative importance of each of the response variables for every mound. Five explanatory variables (age, altitude, trees, poles and ground cover) were then overlain as vectors (together with the vectors representing the response variables) based on Pearson's correlation coefficients between the variables and the first and second NMDS axes.

Multivariate analyses were supported by additional statistical and graphical techniques, including: (1) frequency histograms and descriptive statistics, to describe univariate distributions; (2) correlation and linear regression, to analyse bivariate relationships between response and explanatory variables; (3) parametric one-way analysis of variance (ANOVA) combined with the Tukey method for simultaneous pairwise comparison, together with the equivalent non-parametric Kruskal-Wallis tests and box plots, to investigate relationships between mound characteristics and habitat types, and the association of ants with aphids; and (4) rose diagrams, to demonstrate graphically patterns in the orientation of mounds. MINITAB (2010) statistical software was used for these standard statistical analyses.

Taxonomy

The presence of both *Formica lugubris* Zetterstedt, 1838 and *F. aquilonia* Yarrow, 1955 (Collingwood, 1979; Kvamme and Wetås, 2010) at the study sites was confirmed by specialist identification of 24 individuals sampled from 21 mounds. This represents 12.6% of the total number of mounds investigated in this study.

F. lugubris was by far the more common of the two species, accounting for >80% of the mounds from which individuals were identified. Furthermore, all of the mounds sampled for species identification within the glacier foreland boundaries of Nigardsbreen (11 mounds) and Fåbergstølsbreen (three mounds) belonged to *F. lugubris*. However, two of the three sampled mounds on the Bergsetbreen glacier foreland belonged to *F. aquilonia*. Similarly, no conclusive pattern was observed from the four mounds occupied by *F. aquilonia*, which included two of three relatively large mounds sampled on relatively old terrain at or beyond the glacier foreland boundaries of Nigardsbreen and Fåbergstølsbreen. The latter observation is in agreement with Arnan et al. (2009), Borkin et al. (2012) and Kipeläinen et al. (2008), who suggest that *F. aquilonia* tends to dominate in old-growth stands. More secure differentiation of the mounds of the two species would need the identification of more specimens. Nevertheless, we propose that the results and conclusions of this study relate primarily to *F. lugubris*.

Results

Distribution and density of nest mounds

The distribution of mounds on the three glacier forelands are shown in Figs 2-4 and summarized in Table 1. No mounds were found on terrain younger than about 80 years at both Bergsetbreen and Fåbergstølsbreen, though mounds were present on terrain deglaciated only 49 years ago at Nigardsbreen. On those parts of the glacier forelands where mounds were present, overall densities ranged from 2.5 mounds/hectare at Fåbergstølsbreen to 4.5 and 4.6 mounds/hectare at Nigardsbreen and Bergsetbreen, respectively. These values are typical for red wood ant mounds, the density of which rarely exceeds 5.0 mounds/hectare in European forests (Kilpeläinen et al., 2008; Punttila and Kilpeläinen, 2009; Risch et al., 2016; Vandegehuchte et al., 2017). However, Figs 2-4 indicate variations in density with the clustering of mounds in some areas, which may relate to habitat variations and/or reproductive strategies (see discussion).

Nest mound characteristics: variation in size and composition

Mound size is summarised in Fig. 7A-C and Table 2 and the range of mound sizes is illustrated in Fig. 8. Mean height of mounds across the three glacier forelands is approximately 44 cm and modal height is only 25-30 cm. Maximum mound height lies between 92 cm and 100 cm on each foreland and the mounds are nearly twice as wide as they are high. This low profile agrees with the findings of Sorvari et al. (2016) who note that high-profile mounds in exposed and windy positions pose a high risk for drying of nest material, reducing thermoregulation properties. Mean mound volume across all forelands is only 0.19 m^3, which seems typical of the lower end (young 5 years old forest stands) studied by Domisch et al. (2005) and matches closely the values of 0.25 m^3 and 0.3 m^3 recorded for mean mound volume of *F. lugubris* in the national Finnish and Swiss studies of Punttila and Kilpeläinen (2009) and Vandegehuchte et al. (2017) respectively. Thus, many mounds are very small (Fig. 8A), a feature of the mound-size distributions that is particularly apparent in relation to mound volume (Fig. 7C), and very large mounds (Fig. 8D) are uncommon. However, there is evidence for bimodality in the mound-size distribution (a secondary mode in mound height of around 50-65 cm is clearly apparent in Fig. 7A), which we relate below to the multi-nest structure of ant colonies.

Most mounds are composed largely of organic material collected from the litter layer, which covers 100% of the surface of many (Table 2, Fig. 7F). Gravel and sand, presumably excavated from beneath the nest mounds, generally cover <17% of the mound surface, with gravel (mean cover across all forelands 12%) more common than sand (Fig. 7D-E).

Relationships to terrain age

The strength of the relationships between nest mound characteristics and terrain age are summarised for the three chronosequences in Table 3 using the Pearson's product-moment correlation coefficient (r). It should be pointed out that use of Spearman's non-parametric correlation coefficient yielded closely similar results, with slightly higher coefficients and an almost identical pattern of statistical significance.

The results indicate generally weak relationships between mound characteristics and terrain age with correlation coefficients (and coefficients of determination) no more than 0.53 (28.5 %) at Fåbergstølsbreen (Fig. 9A), –0.36 (12.6 %) at Bergsetbreen (Fig. 9B) and +0.27 (7.3 %) at Nigardsbreen (Fig. 9C). Although few relationships are consistent across all forelands, the strongest relationships relate to mound surface composition rather than mound size. Organic composition tends to increase with terrain age while sand and gravel composition decline. With respect to mound size, the strongest relationships are with height, which tends to increase with age (Figs 9C and 9D). The data indicate that relatively large mounds >50 m high can become established within ~100 years. They also suggest that whereas the maximum height of mounds tends to increase further with terrain age, the presence on relatively old terrain of small mounds as well as large ones reduces the strength of any size/age relationship.

Environmental relationships

Returning to the correlation matrices of Table 3, the explanatory variables relating to foreland vegetation are, in some cases, strongly related to nest mound size, particularly mound height, and to a lesser extent mound surface composition. The strongest relationships are between number of trees and mound volume at Bergsetbreen ($r = 0.62$; $p<0.05$) and Nigardsbreen ($r = 0.52$; $p<0.05$); the statistically insignificant result from Fåbergstølsbreen possibly being affected by the generally higher tree cover on that glacier foreland.

The overall effect of several explanatory variables on mound characteristics, and their interactions with terrain age are shown in the multivariate analyses (Fig. 10A-C).

Details of the variations in mound size and surface composition can be seen in the segmented bubble plots, while the vectors summarize the strength and major alignments of both mound characteristics and potential environmental controls when all the data are taken into account. NMDS provides an effective two-dimensional visual representation of the similarities between mounds in terms of size and surface composition, as shown by very low values of the stress statistic.

At Nigardsbreen (Fig. 10A), variation in surface composition between mounds, with the organic percentage increasing in bubble plots from left to right across the diagram and the sand and gravel percentage increasing from right to left, is effectively captured by NMDS axis 1. Size variation between mounds, with mound size (height, width and volume) increasing from the top towards the bottom of the diagram, is equally well captured by NMDS axis 2. Vectors representing terrain age and environmental characteristics are relatively short, reflecting their relatively weak correlations with mound characteristics (Table 3). However, the moderately strong relationship between trees and mound characteristics is confirmed by the length of the tree vector (the longest of the explanatory variables), while the vector direction confirms that the trees variable is approximately equally effective in accounting for variation in mound size and composition. Shorter vector lengths for ground cover, terrain age and altitude indicate similar weak relationships, whereas the very short poles vector confirms its negligible importance. Although the altitude vector suggests it has some influence on mound characteristics, this is unlikely at Nigardsbreen where altitude varies little across the glacier foreland. There is nevertheless a very strong negative correlation between altitude and terrain age ($r = -0.89$, $p<0.05$, Table 3), which arises from the consistent but small increase in altitude from the glacier foreland boundary towards the glacier snout.

The multivariate analyses from Bergsetbreen (Fig. 10B) and, particularly, Fåbergstølsbreen (Fig. 10C) show some fundamentally similar features to that of Nigardsbreen. The main differences at Fåbergstølsbreen are the relatively strong potential effects of age and altitude (longer vectors), which are more closely aligned with mound surface composition than with the mound size variables, and a relatively weak influence of trees. At Bergsetbreen, age and altitude are more closely aligned with the mound surface composition than at Nigardsbreen but the relationship is again weak. However, the influence of trees is as strong as at Nigardsbreen and, unlike at either of the other two glacier forelands, there is an appreciable potential effect of poles.

Where one-way ANOVA and/or Kruskal-Wallis tests indicated statistically significant differences ($p<0.05$) between habitat types in relation to mound size, Tukey simultaneous comparison tests were carried out to indicate which habitats differed from others. The strongest association was found between mound height and habitat type, which is illustrated for the combined data set from all three glacier forelands in Fig. 11. The boxplot (Fig. 11A) shows that mounds tend to be higher on the moraines and till-covered surfaces than on the glaciofluvial outwash plains and road banks. Simultaneous consideration of the 95 % confidence intervals around the mean height (Fig. 11B) confirms which differences are statistically significant (non-overlap of a 95 % confidence interval with zero on the scale indicating a significant difference at $p<0.05$) and highlights the clear influence of outwash plains in depressing mound height. Similar tests for Nigardsbreen alone revealed the same patterns, whereas at Bergsetbreen and Fåbergstølsbreen differences in mound size were not statistically significant. Use of mound volume rather than height produced similar but weaker patterns, while tests involving mound surface composition revealed no statistically significant associations. Most importantly, it is clear that mounds on moraines are significantly larger than those on the outwash plains, though patterns may be obscured by large and small mounds often occurring together.

Mounds on all three glacier forelands exhibit strong southerly preferred aspects (Fig. 12A-C): modal aspects are SSE (Nigardsbreen), SE (Bergsetbreen) or S (Fåbergstølsbreen) and 82% of all mounds are in the four segments facing SSW to SE. The relatively large number of mounds facing SSW at Fåbergstølsbreen seems to reflect the dominant aspect of the valley-side slope on the north side of the glacier foreland. This contrasts with the occurrence of most of the mounds associated with the south-side transect and also with the other forelands on relatively flat valley floors.

Box plots, one-way ANOVA analyses and Tukey tests of the presence or absence of aphids on trees within 5 m distance of mounds revealed statistically significant differences ($p <0.05$) in relation to mound height at Nigardsbreen, and also for the combined data set from Nigardsbreen and Fåbergstølsbreen (Fig. 11C). Where aphids were present, mounds were higher than where no aphids were present (Fig. 11D). Mound volume produced a similar pattern but no significant differences in mound size were detected at the other two forelands. The only statistically significant relationship involving mound surface composition and aphids was at Nigardsbreen: where aphids were present the sand percentage was lower than where they were absent. Thus, aphids tend to be associated with relatively large mounds rather than mounds with a particular composition.

Discussion

Implications of the observed patterns are both substantive, in relation to the geo-ecology of red wood ants, and methodological, in relation to chronosequences.

Terrain age and succession

The first substantive geo-ecological implications of the observed patterns relate to the colonisation and succession of red wood ants. Our results indicate that red wood ants colonise the glacier forelands 50-80 years after deglaciation. They are not, therefore, true pioneer species but early colonisers (Vater and Matthews, 2013, 2015). Furthermore, the tendency for nest mound size to increase with terrain age on two of the glacier forelands, and for large mounds (~1m in height and ~1m^3 in volume) to occur only on older terrain, suggests that further long-term development affects the mounds for >200 years following deglaciation. This conclusion is reinforced by mound surfaces with a relatively high sand and gravel content during the initial colonisation phase when the terrain is not completely vegetation covered (Fig. 13A). Early mounds with a substantial mineral cover are seemingly transformed into 100% organic mounds later in the chronosequences (Fig. 13B).

Recognition of long-term successional trends across the chronosequences tends to be obscured by the existence of numerous immature mounds. There is little information available on the turnover of mounds. While colonies of wood ants are generally assumed to last for years to decades (Manzaneda and Rey, 2012; Parmentier et al., 2014), individual mounds are dynamic over time, from year-to-year and within years, and small nests have a greater turnover rate than large nests (Boudjema et al., 2006; Chen and Robinson, 2014; Ellis et al., 2014; Klimetzek, 1981). At Nigardsbreen, clusters of mounds including small mounds as close together as 10 m, point to the expansion by 'budding' of socially-connected (polydomous) colonies. This fragmentation of main nests involves small groups of worker ants, accompanied by one or more queens, leaving a nest on foot to establish a new nest (Debout et al., 2007; Ellis and Robinson, 2014; Hölldobler and Wilson, 1990; Maeder et al., 2016). In many instances, nest budding functions as a reproductive strategy. In other cases, ants move their nests to avoid predation, to escape from unfavourable environmental conditions, to increase access to food, or to avoid overcrowding

(Buczkowski and Bennett, 2009). Crucially, polydomy allows colonies to create new nests without resorting to high-risk single-queen nest foundation (Robinson, 2014).

The pattern of mound size and surface composition, together with densities approaching 5 mounds per hectare on the glacier forelands following the initial colonisation phase, suggest that the ants become dominant (keystone) species quite early in the succession. This would be consistent with the addition and persistence model of invertebrate succession proposed by Vater (2012) and developed further by Vater and Matthews (2013, 2015), whereby successive colonisers are added to communities during succession and persist into the later stages with only limited replacement by later colonisers. However, several authors have suggested that *Formica lugubris* is more common in open, young and managed forests, and forest edges, whereas *F. aquilonia* tends to dominate in mature old-growth stands and in coniferous forests (Arnan et al., 2009; Gibb, 2011; Borkin et al., 2012; Chen and Robinson, 2014; Czechowski et al., 2002; Eichorn, 1963; Hågvar, 2005; Kilpeläinen et al., 2008; Punttila, 1996; Savolainen and Vepsäläinen, 1988), possibly due to superior competitive abilities. As the vegetation on our glacier forelands has more in common with young rather than mature forests, it is likely that *F. lugubris* is the dominant species (supportive of our taxonomic evidence).

Vegetation and biological resources

The lag time between deglaciation and establishment of nest mounds on the glacier forelands clearly is indicative of the dependence of red wood ant colonies on the prior establishment of vegetation, particularly trees. Litter provides organic nest material (‘thatch’) for the mounds (Laakso and Setälä, 1998; Weber, 1935), while live vegetation provides food resources. Red wood ants strive to maintain a reliable food source (Lenoir, 2002) and a key way they achieve this is by ant-aphid mutualism (Billick et al., 2007; Domisch et al., 2016; Fowler and Macgarvin, 1985; Stadler and Dixon, 2005). The ants farm aphid herds on trees for honeydew to obtain carbohydrates, the plant sugars having been obtained by the aphids directly from phloem sap (Dixon, 1998; Dixon and Thieme, 2007; Mahdi and Whittaker, 1993). Aphid honeydew is the main food resource of red wood ants, supplying up to 95% of a colony’s nutrition (Gordon et al., 1992; Rosengren and Sundström, 1991). To obtain protein, red wood ants also hunt and scavenge for arthropods on surrounding trees (and to a lesser extent on the forest floor), and a large proportion of their intake may come from feeding on the aphids themselves (Robinson et al., 2008).

Normally, about one third of the diet of red wood ants consists of insect prey (Lenoir, 2002). Minor food sources obtained directly from living vegetation include seeds, tree sap and berry juices (Domisch et al., 2016; Finér et al., 2013; Wellenstein, 1952). Thus, the availability of food resources is likely to positively drive mound size and distribution (Punttila and Kilpeläinen, 2009; Sorvari and Hakkarainen, 2005).

In previous studies, the location of *Formica* species generally (Travan, 1998) and *F. lugubris* more particularly (Arnan et al., 2009) has been positively associated with tree density. The recent study of Swiss forests by Vandegehuchte et al. (2017) found *Formica* species to be significantly related to loose or grouped tree crowns, with *F. lugubris* mounds more likely to occur amongst clusters of trees of different heights, dominated by spruce. The authors related this positive association to the rich vertical structure harbouring more abundant and diverse prey and honeydew-producing insects. Similarly, Hågvar (2005) found *F. lugubris* mounds in relatively open terrain amongst the uppermost birch (*Betula pubescens*) trees on an altitudinal transect in Sogndal, >50 km southwest of our study area. At the glacier forelands investigated in this study, *B. pubescens* is the main source of biological resources for ants, though scattered Scots pine (*Pinus sylvestris*) are utilised where they occur at Nigardsbreen and Bergsetbreen. This is apparent from the statistically significant relationships between mound size, tree numbers and the presence of aphids on trees in close proximity to mounds.

Significant relationships between mound surface composition and ground cover at Nigardsbreen suggest that dwarf shrubs (the dominant species of understorey vegetation) contribute organic thatch material, especially where trees are sparse on the younger parts of the glacier forelands. This is confirmed by the distinctive twigs and leaves of several dwarf shrubs that can be observed in mound thatch on all three glacier forelands (see Fig. 13). Ground vegetation also protects ants from predators and/or provides them with insect prey and other food resources (Vandegehuchte et al., 2017). Ground cover must not be too high, however, because the ants compete with low-growing shrubs for light and space to build their nests (Arnan et al., 2009).

Habitat variation and landscape development

The apparent location of nest mounds in certain physical habitat types – namely moraines and till plains over glaciofluvial outwash and road banks (cf Fig. 5B and 5C) – seems to involve the interaction of a number of abiotic and biotic environmental factors. In particular, moraines and till plains provide a substrate with mixed particle sizes (typically matrix-supported diamictons), whereas glaciofluvial outwash deposits are well sorted, often coarse grained (sands, gravels and/or cobbles) and devoid of silt and clay (Matthews, 1992). In consequence, the diamictons have a greater moisture-holding capacity and higher nutrient status, which leads to more rapid vegetation growth and ecosystem development generally. In other words the biological resources available to support red wood ants tend to be greater in the moraine and till-plain habitats. Trees in particular often remain small and stunted on glaciofluvial deposits on the oldest parts of all three glacier forelands, whereas mature birches occur in the other habitats.

The road banks at Nigardsbreen present a special case. Here, the relatively small mounds may reflect recent disturbance during road building and maintenance (in addition to the infertile substrate where road banks are made mainly from outwash deposits). At the same time, road banks may facilitate colonisation in an otherwise closed-canopy tree cover (Gibb and Hochuli, 2003). In general, therefore, the distribution of mounds in relation to habitats highlights the importance of spatial patterns as well as temporal trends within the developing landscape.

Aspect and mound thermal regime

Temperatures within red wood ant nest mounds from early spring to late autumn tend to be maintained at a relatively constant level, often 10 °C or more higher than in the surrounding soil and some 20 °C above the adjacent air temperature (Frouz et al. 2016; Skinner and Allen, 2015). The preferred southerly aspect of the mounds on our glacier forelands, mirroring the findings of Breen (2014), Kilpeläinen et al. (2008) and Risch et al. (2016), has a bearing on the mechanisms that have been proposed to explain such temperature differences. Risch et al. (2016) recognise three fundamentally different theories all of which, they conclude, probably contribute to the maintenance of the mound thermal regime. First, Forel's 'theory of domes' (Seeley and Heinrich, 1981) depends on the geometry of the mound and the interception of solar radiation. Second, the 'heat carrying theory' (Zahn, 1958) depends on ants being heated by the sun on top of the mound, and the subsequent release of heat when they move back into the mound. Third, the 'metabolic heat theory', requires heat to be generated within the mound, either by microbial decomposition (Coenen-Stass et al., 1980) or by the ants themselves contributing actively to thermoregulation (Kneitz, 1965). All three theories are supported by the thermal insulating properties of loosely packed mound thatch, which reduces the rate of heat loss from the mound once the internal temperature has been raised.

A preferred southerly aspect certainly supports solar radiation as an external heat source during the season when the ants themselves are most active, and therefore the first two theories, but cannot account for mounds heating up when they are still buried by snow in early spring when sunlight does not reach the surface of the mound (Rosengren et al., 1987). Small mounds, in particular, may require a sunny location as they are less capable of independent thermoregulation (Rosengren et al., 1987).

Geo-ecological processes and a conceptual model

From the above discussion it can be concluded that an understanding of geo-ecological processes – i.e. interacting abiotic and biotic processes in their spatio-temporal context – is necessary to explain the chronosequences described and analysed in this paper. The main interactions identified in this study are summarized in Fig. 14.

Central to our conceptual model is the development of a tree canopy, which increases gradually during primary succession and is modulated by the physical habitat type. On moraines and till plains the development of the tree cover increases more rapidly than on outwash deposits (probably due to the fertility and moisture-retention properties of the substrate) until, some 50 years after deglaciation, tree biomass is sufficient to sustain wood ant populations as evidenced by the first appearance of nest mounds. Key to successful establishment of the wood ants is the development of sufficient resources from the dominant tree, *Betula pubescens*, which establishes early in the vegetation succession (cf. Robbins and Matthews, 2010). The resulting birch woodland provides the biological resources required by foraging ants, namely plant litter for mound building and the ant's main carbohydrate food source (honeydew) from aphids. Statistically significant relationships between the number of trees and mound size, and between mound size and aphids, provide evidence for these interactions. As our data indicate that the ground cover of largely dwarf shrubs plays a similar but lesser role to the tree canopy, a ground-cover box has been omitted from the model.

The second major theme of our model is the interactions between the tree canopy, the microclimate (external and internal thermal climate) of the mounds, and the ant population. On the glacier forelands, the immature birch woodland is characteristically open with tree clusters rather than closed-canopy woodland. The preferred southerly aspect of mounds sited in clearings therefore results in the heating up of the mound surface (and any ants occupying that surface) by direct solar radiation, an external microclimatic effect that is unlikely to occur in mature, closed-canopy woodland. This is consistent with the findings of Vandegehuchte et al. (2017) who found that the occurrence and size of *Formica lugubris* mounds were strongly related to July radiation receipt and that relatively low mound densities were characteristic of homogeneous closed-canopy forests in Switzerland. Indeed, Chen and Robinson (2014) found a relatively cool microclimate characterised mounds of *Formica lugubris* in close-canopy woodland in the Peak District, UK, and proposed that this necessitated the construction of larger mounds (see also Geiger et al., 2003; Huang et al., 2014; Kilpeläinen et al., 2008; Rodrigues-Garcia et al., 2011).

Our data further indicate that the negative effect on internal mound temperature of an increasing canopy cover is more than compensated for by the positive effect of a southerly aspect in the open habitats of glacier forelands. In addition, as indicated in our model, self-regulation of the internal thermal microclimate of mounds by large numbers of socially-organised ants contributes to the maintenance of higher temperatures than outside the mounds (alongside the other possible mechanisms, including microbial decomposition of organic matter within the mound and the transportation of heat into the mound by ants).

Chronosequence methodology, autecology, geo-ecology and multivariate analysis

The main methodological implications of this study relate to chronosequences in the context of geo-ecology and autecology. Previous studies of chronosequences on glacier forelands have emphasised community ecology (synecology) and have restricted their analyses to plant communities, animal communities or other compartments of the geo-ecological system. As indicated in the introduction to this paper, autecological investigations have rarely been attempted. In contrast, we have explored the potential of glacier foreland chronosequences for the autecological study of red wood ants. Although two species have been identified at the study sites, the available evidence from the nest mounds suggests that *Formica lugubris* is far more abundant than *F. aquilonia* and therefore the study can be regarded as essentially an autecological investigation of the former.

By focusing on keystone species, it can be argued that we have opened a window onto the complex geo-ecological interactions that characterise succession in glacier-foreland chronosequences. The strictly ‘ecological’ approaches of the past have clearly overemphasised the biological elements, with consequent neglect of both spatial variation (the geographical element) and the abiotic interactions that are apparent in glacier foreland landscapes. Our ‘geo-ecological’ approach, on the other hand, effectively integrates the biotic and abiotic elements in the landscape to achieve a deeper understanding of spatio-temporal variation (cf. Cutler et al., 2008; Matthews, 1992; Matthews and Vater, 2015; Matthews and Whittaker, 1987; Robbins and Matthews, 2010; Vater and Matthews, 2015). Furthermore, the focus on the autecology of the keystone species has revealed important interactions of broad significance within the glacier foreland landscape while reducing somewhat its inherent complexity. This can be viewed as exploiting the natural experiment implicit in chronosequence methodology (cf. Deevey, 1969; Diamond, 1986; Fukami and Wardle, 2005). Such holistic understanding is becoming more important as red wood ant populations are experiencing increasing human pressure, both locally at our study site, and more widely (Dekoninck et al., 2010; Parmentier et al., 2014; Sorvari, 2016; Vandegehuchte et al., 2017).

Finally, we have demonstrated the suitability of multivariate analysis in general and NMDS ordination in particular for detecting and investigating relatively weak geo-ecological interactions between mound characteristics and explanatory variables in chronosequences. Although only a limited number of biotic environmental variables (trees, poles and ground cover) were used in our analyses alongside terrain age as explanatory variables, we have supplemented the multivariate NMDS ordination with simpler analyses of abiotic data relating to aspect and the physical habitat. It can be concluded therefore that NMDS and associated visualisation techniques should be capable of wider application in ecology and geo-ecology.

Summary and conclusion

(1) Chronosequences of red wood ant nest mounds (predominantly *Formica lugubris*) were investigated using belt transects and a geo-ecological approach on three southern Norwegian glacier forelands – Nigardsbreen, Bergsetbreen and Fåbergstølsbreen. Mounds occurred at a density of 2.5-4.6 mounds/hectare. The distribution of mounds indicates that colonisation first occurs on terrain deglaciated for 50-80 years.

(2) Mean mound height across all forelands was 44 cm (maximum 92-100 cm) but numerous small mounds, attributed to the expansion of polydomous ant colonies by

budding, resulted in a modal height of 20-30 cm and a mean mound volume of 0.19 m^3. Nevertheless, mound height showed a weak but statistically significant ($p<0.05$) increase with terrain age at Fåbergstølsbreen ($r = 0.47$; $p<0.05$) and Nigardsbreen ($r = 0.27$; $p<0.05$). Mound surface composition, also weakly related to terrain age, was largely organic with up to 17 % mineral material (mostly gravel), especially on relatively young terrain.

(3) Interrelationships between mound characteristics, terrain age and potential explanatory variables were examined using non-metric multidimensional scaling (NMDS) with superimposed bubble plots (Fig. 10A-C) and a variety of simpler statistical techniques. Mound height was found to be related to the number of trees (almost entirely *Betula pubescens*) occurring within 5 m of each mound at Bergsetbreen ($r = 0.61$; $p<0.05$) and Nigardsbreen ($r = 0.47$; $p<0.05$), which points to the importance of biological resources for the establishment and expansion of ant populations.

(4) In addition to the necessity for organic thatch for mounds, the presence of sufficient trees promotes the development of ant-aphid mutualism, a conclusion supported by mounds being significantly larger where aphids were present than where they were absent.

(5) Mound size was related to physical habitat type. Mounds located on moraines and till-plain habitats tended to be larger than those located on coarse-grained outwash deposits. This pattern may be explained by substrate differences related to moisture retention and fertility, both of which promote tree growth.

(6) The strong preferred southerly aspect of mounds on all three glacier forelands indicates the importance of direct solar radiation in maintaining mound temperatures when the ant populations are active. This effect appears particularly important on glacier forelands in the absence of a complete tree canopy cover.

(7) Our geo-ecological conceptual model (Fig. 14) summarizes the complex interrelationships between geo-ecological processes affecting ant populations on glacier forelands. In these landscapes, successional trends are modulated by spatial patterns in both the biotic and abiotic environment. Other key features of the model are the interactions between the developing tree canopy, mound building, the microclimate of nest mounds and the development of ant-aphid mutualism.

(8) Thus, the chronosequence methodology can be appropriately combined with a geo-ecological approach in the context of the autecology of keystone species. Furthermore, multivariate ordination techniques, such as NMDS, seem necessary for effective analysis in this context, where complex interrelationships are characteristic, rather than simple one-to-one causal relationships between particular variables.

Acknowledgements

Field work was carried out on the Swansea University Jotunheimen Research Expeditions, 2013 and 2015. We are grateful to Ross Pinnuck for field assistance, Torstein Kvamme (Norwegian Institute of Bioeconomy Research) for the identification of ant specimens, Anna Ratcliffe (Swansea University) for preparing the figures for publication, and the University of the West of England for a contribution to the expedition costs of JLH. This paper is Jotunheimen Research Expeditions, Contribution No. 204 (see http://jotunheimenresearch.wixsite.com/home)

References

Andreassen LM and Winsvold SH (eds) (2012) *Inventory of Norwegian Glaciers*. Oslo: Norwegian Water Resources and Energy Directorate (NVE).

Arnan X, Gracia M, Comas L et al. (2009) Forest management conditioning ground ant community structure and composition in temperate coniferous forests in the Pyrenees Mountains. *Forest Ecology and Management* 258: 51-59.

Aune B (1993) *Temperatur normaler, normalperiode 1961-1990. Rapport 02/93.* Den Oslo: Norske Meteorologiske Institutt.

Bardgett RD and Walker LR (2004) Impact of coloniser plant species on the development of decomposer microbial communities following deglaciation. *Soil Biology and Biochemistry* 36: 555-559.

Bardgett RD, Bowman WD, Kaufmann R et al. (2005) A temporal approach to linking aboveground and belowground ecology. *Trends in Ecology and Evolution* 20: 634-641.

Bickerton RH and Matthews JA (1992) On the accuracy of lichenometric dates: an assessment based on the 'Little Ice Age' moraine sequence of Nigardsbreen, southern Norway. *The Holocene* 2: 227-237.

Bickerton RH and Matthews JA (1993) 'Little Ice Age' variations in outlet glaciers from the Jostedalsbreen ice-cap, southern Norway: a regional lichenometric-dating study of icemarginal moraine sequences and their climatic significance. *Journal of Quaternary Science* 8: 45-66.

Billick I, Hammer S, Reithel JS et al. (2007) Ant-aphid interactions: are ants friends, enemies or both? *Annals of the Entomological Society of America* 100: 887-892.

Blüthgen N and Feldhaar H (2010) Food and shelter: how resources influence ant ecology. In: Lach L, Parr CL and Abbott KL (eds), *Ant Ecology*. Oxford: Oxford University Press, pp. 115-136.

Borkin KM, Summers RW and Thomas L (2012) Surveying abundance and stand type associations of *Formica aquilonia* and *F. lugubris* (Hymenoptera: Formicidae) nest mounds over an extensive area: trialing a novel method. European *Journal of Entomology* 109: 47-53.

Boudjema G, Lempérière G, Deschamps-Cottin M et al. (2006) Analysis and nonlinear modeling of the mound-building ant *Formica lugubris* spatial multi-scale dynamic in a larch-tree stand of the southern French Alps. *Ecological Modelling* 190: 147-158.

Boulay R, Coll-Toledano J, Manzaneda AJ et al. (2007) Geographic variations in seed dispersal by ants: are plant and seed traits decisive? *Naturwissenschaften* 94: 242-246.

Bradley JA, Singarayer JS and Anesio AM (2014) Microbial community dynamics in the forefield of glaciers. *Proceedings of the Royal Society B (Biological Sciences)* 281: 20140882. http://dx.doi.org/10.1098/rspb.2014,0882.

Breen B (1979) Nest sites of *Formica lugubris* (Hymenoptera: Formicidae) in Irish plantation woods. *Journal of Life Sciences, Royal Dublin Society* 1: 13-32.

Breen B (2014) Species dossier, range and distribution data for the hairy wood ant, *Formica lugubris,* in Ireland. *Irish Wildlife Manuals 68. National Parks and Wildlife Service, Ireland.*

Buczkowski G and Bennett G (2009) Colony budding and its effects on food allocation in the highly polygynous ant, *Monomorium pharaonis*. *Ethology* 115: 1091-1099.

Carlson ML, Flagstad LA, Gilet F et al. (2010) Community development along a proglacial chronosequence: are above-ground and below-ground community structure controlled more by biotic than abiotic factors? *Journal of Ecology* 98, 1084–1095.

Chen Y-H and Robinson EJH (2013) A comparison of mark-release-recapture methods for estimating colony size in the wood ant *Formica lugubris*. *Insectes Sociaux* 60, 351-359.

Chen Y-H and Robinson EJH (2014) The relationship between canopy cover and colony size of the wood ant *Formica lugubris* - implications for the thermal effects on a keystone ant species. *PLoS ONE* 9(12): e116113, 1-18.

Clarke KR, Gorley RN, Somerfield PJ et al. (2014) *Change in Maritime Communities: An Approach to Statistical Analysis and Interpretation*, *3rd edition*. Plymouth: PRIMER-E.

Clarke KR and Gorley RN (2015) *PRIMER v7: User Manual/Tutorial.* Plymouth: PRIMER-E.

Coenen-Stass D, Schaarschmidt B and Lamprecht I (1980) Temperature distribution and calorimetric determination of heat production in the nest of the wood ant, *Formica polyctena* (Hymenoptera, Formicidae). *Ecology* 61: 238-244.

Collingwood CA (1979) The Formicidae (Hymenoptera) of Fennoscandia and Denmark. *Fauna Entomologica Scandinavica* 8: 1-156.

Cox TF and Cox MAA (2000) *Multidimensional Scaling, 2nd edition.* Boca Raton, FL: Chapman and Hall/CRC Press.

Cutler N, Belyea LR and Dugmore AJ (2008) The spatiotemporal dynamics of a primary succession. *Journal of Ecology* 96: 231-246.

Czechowski W, Radchenko A and Czechowska W (2002) *The ants (Hymenoptera, Formicidae) of Poland*. Warsaw: Museum and Institute of Zoology, Polish Academy of Sciences.

Dahl SO, Nesje A, Lie Ø et al. (2002) Timing, equilibrium-line altitudes and climatic implications of two early-Holocene glacier readvances during the Erdalen Event at Jostedalsbreen, western Norway. *The Holocene* 12: 17-25.

Darmody RG, Allen CE and Thorn CE (2005) Soil topochronosequences at Storbreen, Jotunheimen, Norway. *Soil Science Society of America Journal* 69: 1275-1287.

Debout G, Schatz B, Elias M et al. (2007) Polydomy in ants: what we know, what we think we know, and what remains to be done. *Biological Journal of the Linnean Society* 90: 319-348

Deevey ES (1969) Coaxing history to conduct experiments. *Bioscience* 19: 40-43.

Dekoninck W, Hendrickx F, Grootnaert P et al. (2010) Present conservation status of red wood ants in north-western Belgium: worse than previously, but not a lost cause. *European Journal of Entomology* 107: 209-218.

Diamond J (1986) Overview: laboratory experiments, field experiments, and natural experiments. In: Diamond Jand Case TJ (eds) Community Ecology. New York: Harper and Row, pp. 3-22.

Dixon AFG (1998) *Aphid Ecology: An Optimization Approach, 2nd edition*. London: Chapman and Hall.

Dixon AFG and Thieme T (2007) *Aphids on Deciduous Trees*. Slough, UK: Richmond Publishing.

Doblas-Miranda E, Wardler DA, Peltzer DA et al. (2008) Changes in community structure and diversity of soil invertebrates across the Franz Josef Glacier chronosequence. *Soil Biology and Biochemistry* 40: 1069-1081.

Domisch T, Finér L and Jurgensen MF (2005) Red wood ant mound densities in managed boreal forests. *Annales Zoologici Fennici* 42: 277-282.

Domisch T, Neuvonen S, Sundstrom L et al. (2011) Sources of variation in the incidence of ant-aphid mutualism in boreal forests. *Agricultural and Forest Entomology* 13: 239-245.

Domisch T, Risch AC and Robinson EJH (2016) Wood ant foraging and mutualism with aphids. In: Stockan JA and Robinson EJH (eds), *Wood Ant Ecology and Conservation*. Cambridge: Cambridge University Press, pp. 145-176.

Eichorn O (1963) Die höhen- und waldtypenmässige Verbreitung der nützlichen Waldameisen in den Ostalpen. *Waldhygiene* 5: 129-135.

Ellis S and Robinson EJH (2014) Polydomy in red wood ants. *Insectes Sociaux* 61: 111-122.

Ellis S, Franks DW and Robinson EJH (2014) Resource redistribution in polydomous ant nest networks: local or global. *Behavioural Ecology* 25: 1183-1191.

Erschbaumer B and Caccianiga MS (2016) Glacier forelands: lessons of plant population and community development. *Progress in Botany* 78: 259-284.

Everitt BS and Hothorn T (2011) *An Introduction to Applied Multivariate Analysis with R*. New York: Springer.

Fernández-Martínez MA, Pérez-Ortega S, Pointing SB et al. (2017) Microbial succession dynamics along glacier forefield chronosequences in Tierra del Fuego (Chile). *Polar Biology* doi 10.1007/s00300-017-2110-7.

Finér L, Jurgensen MF, Domisch T et al. (2013) The role of wood ants (*Formica rufa* group) in carbon and nutrient dynamics of a boreal Norway spruce forest ecosystem. *Ecosystems* 16: 196-208.

Førland EJ (1993) *Nedbørnormaler, normalperiode 1961-90. Rapport 39/93.* Oslo: Den Norske Meteorologiske Institutt.

Fowler SV and Macgarvin M (1985) The impact of hairy wood ants, *Formica lugubris*, on the guild structure of herbivorous insects on birch, *Betula pubescens*. *Journal of Animal Ecology* 54: 847-855.

Freitag A, Stockan JA, Bernasconi C et al. (2016) Sampling and monitoring wood ants. In: Stockan JA and Robinson EJH (eds) *Wood Ant Ecology and Conservation*. Cambridge: Cambridge University Press, pp. 238-263.

Frouz J and Jílková V (2008) The effects of ants on soil properties and processes (Hymenoptera: Formicidae). *Myrmecological News* 11: 191-199.

Frouz J, Jílková V and Sorvari J (2016) Contribution of wood ants to nutrient cycling and ecosystem function. In: Stockan JA and Robinson EJH (eds), *Wood Ant Ecology and Conservation*. Cambridge: Cambridge University Press, pp. 207-220.

Fukami T and Wardle DA (2005) Long-term ecological dynamics: reciprocal insights from natural and anthropogenic gradients. *Proceedings of the Royal Society B (Biological Sciences)* 272: 2105-2115.

Garibotti IA, Pissolito CL and Villalba R (2011) Spatiotemporal pattern of primary succession in relation to meso-topographic gradients on recently deglaciated terrain in the Patagonian Andes. *Arctic, Antarctic and Alpine Research* 43: 555-567.

Geiger R, Aron RH Todhunter P (2003) *The Climate Near the Ground. 6th edition*. Lanham, MD: Rowman and Littlefield.

Gibb H (2011) Experimental evidence for mediation of competition by habitat succession. *Ecology* 92: 1871-1878.

Gibb H and Hochuli DF (2003) Anthropogenic disturbance facilitated colonisation by a dominant ant: effects on ant community composition, biomass and resource use. *Oikos* 103: 469-478.

Gibb H and Johansson T (2010) Forest succession and harvesting of Hemipteran honeydew by boreal ants. *Annales Zoologici Fennici* 47: 99-110.

Gibb H, Andersson J and Johansson T (2016) Foraging loads of red wood ants: Formica aquilonia (Hymenoptera: Formicidae) in relation to tree characteristics and stand age. *PeerJ* 4, e2049, DOI 10.7717/peerj.2049.

Gobbi M, De Bernardi F, Pelfini M et al. (2006) Epigean arthropod succession along a 154-year glacier foreland chronosequence in the Forni Valley (Central Italian Alps). *Arctic, Antarctic and Alpine Research* 38: 357-362.

Gorb SN and Gorb EV (1995) Removal rates of seeds of five myrmecochorous plants by the ant *Formica polyctena* (Hymenopters: Formicidae). *Oikos* 73: 367-374.

Gordon DM, Rosengren R and Sundström L (1992) The allocation of foragers in red wood ants. *Ecological Entomology* 17: 114-120.

Goropashnaya AV, Fedorov VB and Pamilo P (2004) Recent speciation in the *Formica rufa* group ants (Hymenoptera, Formicidae): inference from mitochondrial DNA phylogeny. *Molecular Phylogenetics and Evolution* 32: 198-206.

Hågvar S (2005) Altitudinal zonation of ants (Formicidae) in a steep fjord landscape in Sogndal, Western Norway. *Norwegian Journal of Entomology* 52: 3-12.

Hågvar S (2012) Primary succession on glacier forelands: how small animals conquer new land around melting glaciers. In: Young SS and Silvern SE (eds) *International Perspectives on Global Environmental Change*. Intech Open Access Publisher, pp. 151-172 (Available at: http://www.intecopen.com).

Hågvar S and Flø D (2015) Succession and phenology of the generalist predator *Mitopus morio* (Fabricius, 1799) (Opiones) in a glacier foreland. *Norwegian Journal of Entomology* 62: 210-215.

Hodkinson ID, Coulson SJ and Webb NR (2004) Invertebrate community assembly along proglacial chronosequences in the high Arctic. *Journal of Animal Ecology* 73: 556-568.

Hölldobler B and Wilson EO (1990) *The Ants*. Berlin: Springer.

Huang SP, Porter WP, Tu MC et al. (2014) Forest cover reduces thermally suitable habitats and affects responses to warmer climate predicted in a high-elevation lizard. *Oecologia* 175: 25-35.

Hughes J (1999) The status of *Formica lugubris* Zett. and *Formica aquilonia* Yarrow [Hym: Formicidae] in Ross-shire and Sutherland. *Entomologists Record and Journal of Variation* 111: 277-284.

Hughes J (2006) *A Review of Wood Ants (Hymenoptera: Formicidae) in Scotland*. Inverness: Scottish Natural Heritage. [Commissioned Report 178]

Jílková V, Šebek O and Frouz J (2012) Mechanisms of pH change in wood ant (*Formica polyctena*) nests. *Pedobiologia* 55: 247-251.

Johnson E and Miyanishi K (2008) Testing the assumptions of chronosequences in succession. *Ecological Letters* 11: 419-431.

Jones CC and del Moral R (2009) Dispersal and establishment both limit colonization during primary succession on a glacier foreland. *Plant Ecology* 204: 217-230.

Jurgensen M, Finér L, Domisch T et al. (2008) Organic mound-building ants: their impact on soil properties in temperate and boreal forests. *Journal of Applied Entomology* 132: 266-275.

Kadochová Š and Frouz J (2014) Thermoregulation strategies in ants in comparison to other social insects, with a focus on red wood ants (*Formica rufa* group). *F1000Research* 2-280: v2, 1-16.

Kaštovská K, Elster J, Stibal M et al. (2005) Microbial assemblages in soil microbial succession after glacial retreat in Svalbard (High Arctic). *Microbial Ecology* 50: 396-407.

Kaufmann R (2001) Invertebrate succession on an alpine glacier foreland. *Ecology* 82: 2261-2278.

Kilpeläinen J, Punttila P, Sundström L et al. (2005) Forest stand structure, site type and distribution of antmounds in boreal forests in Finland in the 1950s. *Annales Zoologici Fennici* 42: 243-258.

Kilpeläinen J, Punttila P, Finér L et al. (2008) Distribution of ant species and mounds (Formica) in different-aged managed spruce stands in eastern Finland. *Journal of Applied Entomology* 132: 315-325.

King, TJ (1977) The plant ecology of ant hills in calcareous grasslands I. Patterns of species in relation to ant-hills in southern England. *Journal of Ecology* 65: 235-256.

Klimetzek D (1981) Population studies on hill building wood-ants of the *Formica rufa* group. *Oecologia* 48: 418-421.

Kneitz G (1965) *Formica*-Arten mit vegetabilischen Nestbau in den Gurktaer Alpen (Kärnten). *Waldhygiene* 5: 240-250.

Koivula M and Niemelä J (2003) Gap felling as a forest harvesting method in boreal forests: responses of carabid beetles (Coleoptera, Carabidae). *Ecography* 26: 179-187.

Kvamme T and Wetås Å (2010) *Revidert liste over norske maur [Revised list of Norwegian ants]. Nationalt senter for insektbiodiversity*. Ås: Norsk Institutt for Skog og Landskap,.

Laakso J and Setälä H (1998) Composition and trophic structure of detrital foodweb in ant nest mounds of *Formica aquilonia* and in the surrounding forest soil. *Oikos* 81: 266-278.

Laine KJ and Niemelä P (1989) Nests and nest sites of red wood ants (Hymenoptera, Formicidae) in Subarctic Finland. *Annales Entomologici Fennici* 55: 81-88.

Lawrence LR, Wardle DA, Bargett RD et al. (2010) The use of chronosequences in studies of ecological succession and soil development. *Journal of Ecology* 98: 725-736.

Lenoir L (2002) Can wood ants distinguish between good and bad food patches on the forest floor? *European Journal of Soil Biology* 38: 97-102.

Lenoir L, Persson T and Bengtsson J (2001) Wood ant nests as potential hot spots for carbon and nitrogen mineralization. *Biology and Fertility of Soils* 34: 235-240.

Losapio G, Jordán F, Caccianiga M etal. (2015) Structure-dynamic relationship of plant-insect networks along a primary succession gradient on a glacier foreland. *Ecological Modelling* 314: 73-79.

Lutro O and Tveten E (1996) *Geologisk kart over Norge, bergrunnskart Årdal M 1:250,000.* Trondheim: Norges Geologiske Undersøkelse.

Mabelis AA (1984) Interference between wood ants and other ant species (Hymenoptera, Formicidae). *Netherlands Journal of Zoology* 34: 1-20.

Maeder A, Cherix D, Bernasconi C et al. (2016) Wood ant reproductive biology and social systems. In: Stockan JA and Robinson EJH (eds) *Wood Ant Ecology and Conservation*. Cambridge: Cambridge University Press. pp. 37-50.

Mahdi T and Whittaker JB (1993) Do birch trees (*Betula pendula*) grow better if foraged by wood ants? *Journal of Animal Ecology* 62: 101-116.

Manzaneda AJ and Rey PR (2009) Assessing ecological specialization of an ant-seed dispersal mutualism through a wide geographic range. *Ecology* 90: 3009-3022.

Manzaneda AJ and Rey PR (2012) Geographical and interspecific variation and the nutrient-enrichment hypothesis as an adaptive advantage of myrmecochory. *Ecography* 35: 322-332.

Matthews JA (1992) *The Ecology of Recently-Deglaciated Terrain: a Geo-ecological Approach to Glacier Forelands and Primary Succession*. Cambrisdge: Cambridge University Press.

Matthews JA (1999) Disturbance regimes and ecosystem response on recently-deglaciated substrates. In: Walker LR (ed.) *Ecosystems of Disturbed Ground.* Amsterdam: Elsevier, pp. 17-37.

Matthews JA and Vater AE (2015) Pioneer zone geo-ecological change: observations from a chronosequence on the Storbreen glacier foreland, Jotunheimen, southern Norway. *Catena* 135: 219-230.

Matthews JA and Whittaker RJ (1987) Vegetation succession on the Storbreen glacier foreland, Jotunheimen, Norway: a review. *Arctic and Alpine Research* 19: 385-395.

Matthews JA, Shakesby RA, Berrisford MS et al. (1998) Periglacial patterned ground on the Styggedalsbeen glacier foreland, Jotunheimen, southern Norway: micro-topographic, paraglacial and geoecological controls. *Permafrost and Periglacial Processes* 9: 147-166.

Mellor A (1985) Soil chronosequences on Neoglacial moraine ridges, Jostedalsbreen and Jotunheimen, southern Norway: a quantitative pedogenic approach. In: Richards KS, Arnett RR and Ellis S (eds) *Geomorphology and Soils*. London: George Allen and Unwin, pp. 289-308.

Messer AC (1988) Regional variation in rates of pedogenesis and the influence of climatic factors on moraine chronosequences, southern Norway. *Arctic and Alpine Research* 20: 31-39.

MINITAB (2010): *MINITAB Version 17 Statistical Software.* State College, PA: Minitab Inc. [www.minitab.com]

Moen A (1999) *National Atlas of Norway: Vegetation*. Hønefoss: Norwegian Mapping Agency.

Ohashi M, Kilpeläinen J, Finér L et al. (2007) The effect of red wood ant (*Formica rufa* group) mounds on root biomass, density and nutrient concentrations in boreal managed forests. *Journal of Forest Research* 12: 113-119.

Owen G, Matthews JA and Albert PG (2007) Rates of Holocene chemical weathering, 'Little Ice Age' glacial erosion and implications for Schmidt-hammer dating at a glacier-foreland boundary, Fåbergstølsbreen, southern Norway. *The Holocene* 17: 829-834.

Parmentier T, Dekoninck W and Wenseleers T (2014) A highly diverse microcosm in a hostile world: a review on the associates of red wood ants (*Formica rufa* group). *Insectes Sociaux* 61: 229-237.

Polyanin AD and Manzhirov AV (2006) *Handbook of Mathematics for Engineers and Scientists*. Boca Raton, FL.

Porter SD, Fowler HG and MacKay WP (1992) Fire ant mound densities in the United States and Brazil (Hymenoptera: Formicidae). *Journal of Economic Entomology* 84: 1154-1161.

Prach K and Rachlewicz G (2012) Succession of vascular plants in front of retreating glaciers in central Spitsbergen. *Polish Polar Research* 33: 319-328.

Punttila P (1996) Succession, forest fragmentation, and the distribution of wood ants. *Oikos* 75: 291-298.

Punttila P and Kilpeläinen J (2009) Distribution of mound-building ant species (Formica spp., Hymenoptera) in Finland: preliminary results of a national survey. *Annales Zoologici Fennici* 46: 1-15.

Punttila P, Niemelä P and Karhu K (2004) The impact of wood ants (Hymenoptera Formicidae) on the structure of invertebrate community on mountain birch (*Betula pubescens ssp. czerepanovii*). *Annales Zoologici Fennici* 41: 429-446.

Reznikova Z and Dorosheva H (2004) Impacts of red wood ants Formica polyctena on the spatial distribution and behavioural patterns of ground beetles (Carabidae). *Pedobiologia* 48: 15-21.

Risch AC, Ellis S and Wiswell H (2016) Where and why? Red wood ant population ecology. In: Stockan JA and Robinson EJH (eds) *Wood Ant Ecology and Conservation*. Cambridger: Cambridge University Press, pp. 81-105.

Robbins JA and Matthews JA (2010) Regional variation in successional trajectories and rates on glacier forelands in south-central Norway. *Arctic, Antarctic and Alpine Research* 42: 351–361.

Robinson EJH (2014) Polydomy: the organisation and adaptive function of complex nest systems in ants. *Current Opinion in Insect Science* 5: 37-43.

Robinson NA and Robinson EJH (2013) Myrmecophiles and other invertebrate nest associates of the red wood ant *Formica rufa* (Hymenoptera: Formicidae) in north-west England. *British Journal of Entomology and Natural History* 26: 67-88.

Robinson EJH and Stockan JA (2016) Future directions for wood ant ecology and conservation. In: Stockan JA and Robinson EJH (Eds) *Wood Ant Ecology and Conservation.* Cambridge: Cambridge University Press, pp, 287-299.

Robinson EJH, Stockan JA and Iason GR (2016) Wood ants and their interaction with other organisms. In: Stockan JA and Robinson EJH (eds) *Wood Ant Ecology and Conservation*. Cambridge: Cambridge University Press, pp. 177-206.

Robinson EJH, Tofilski A and Ratnieks FLW (2008) The use of native and non-native tree species for foraging and nesting habitat by the wood-ant *Formica lugubris* (Hymenoptera: Formicidae). *Myrmecological News* 11: 1-7.

Rodrigues-Garcia E, Ordonez C and Bravo F (2011) Effects of shrub and canopy cover on the relative growth rate of *Pinus pinaster* Alt. seedlings of different sizes. *Annals of Forest Science* 68: 337-246.

Rosengren R, Fortelius W, Lindström K et al. (1987) Phenology and causes of nest heating and thermoregulation in red wood ants of the *Formica rufa* group studied in coniferous forest habitats in southern Finland. *Annales Zoologici Fennici* 24: 147-155.

Rosengren R and Sundström L (1991) The interaction between red wood ants, *Cinara* aphids, and pines - A ghost of mutualism past? In: Huxley CR and Cutler DF (eds) *Ant-Plant Interactions.* Oxford: Oxford University Press pp. 80-91.

Savolainen R and Vepsäläinen K (1988) A competition hierarchy among boreal ants: impact on resource partitioning and community structure. *Oikos* 51: 135-155.

Savolainen R and Vepsäläinen K (1989) Niche differentation of ant species within territories of the dominant *Formica polyctena. Oikos* 56: 3-16.

Schmidt SK, Reed SC, Nemergut DR et al. (2015) The earliest stages of ecosystem succession in high-elevation (5000 metres above sea level), recently-deglaciated soils. *Proceedings of the Royal Society B (Biological Sciences)* 275: 2793-2802.

Seeley TD and Heinrich B (1981) Regulation in temperature in the nests of social insects. In: Heinrich, B. (Ed.), Insect Thermoregulation. John Wiley, New York, pp. 160-234.

Skinner GJ and Allen GW (2015) *Ants.* Exeter: Pelagic Publishing. [Naturalist Handbooks 24]

Sorvari J (2016) Threats, conservation and management. In: Stockan JA and Robinson EJH (eds) *Wood Ant Ecology and Conservation*. Cambridge: Cambridge University Press, pp. 264-285.

Sorvari J and Hakkarainen H (2005) Deforestation reduces nest mound size and decreases the production of sexual offspring in the wood ant *Formica aquilonia*. *Annales Zoologici Fennici* 42: 259-267.

Sorvari J, Elo RA and Härkönen SK (2016) Forest-built nest mounds of red wood ant *Formica aquilonia* are no good in clear fells. *Applied Soil Ecology* 101: 101-106.

Stadler B and Dixon AFG (2005) Ecology and evolution of aphid-ant interactions. *Annual Review of Ecology, Evolution and Systematics* 36: 345-372.

Stevens PR and Walker TW (1970) The chronosequence concept and soil formation. *Quarterly Review of Biology* 45: 333-350.

Stockan JA and Robinson EJH (eds) (2016) *Wood Ant Ecology and Conservation*. Cambridge: Cambridge University Press.

Stockan JA, Robinson EJH, Trager JC et al. (2016) Introducing wood ants: evolution, phylogeny, identification and distribution. In: Stockan JA and Robinson EJH (eds) *Wood Ant Ecology and Conservation*. Cambridge: Cambridge University Press, pp. 1-36.

Styrsky J and Eubanks M (2007) Ecological consequences of interactions between ants and honeydew producing insects. *Proceedings of the Royal Society B (Biological Sciences)* 274: 151-164.

Sudd JH (1983) The distribution of foraging wood ants (Formica lugubris Zett.) in relation to the distribution of aphids. *Insectes Sociaux* 30: 298-307.

Sudd JH, Douglas JM, Gaynard T et al. (1977) Distribution of wood ants (*Formica lugubris* Zetterstedt) in a northern English forest. *Ecological Entomology* 2: 301-313.

Tampucci D, Gobbi M, Boracchi P et al. (2015) Plant and arthropod colonisation of a glacier foreland in a peripheral mountain range. *Biodiversity* 16: 213-223.

Travan J (1998) The impact of habitat factors on the colonization of red wood ants (*Formica* spp.) in the Bavarian Alps. *Anzeiger fur Schadlingskunde Pflanzenschutz umweltschutz* 71: 105-109.

Tscherko D, Hammesfahr H, Zeltner G et al. (2005) Plant succession and rhizosphere microbial communities in a recently deglaciated alpine terrain. *Basic and Applied Ecology* 6: 367-383.

Vandegehuchte ML, Wermelinger B, Fraefel M et al. (2017) Distribution and habitat requirements of red wood ants in Switzerland: implications for conservation. *Biological Conservation* 212: 366-375.

Vater AE (2012) Insect and arachnid colonization on the Storbreen glacier foreland, Jotunheimen, Norway: persistence of taxa suggests an alternative model of succession. *The Holocene* 22: 1123-1133.

Vater AE and Matthews JA (2013) Testing the ‘addition and persistence’ model of invertebrate succession on a subalpine glacier–foreland chronosequence, Fåbergstølsbreen, southern Norway. *The Holocene* 23: 1151-1162.

Vater AE and Matthews JA (2015) Succession of pitfall-trapped insects and arachnids on eight Norwegian glacier forelands along an altitudinal gradient: patterns and models. *The Holocene* 25: 108-129.

Vilmundardóttir OK, Gísladóttir G and Lal R (2017) A chronosequence approach to estimate the regional soil organic stock on moraines of two glacial fore-fields in SE-Iceland. *Geografiska Annaler, Series A, Physical Geography* 99: 207-221.

Vogt JT (2007) Three-dimensional sampling method for characterizing ant mounds. *Florida Entomologist* 90: 553-558.

Walker LR, Wardle DA, Bardgett RD et al. (2010) The use of chronosequences in studies of ecological succession and soil development. *Journal of Ecology* 98: 725-736.

Weber NA (1935) The biology of the thatching ant *Formica rufa obscuripes* Forel, in North Dakota. *Ecological Monographs* 5: 165-206.

Wellenstein G (1952) Zur Ernahrungsbiologie der Roten Waldameise. *Zeitschrift für Pflanzenkrankheiten, Pflanzenpathologie und Pflanzenschutz* 59: 430-445.

Whittaker RJ (1993) Plant population patterns in a glacier foreland succession: pioneer herbs and later-colonizing shrubs. *Ecography* 16: 117-136.

Zahn M (1958) Temperatursinn, Wärmehaushalt und Bauweise der rotten Waldameise (*Formica rufa* L.). *Zoologische Beiträge* 3: 127-194.

FIGURE CAPTIONS

Figure 1. Location of the glacier forelands of Nigardsbreen, Bergsetbreen and Fåbergstølsbreen in southern Norway, and the areas shown in detail in Figs 2, 3 and 4, respectively. Note the Jostedalsbreen ice-cap (stipple shading), main settlements and roads, and the 500 m contour intervals.

Figure 2. Nigardsbreen glacier foreland showing the location of the ant nest mounds (numbered 1–100), glacier snout retreat positions since the Little Ice Age maximum in ~AD 1750, and altitude (20 m contour intervals).

Figure 3. Bergsetbreen glacier foreland showing the location of the ant nest mounds (numbered 1–35), glacier snout retreat positions since the Little Ice Age maximum in ~AD 1750, and altitude (20 m contour intervals). For key, see Fig. 2.

Figure 4. Fåbergstølsbreen glacier foreland showing the location of the ant nest mounds (numbered 1–18 on the north side of the foreland and 1-15 on the south side), glacier snout retreat positions since the Little Ice Age maximum in ~AD 1750, and altitude (20 m contour intervals). For key, see Fig. 2.

Figure 5. (A) Typical ant nest mound on the glacier foreland of Bergsetbreen (mound height ~30 cm, ground cover largely *Calluna vulgaris* and *Vaccinium myrtillus* with small *Betula pubescens* trees in the background); (B) ant nest mound on a low moraine ridge surrounded by shrubby *Betula pubescens* (Bergsetbreen in the background, water bottle is 15 cm high); (C) ant nest mound at Nigardsbreen on glaciofluvial outwash deposits with partial ground cover of *Calluna vulgaris* and, in the background, patchy *Betula pubescens* woodland and a solitary *Pinus sylvestris* tree (Note A4 sheet for scale to right of mound).

Figure 6. Ants herding aphids and aphid eggs on *Betula pubescens* at Fåbergstølsbreen glacier foreland.

Figure 7. Frequency histograms of mound size and surface characteristics, including all the mounds measured on the three glacier forelands: (A) mound height; (B) mound width; (C) mound volume; (D) sand % cover; (E) gravel % cover; (F). organic % cover.

Figure 8. Ant nest mounds of different sizes: (A) the smallest mound (height <10 cm) at Nigardsbreen surrounded by *Empetrum hermaphroditum* heath; (B) mound of intermediate size at Bergsetbreen surrounded by *Empetrum hermaphroditum* heath with individual poles of *Betula pubescens* and *Salix* sp.; (C) moderately large mound at Fåbergstølsbreen surrounded by *Vaccinium myrtillus* heath and scattered trees of *Betula pubescens*; (D) the largest mound (height 92 cm) at Fåbergstølsbreen in relatively dense *Betula pubescens* woodland outside the glacier foreland boundary. Note the water bottle is 25 cm high.

Figure 9. Selected statistically significant linear relationships between mound size and surface characteristics and terrain age ($p<0.05$): (A) sand % cover at Fåbergstølsbreen ($r = –0.53$, $n = 33$); (B) organic % cover at Bergsetbreen ($r = 0.36$, $n = 35$); (C) mound height at Nigardsbreen ($r = 0.27$, $n = 100$); (D) mound height at Fåbergstølsbreen ($r = 0.47$, $n = 33$). 95% confidence intervals are shown.

Figure 10. Non-metric multidimensional scaling and segmented bubble plots summarizing the interaction between mound characteristics, terrain age and environmental variables: (A) Nigardsbreen (stress = 7%); (B) Bergsetbreen (stress = 10%); and (C) Fåbergstølsbreen (stress = 8%). Six scaled mound size and surface composition characteristics are shown for each individual mound (see key). The length and direction of the vectors, which relate to both mound characteristics and environmental variables, indicate the strength and direction of their correlation with the axes defining the NMDS two-dimensional space. Extension of vectors to the full diameter of the circle, the position of which is arbitrary, would indicate perfect correlation. Note the ‘poles’ vector in (A) is too short to be seen.

Figure 11. (A) Boxplot of mound height in four habitat types (boxes define the interquartile range around the median; tails define the full range) based on the combined data set from the three glacier forelands; (B) Tukey simultaneous pairwise comparison of mound height in relation to the four habitat types using the same data set as in (A) – 95% confidence intervals are shown around the difference in means between each habitat pair (means are significantly different where corresponding confidence intervals do not contain zero); (C) boxplot of mound height where aphids are present or absent on trees within 5 m of the mound based on the combined data set from Nigardsbreen and Fåbergstølsbreen (aphids not

having been investigated at Bergsetbreen); (D) Tukey pairwise comparison of mound height where aphids are present or absent using the same data set as in (C).

Figure 12. Rose diagrams showing mound aspect on the three glacier forelands: (A) Nigardsbreen (n = 100 mounds); (B) Bergsetbreen (n = 35); and (C) Fåbergstølsbreen (n = 33). Percentage of mounds is shown in relation to 16 compass points; circles define 10% of mounds (labels highlight the aspects with >10% of mounds).

Figure 13. Surface composition of (A) a relatively young mound with prominent gravel cover and (B) a relatively old mound with ~100% organic cover, Bergsetbreen glacier foreland.

Figure 14. Conceptual model of the main geo-ecological processes (lower case lettering) affecting red wood ant populations on glacier forelands in southern Norway. Arrows indicate the direction of the main effects between compartments of the geo-ecosystem (upper case lettering in solid boxes). The dashed box encloses components of the internal environment of the nest mounds.

Table 1. Summary of the distribution and density of ant nest mounds on the three glacier forelands. 'Youngest terrain' refers to the most recently deglaciated terrain on which mounds occur.

Glacier foreland	No. of mounds	Area searched (m^2)	Density (No./hectare)	Youngest terrain (years)
Nigardsbreen	100	220,320	4.5	49
Bergsetbreen	35	74,440	4.6	83
Fåbergstølsbreen	33	127,800	2.5	78

Table 2. Summary of mound characteristics (size and surface composition) on the three glacier forelands (SD = standard deviation; * = evidence of bimodality).

	Mean	Max.	Min.	Mode	SD
***Nigardsbreen** (n = 100)*					
Height (cm)	42.0	100	10	30-35*	19.9
Width (cm)	78.0	137	23	65-70	23.1
Volume (m^3)	0.17	0.98	0.003	0-0.05	0.17
Organic (%)	85.2	100	15	95-100	19.8
Sand (%)	2.7	15	0	0-1	3.5
Gravel (%)	12.4	80	0	0-55	18.1
***Bergsetbreen** (n = 35)*					
Height (cm)	43.5	92	8	40-45	20.1
Width (cm)	81.2	121	17	70-80	26.4
Volume (m^3)	0.20	0.79	0.001	0-0.05	0.19
Organic (%)	82.7	100	25	95-100	18.7
Sand (%)	2.7	10	0	0-1	3.5
Gravel (%)	14.2	65	0	0-5	17.2
***Fåbergstølsbreen** (n = 33)*					
Height (cm)	48.2	95	18	50-55*	18.2
Width (cm)	86.2	160	43	80-90	23.6
Volume (m^3)	0.23	1.37	0.016	0.1-0.3	0.24
Organic (%)	88.4	100	47	95-100	13.48
Sand (%)	3.3	10	0	0-1	3.2
Gravel (%)	10.10	46	0	0-5	13.6

Table 3. Pearson correlation coefficients between mound characteristics and potential response variables from the three glacier forelands. Values in bold italics and underlined are statistically significant ($p<0.05$).

A. Nigardsbreen (n = 100)

	Height	Width	Volume	Sand	Gravel	Organic	Altitude	Age	Trees	Poles
Width	***0.698***									
Volume	***0.872***	***0.825***								
Sand	***-0.212***	-0.047	-0.119							
Gravel	***-0.295***	-0.083	***-0.239***	***0.536***						
Organic	***0.273***	0.039	***0.219***	***-0.617***	***-0.968***					
Altitude	***-0.243***	***-0.271***	***-0.237***	0.006	0.077	-0.027				
Age	***0.267***	***0.200***	***0.206***	-0.018	-0.063	0.026	***-0.890***			
Trees	***0.469***	***0.416***	***0.523***	-0.164	***-0.380***	***0.368***	-0.124	0.044		
Poles	-0.001	0.044	0.033	-0.051	0.002	0.034	***0.303***	***-0.346***	0.075	
Ground cover	0.161	0.101	0.155	***-0.294***	***-0.271***	***0.311***	-0.063	0.016	***0.303***	0.177

B. Bergsetbreen (n = 35)

	Height	Width	Volume	Sand	Gravel	Organic	Altitude	Age	Trees	Poles
Width	***0.749***									
Volume	***0.923***	***0.765***								
Sand	0.108	0.227	0.055							
Gravel	-0.217	-0.084	-0.192	0.300						
Organic	0.159	0.048	0.169	***-0.476***	***-0.963***					
Altitude	-0.028	-0.033	-0.188	***0.361***	0.125	-0.223				
Age	0.146	0.059	0.270	-0.287	-0.307	**0.355**	***-0.838***			
Trees	***0.609***	***0.417***	***0.619***	-0.157	-0.248	0.277	***-0.338***	***0.334***		
Poles	***0.383***	0.355	***0.434***	-0.152	-0.340	0.327	-0.353	***0.546***	0.355	
Ground cover	0.137	0.131	0.156	-0.170	-0.100	0.122	-0.115	0.283	0.081	0.125

C. Fåbergstølsbreen (n = 33)

	Height	Width	Volume	Sand	Gravel	Organic	Altitude	Age	Trees	Poles
Width	***0.529***									
Volume	***0.769***	***0.781***								
Sand	-0.265	-0.009	-0.251							
Gravel	-0.311	-0.189	-0.246	***0.566***						
Organic	0.268	0.105	0.239	***-0.793***	***-0.830***					
Altitude	***-0.459***	-0.175	***-0.368***	***0.537***	***0.388***	***-0.457***				
Age	***0.474***	0.193	***0.351***	***-0.534***	***-0.439***	***0.478***	***-0.821***			
Trees	0.025	0.053	0.014	-0.157	-0.063	0.274	-0.118	-0.127		
Poles	0.048	-0.060	0.036	-0.242	-0.120	0.110	-0.335	0.307	-0.288	
Ground cover	0.176	0.247	0.170	-0.285	-0.240	0.320	-0.285	0.230	0.089	***0.347***