

RESEARCH ARTICLE

Ant-hill heterogeneity and grassland management

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Abstract

1. In many grasslands, some ants act as ecological engineers to produce long-lasting soil structures which have a considerable influence on the patterns and dynamics of plant, vertebrate and invertebrate species. They promote species richness and diversity.

2. The yellow meadow ant, *Lasius flavus*, is the most abundant allogenic ecological engineer in grazed European grasslands, producing vegetated long-lasting mounds. It is so frequent and abundant that it must be regarded as a keystone species. Grassland restoration projects frequently attempt to re-introduce grasslands on abandoned arable fields. When this ant does not colonize naturally it should be introduced. It probably limits the abundance of grasses in a similar manner to hemi-parasitic plant species.

3. Ant-hills make a distinctive contribution to grassland heterogeneity. Measurements on mounds in a single grassland over 45 years document the dynamics of the same 200+ ant-hills in volume, surface area and basal area. As the mounds aged, they increased in size and took over a higher proportion of the grassland surface. Occupied mounds continued to grow, abandoned mounds decreased in volume and some disappeared entirely.

4. Four plant species favoured by the soil heaped by the ants were also monitored. Two woody perennials grew up through heaped soil and two short-lived species colonized its surface. As the mounds became occupied, some of these species significantly increased, and when they were abandoned some decreased.

5. In a grassland, the ant-hill population provides a fluctuating subset of plant and animal species which are characteristic of temporary habitats. This seems likely to reduce the rate of local extinctions which might otherwise result from fluctuations in grazing pressure. In conservation settings, ant-hills should be introduced or maintained where possible, and considered in planning grassland maintenance and management.

KEYWORDSant-hills, ecological engineers, grasslands, *Lasius flavus*, restoration, resilience, spatial variability, species richness

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1 | INTRODUCTION

Grasslands cover about 2 million km² of the planet's surface. Many support ant-hills and termite mounds on a grand scale (Martin, Funch, Hanson, & Yoo, 2018; Tarnita et al., 2017; Wells, Sheail, Ball, & Ward, 1976). Whether created from heaped soil or carton, these considerably increase environmental heterogeneity. They often offer bare soil, hotspots, feeding stations for vertebrates and provide microhabitats for many plant and invertebrate species. They sometimes have a major effect on vegetation patterns (e.g. King, 1977a; Okullo & Moes, 2012; Schutz, Kretz, Dekoninck, Iravani, & Risch, 2008; Wills & Landis, 2018).

Some ant species, such as *Lasius flavus* (F.) in grasslands, produce long-lasting mounds which harbour a distinct flora and animal life. They frequently increase the species richness of the habitat, both on the mounds and between them. Their presence is important in the conservation of old grasslands and the creation of new ones (Jouquet, Dauber, Lagerhof, Lavelle, & Lepage, 2006; King, 2006). Their maintenance and long-term survival need to be carefully considered as an integral component of management plans, because they increase the range of micro-environments and may contribute to the ability of the grassland to withstand perturbations.

The yellow meadow ant, *L. flavus*, is the most important allogenic ecological engineer (sensu Jones, Lawton, & Shachak, 1994), apart from *Homo sapiens*, over much of its range, which stretches within the Palaearctic to northern Spain, and across most of Europe to China. Its mounds are the most abundant and persistent of all the extended phenotype structures created by organisms in the northern hemisphere. In grazed grasslands this species can reach a higher fresh mass than any other ant species, 165 kg/ha, and shift up to 7 tonnes of mineral soil/ha/yr (Seifert, 2018). Its mounds sometimes cover over 20% of the ground area (Bushy Park SSSI. London, UK NGR TQ 154 708, grassland 519 years old, 26.33%, unpublished data) and contribute annually most of the bare soil within a grassland habitat. Despite this subterranean ant's reluctance to enter pitfall traps (Fagan, Pywell, Bullock, & Marrs, 2008a), it is likely to greatly outnumber other ant species in most European pastures.

Its mounds certainly have a profound effect on the distribution patterns of plant species (e.g. Kay & Woodell, 1976; Grubb, Green & Merrifield, 1969; Dean, Milton, & Klotz, 1997; King, 1977a, 1977b, 1977c, 1981a, 2006, 2020; Kovar, Kovarova, Dostal, & Herben, 2001; Smith, 1980; Wells et al., 1976; Woodell & King, 1991; Platner, 2006; Streitberger, Schmidt, & Fartmann, 2017; Veen, Geuverink, & Olf, 2012). They increase the range of insolation, soil temperature and moisture for mammals, birds, the soil mesofauna and many invertebrates which have the early stages of their life cycles in the soil (Haarlov, 1960; King, 2006, 2020). Ant-hills built by *L. flavus* display a variety of aspects, patches of bare soil ripe for colonization, and dryer soil with a lower content of organic matter, lower bulk density and altered level of mineral nutrients. They provide distinct island microhabitats, supporting small-scale meta-populations of plant species and invertebrates which would otherwise become locally extinct (King, 2006, 2020). They impart distinctive qualities to grasslands, providing 'alternative stable

states' to grassland soils, fauna and vegetation (Beisner, Haydon, & Cuddington, 2003). The diversity of sizes, shapes and activities within an ant-hill population also contribute to heterogeneity, species richness and alpha diversity. This depends particularly on the grassland's grazing history. Although many static measurements have been published, the ways in which populations of ant-hills are born, grow and die have only sketchily been investigated (Ehrle et al., 2017, King, 2020; Nielsen, 1992; Nielsen, Skyberg, & Winther, 1976; Waloff & Blackith, 1962). The implications of the presence of ant-hills for identifying ancient sites likely to be species-rich, and for grassland management, should also be taken into account in conservation practice.

This study encompasses 45 years on the same site, illuminates the fates of the ant-hills and discusses the relevance of ant-hills to grassland conservation. This ant species may be a useful tool in the restoration of typical species-rich grasslands. It tests the hypotheses that

1. as an ant-hill population grows, the mounds come to play an increasingly important role in the grassland, covering a higher proportion of its area,
2. the abandonment of ant-hills and their recolonization may play a significant role in the dynamics of grassland plants. The characteristic ant-hill species should expand when soil heaping by ants occurs and contract after ant colonies abandon a mound.

Four plant species were recorded on each ant-hill as indicators of soil heaping activity by the ants. The dwarf shrubs *Thymus drucei* (= *T. polytrichus* = *T. praecox*) and *Helianthemum nummularium* are characteristic ant-hill species which respond to soil heaping by repeatedly branching and growing through the heaped soil (King, 1977c). The winter annual *Arenaria serpyllifolia* and the paucennial *Cerastium fontanum* are largely restricted to ant-hills in continuous calcareous grassland (Dostal, 2007, King, 1977a).

2 | MATERIALS AND METHODS

The progress of a single ant-hill population was measured by the same observer in 1970, 2007 and 2015 in the same calcareous grassland at Beacon Hill, Aston Rowant National Nature Reserve (UK NGR SU727972, 230–244 m altitude) at which the vegetation on the ant-hills has been investigated (e.g. King, 1977a, 1977b, 1977c, 2007). This plot (Figure 1) is described in detail in King (1977b). It was last ploughed about 1904, although it was a rabbit farm from 1935–1954 (local farmer, personal communication, 2009). The size of every fifth ant-hill in the northern-eastern half of this field, a total of 206, was measured in 1969. In 2007, the 333 ant-hills in 800 m² of this area were all mapped and their volumes estimated. The same area was sampled once more in 2015, when each individual ant-hill mapped in 2007 was measured again, without reference to the 2007 data.

On each ant-hill, two measurements were recorded of its horizontal diameter and four of its height according to established methodology (King, 1977b, 1981a). To calculate volumes and surface areas, ant-hills were regarded as spherical caps. If the average radius of the base of the cap is a centimetre, and its average height is h cm, then the volume



FIGURE 1 The sampled site at Aston Rowant NNR, Oxfordshire (April 2015). This grassland was intensively sheep-grazed at 8 sheep per hectare during winter every 3 years. Photograph Courtesy Robert Barber

of the ant-hill is $\pi h (3a^2 + h^2)/6000$ L, and its surface area is $\pi(a^2 + h^2)/10000$ m². The percentage cover of bare soil was estimated by eye. The presence or otherwise of a *L. flavus* colony within the mound was recorded on each occasion. In fewer than 3% of cases, some individuals of *Lasius niger* or *Myrmica* spp. were present.

The percentage cover of *Thymus drucei* and *Helianthemum chamaecistus* was recorded by eye and the numbers of flowers of *Arenaria serpyllifolia* and *Cerastium fontanum* were counted. The calculated surface areas of each mound allowed the areas of bare soil, *T. drucei* and *H. chamaecistus* to be estimated. The non-parametric Wilcoxon signed-ranks test for matched pairs (Sokal & Rohlf, 2012) was used to compare the 2007 and 2015 data for the same ant-hills because the underlying distribution pattern of the data was sometimes difficult to transform to normality. Plant nomenclature follows Stace (2019).

3 | RESULTS

The ant-hill volumes on the Aston Rowant plot averaged 14.6 L in 1970, 24.21 L in 2007 (95% confidence limits [21.99–26.62]) and 31.05 L in 2015 (95% confidence limits [28.03–34.36]). The proportion of ant-hills > 70 L in volume increased from 0% (1969) to 7.6% (2007) to 15.9% (2015). The proportion < 10 L in volume decreased from 52.4% (1970) to 18.6% (2007) to 14.6% (2015).

The basal areas of all the ant-hills covered 5.6% of the plot in 1970, 11.52% in 2007 and 11.74% in 2015. The basal areas in 1970 and 2007 were significantly different by a Wilcoxon two-sample test ($p < 0.001$), but not significantly different between 2007 and 2015 by a Wilcoxon test for matched pairs (Sokal & Rolf, 2012). The ant-hill surfaces made up 7.59% of the total surface of the plot in 1970, 15.4% in 2007 and 17.01% in 2015. The ant-hill surface areas in 1970 and 2007 were significantly different by a Wilcoxon two-sample test ($p < 0.001$) and sig-

nificantly higher in 2015 than 2007 ($p < 0.001$) by a Wilcoxon test for matched pairs.

In 1970, the distribution of ant-hill volumes on a logarithmic scale appears bimodal (Figure 2), suggesting two major episodes of establishment followed by variable rates of volume increase. Kolmogorov–Smirnov and G-tests confirmed that the pattern is consistent with two overlapping log-normal distributions, one of 141 mounds with a mean of 12.06 L (95% confidence limits 10.9–14.5 L) and the other with a mean of 1.28 L (95% confidence limits 1.01–1.61 L). In 1970 *Thymus drucei* and *Helianthemum nummularium* were both significantly more abundant on the ant-hill surfaces than in the grassland ($p < 0.001$). *T. drucei* had a mean cover of 13.9% on ant-hills and 2.4% in the surrounding grassland, and *H. nummularium* had covers of 13.5% on the mounds and 5.2% in the grassland. *Arenaria serpyllifolia* occurred on five ant-hills, and *Cerastium fontanum* on 11, out of 206 sampled.

In 2007 and 2015, the frequency distribution of ant-hill volumes was close to being log-normal (Figure 2). However, the probability that it was log-normal by Kolmogorov–Smirnov and G-tests was about 5%. This was because of the heterogeneity of ant-hills by then; some had become abandoned, some abandoned and recolonized by new colonies, and some new colonies had become established in the grassland.

Between 2007 and 2015, the changes in mound volume, surface area and bare soil seemed to depend on occupancy (Table 1). Whether occupied or abandoned in 2007, by 2015 the occupied ant-hills had increased significantly in volume, surface area and bare soil. On the other hand, whether occupied or abandoned in 2007, by 2015 the abandoned mounds had significantly decreased in volume, surface area and bare soil. Of course the occupation and abandonment between 2007 and 2015 could have taken place in any of the intervening years.

The abundances of four plant species characteristic of ant-hills were also estimated. The dwarf shrubs *Thymus drucei* and *Helianthemum nummularium* sometimes dominate the whole mound surfaces, whereas the short-lived species *Cerastium fontanum* and the winter annual *Arenaria serpyllifolia* colonize bare soil (King, 1977c). Between 2007 and 2015, the area of *T. drucei* decreased significantly on abandoned mounds, but so did the surface area of the mounds themselves. *H. nummularium* increased significantly on continuously occupied ant-hills, more markedly than the significant increase in ant-hill surface area. Between 2007 and 2015, the area of bare soil on occupied mounds increased, and on abandoned mounds decreased. Despite the relatively unpredictable population fluctuations of the annuals, the significant increase in *C. fontanum* on continuously occupied mounds, and the significant decrease of *A. serpyllifolia* on occupied mounds which were later abandoned, were expected.

Eight mounds disappeared altogether between 2007 and 2015, indicating that they had been incorporated in the ‘grassland’. In addition, nine new ant-hills which were not present in 2007 had appeared by 2015.

By 2015, the surface area of the ant-hills was 18.1% of the surface area of the 800 m² plot. The total bare soil on their surfaces had been estimated at 11.1 m² in 2007, but by 2015, it was 21.5 m², 2.7% of the area of the plot.

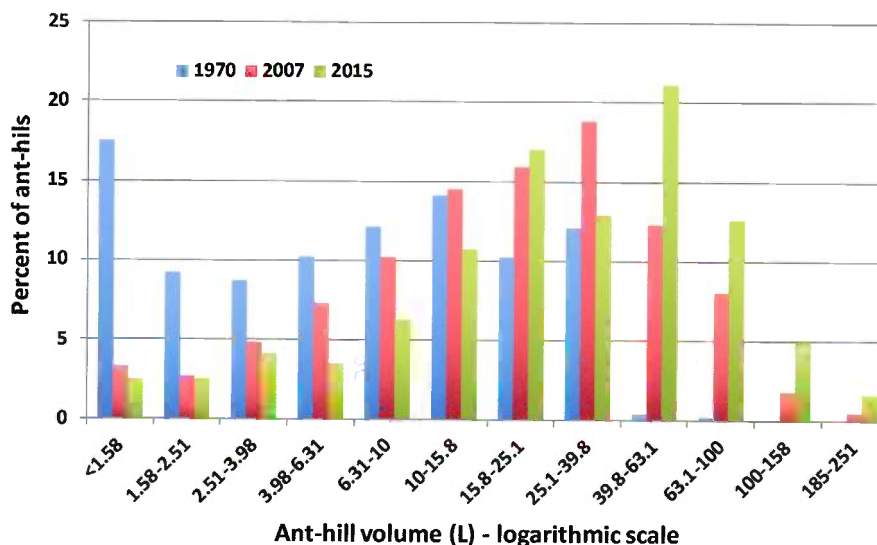


FIGURE 2 Beacon Hill, Aston Rowant. Frequency distribution of ant-hill volumes, both occupied and abandoned, in 1970, 2007 and 2015

TABLE 1 Comparison of the 327 ant-hills sampled in both 2007 and 2015. Significant differences are in bold. NS = $p > 0.05$

Variable	Year Probability	Occupied to occupied (n = 228)	Occupied to abandoned (n = 28)	Abandoned to abandoned (n = 53)	Abandoned to occupied (n = 18)
Mean mound volume (L)	2007	38.4	30.6	17.4	16.8
	2015	52.5	23.3	12.6	25.0
	P	< 0.001	< 0.01	< 0.001	< 0.005
Mean mound surface area (cm ²)	2007	4396	3807	2471	2544
	2015	5257	3107	1932	3306
	P	< 0.001	< 0.01	< 0.001	< 0.005
Mean mound basal area (cm ²)	2007	3136	2735	1904	1636
	2015	3403	2104	1423	1627
	P	< 0.001	< 0.01	< 0.001	NS
Mean area bare soil per mound (cm ²)	2007	57.1	236.8	31.2	21.0
	2015	88.2	104.1	27.7	496
	P	< 0.001	< 0.01	NS	< 0.001
Mean cover per mound <i>Thymus drucei</i> (cm ²)	2007	595	335	96.9	191
	2015	330	171	61.4	175.5
	P	NS	0.05	< 0.03	NS
Mean cover per mound <i>Helanthenum nummularium</i> (cm ²)	2007	781	369	203	473
	2015	1327	329	261	788
	P	< 0.001	NS	NS	< 0.02
Mean flowers <i>Arenaria serpyllifolia</i> per mound (cm ²)	2007	34.2	17.6	0.1	0
	2015	45.3	0.1	0	5.1
	P	NS	< 0.01	NS	NS
Mean flowers <i>Cerastium fontanum</i> per mound	2007	1.6	1.1	0.2	0.7
	2015	36.0	1.0	0	2.8
	P	< 0.001	NS	NS	NS

4 | DISCUSSION

Since, in many grasslands over such a wide geographical area, *L. flavus* ant-hills make a major contribution to plant and animal species richness, this study of the dynamics of an ant-hill population has

considerable implications for the conservation of existing grasslands and the establishment of new ones.

Some ant-hills probably continue to increase in volume over ten or hundreds of years (King, 1981a). Particular ant-hills have been followed over 62 years (King, 2020). In this study, as the ant-hill

population developed, the mounds increased significantly in volume and surface area between 1970 and 2007, and between 2007 and 2015. They also (Hypothesis 1) increased significantly ($p < 0.001$) in basal area between 1970 and 2007, but not between 2007 and 2015. In 1970, their curved surfaces covered 7.59% of the plot. On the plot of 800 m², the curved ant-hill surfaces covered 128.8 m² (16.1%) in 2007 and 144.8 m² (18.01%) in 2015. Ultimately, once the habitat becomes saturated with ant colonies, the area of ant-hills should stabilize (Steinmeyer, Pennings, & Foltz, 2012). So Hypothesis 1 was largely supported statistically, with the caveat that by 2015 expansion sideways seemed to have been sacrificed to expansion upwards.

Between 2007 and 2015, the ant-hill population was unexpectedly dynamic. Continuously-occupied ant-hills increased by 37% in volume (Table 1), but some ant-hills were abandoned (Table 1). The majority of ant-hills abandoned in 2007 were still unoccupied in 2015, but 25% had been recolonized. Some disappeared entirely, being incorporated into the grassland, but others became established.

The four indicator plant species responded as expected to the presence or absence of heaped soil (Hypothesis 2), on 15 of the 16 cases, although only six of the changes achieved statistical significance ($p < 0.05$). The importance of bare soil for the expansion of these species was investigated experimentally by King (1975, 1977c). The results were consistent with the concept that those dwarf shrubs and short-lived species which are much more abundant on ant-hills than in the surrounding pasture will increase when the ant-hills are occupied by *L. flavus* and decrease when they are abandoned.

It is reasonable to expect that as occupied ant-hills expand in volume and take over an increasing proportion of the grassland area, their populations of other distinctive plants and animal species will increase. Occupied ant-hills tend to be the only grassland sites for winter annuals (Grubb, 1976; Dostal, 2007; King, 1975, 1977a) and acrocarpous bryophytes (King, 1981a, 2020) particularly on their south-facing slopes (Streitberger et al., 2017), with pleurocarpous bryophytes on the north (King, 1981b, 2003; Streitberger et al., 2017). Once they are abandoned, grasses, rhizomatous and rosette species invade from the surrounding grassland in concentric zones. The relative abundances of the species on their surfaces change to resemble that of the surrounding grassland (Dostal, Breznova, Kozlickova, Herben, & Kovar, 2005; King, 1977b; Woodell & King, 1991).

The bare soil on ant-hills (2.7% of the ground area in 2015 in the current study), annually replenished, would not otherwise exist on this scale. The bare soil provides oviposition sites for grasshoppers, butterflies and moths (King, 2006, Richards & Waloff, 1954, Streitberger & Fartmann, 2016). Many other invertebrates (listed in King, 2020) are confined to ant-hills or owe their presence in the grassland to the ants. The ants provide important winter food for green woodpeckers (*Picus viridis*) (e.g. Alder & Marsden, 2010).

Furthermore, differences between ant-hill soils and the surrounding soils increase with increasing ant-hill volume (Ehrle et al., 2017). As the mounds grow, their north and south-facing aspects constitute an increasing proportion of the grassland area. Significant ($p < 0.05$) differences in their soils from the surrounding grassland are well-documented. For example, their soils have a lower bulk density (in

occupied mounds), a lower water content, less organic matter, less total carbon, a higher pH, a greater cation exchange capacity and more exchangeable nitrate, potassium and phosphate ions (e.g. Blomqvist, Olf, Blaauw, Bongers, & van der Putten, 2000; Boots et al., 2012; Dostal et al., 2005; Ehrle et al., 2017). They also differ from the surrounding grassland in their microflora and nematodes (Blomqvist et al., 2000; Boots et al., 2012).

These long-term data from Beacon Hill, Aston Rowant suggests that the mounds, once built, exist as distinct structures which go through phases of abandonment and recolonization (Hypothesis 2) This is to be expected in view of the limited longevity of fertilized queens, and the presence of bare soil on top of the mounds into which newly-fertilized queens can burrow after the nuptial flight (Boomsma, Wright, & Brouwer, 1993). At least in captivity, existing colonies can accept additional queens (Waloff, 1957). Some established mounds have secondary summits, reflecting perhaps two or three successful invasions.

On abandoned ant-hills the vegetation closes over the bare soil and the species composition ultimately resembles that of the surrounding grassland (King, 1977b). Abandoned ant-hills may therefore become less suitable for recolonization with time. These Aston Rowant data illustrate that they may also decline in volume. Ant-hills containing vigorous colonies have a soil bulk density < 0.8 times that of the soil beneath the surrounding grassland (Dostal et al., 2005; Haarlov, 1960; Wells et al., 1976). When an ant-hill is abandoned, its chambers and channels cease to be excavated by the ant-colony and erosion exceeds growth. In abandoned ant-hills, characteristic root aphids and inquilines (King, 2020) should be lacking, soil organic matter, bulk density and the sizes of structural aggregates increase, and exchangeable cations such as K⁺ are lower, than in active mounds (Dostal et al., 2005). Ultimately, the soil may be eroded so much that ant-hills disappear.

These data confirm that there is considerable heterogeneity amongst an ant-hill population. Many mounds may be occupied by colonies, but others will be in various stages of abandonment.

Ultimately, when the ant-hills become large, their summits expand and become closer together, allowing optimal dispersal of the characteristic plant and animal species which form metapopulations on their surfaces. The presence of ant-hills ensures that a site maintains a wider range of plant and animal species than if they are absent (Jouquet et al., 2006).

4.1 | Established ant-hill populations

Because of the striking mounds it builds, the 'antscape' erected by *L. flavus* needs to be considered alongside the grazing regime in the conservation of grazed pastures. As the influence of the ant-colonies increases as the underground territories saturate the grassland, *L. flavus* becomes a keystone species (Platner, 2006). The recent large-scale expansion of abandoned pastures in central Germany (Poschlod & WallisDeVries, 2002) has been accompanied by a wholesale invasion of *L. flavus* colonies (Streitberger et al., 2017). They used to be characteristic of British grazed grasslands before they were eliminated from pastures in the 'improvements' between 1780 and 1820. The comment

by Pitt (1809) is typical: 'ant-hills occupy a large proportion of the grazing land of this county, in some of which ant-hills are so abundant, that it is possible to walk over many acres, step by step, from one ant-hill to another, without coming upon the level ground ...'

The ant-hills on this site have been growing for at least 70 years. Sites with large ant-hills are likely to be old grasslands which have accumulated more species (Fagan, Pywell, Bullock, & Marrs, 2008b; Gibson, 2010; Gibson & Brown, 1991; Karlik & Poschlod, 2019; Poschlod & WallisDeVries, 2002; Wagner et al., 2019). Similar ant-hills are prominent features in many sand dunes, salt marshes where the ants can withstand periodic inundation by sea water, freshwater marshes, mountain pastures and acidic grasslands. In many of these areas, they cover 10–20% of the surface, and the dynamic heterogeneity created by the variation in their sizes, aspects, bare soil, degree of abandonment and nutrient accumulation contributes to the range of micro-habitats available for both plants and animals.

Old, well managed, calcareous grasslands are prized and in general, older mature grasslands support more species-rich vegetation and fauna (Gibson, 2010). In some places, this may be partly because the ant-hills are larger and contribute more environmental heterogeneity, as the data in the current paper suggests.

They appear particularly resistant to erosion by normal densities of sheep, cattle deer and rabbits. The number of established colonies stabilizes, as the available territory space becomes fully utilized. Just a few mounds continue to grow rapidly; on the Porton Ranges, the largest ant-hills probably grew at about a litre a year in volume (King, 1981a).

The extent of the influence of the underground *L. flavus* workers on the flora between the mounds, its energy flow and nutrient cycling, is unknown but is likely to be considerable (Bardgett & Wardle, 2014). Where the density of *L. flavus* colonies is considerable and the mounds have been established for some time so that the worker populations in the mounds are high, it is even possible that the ants compete effectively with mammalian grazers for plant net photosynthate. After all, the aphid populations on which they rely are clumped on grass roots between the mounds (Ivens, Kronauer, Pen, Weissing, & Boomsma, 2012; Langley, 1986; Pontin, 1978). They may limit grass growth between the mounds in a similar manner to yellow rattle, *Rhinanthus minor*, frequently sown in the early stages of grassland restoration to limit grass growth and increase the successful establishment of herbs (Pywell et al., 2004).

4.2 | Ant-hill establishment in restored pastures

It is therefore desirable that grasslands restored from arable should accumulate ant-hills as soon as possible. A dynamic ant-hill population is worth establishing and managing in an active state for its positive influence on the species richness of the grassland. The invasion or re-invasion of many plant species to an isolated reserve or reversion locations may depend on the vagaries of chance dispersal by human agency (Fagan et al., 2008b; Gibson, 1986, 2010). Now that suitable donor sites are rarer in the landscape (Ridding, Redhead, & Pywell, 2015), it is much less likely that desirable plant species reach isolated

sites, unless sheep are introduced from elsewhere with suitable seeds in their fleeces (Manzano & Malo, 2006; Fischer, Poschlod, & Beinlich, 1996). A study on habitat fragments in Sweden suggested that ants are better dispersed than plant species (Dauber, Bengtsson, & Lenoir, 2006). It is likely that a grazed arable reversion site will accumulate root aphids and *L. flavus* colonies without help. Vigorous *L. flavus* colonies produce up to 410 queens a year (Pontin, 1963) dispersed over the local landscape for perhaps up to 5 km. Some specialist root aphids 'farmed' by *L. flavus*, such as *Anoecia corni* and *Tetraneura ulmi*, have winged morphs in their life cycles (Langley, 1986).

These ants sometimes invade early in grassland establishment (Woodell & King, 1991). In Dutch sand dunes and grasslands reverted from arable in Central Germany, *L. flavus* colonies begin to predominate amongst ant colonies in pastures more than 10–28 years old (Boomsma & van Loon 1982; Dauber & Wolters, 2005). The successful invasion and establishment of *L. flavus* probably depends to some extent on the prior colonization of the root aphids on which this species largely feeds (Pontin, 1978; Seifert, 2018). Once ant-hills become established they are likely to persist for at least as long as grazing continues, reducing grass growth and representing a continual source of environmental heterogeneity and bare soil.

If newer grasslands are far from source populations, existing ant-hills may have to be imported to establish this ant in the pasture, for example by the mechanical transfer method suggested by King and Balfour (2020), which is likely to introduce their myrmecophilous aphids at the same time. This technique seems more likely to succeed in establishing some species than artificial methods to create microtopographical heterogeneity (Wagner et al., 2016). Several plant species characteristic of mature calcareous grassland (Wagner et al., 2019) have ant-hill affinity indices over 60% (King, 1977a; Streitberger et al., 2017): *Trisetum flavescens*, *Galium verum*, *Thymus drucei*, *Scabiosa columbaria*, *Asperula cynanchica*, *Campanula rotundifolia* and *Helianthemum nummularium*. Establishing ant-hills could not only introduce these species, but winter annuals and essential myrmecophilous aphids, at an earlier stage than otherwise.

4.3 | Conservation relevance of *L. flavus*

It is well known amongst reserve managers that in spring ant-hill vegetation becomes green before the surrounding grassland, providing an early 'bite' for cattle, deer or sheep. Experimental evidence for the grazing preference of European brown hares (*Lepus europaeus*) and cattle for ant-hills comes from a salt marsh off the Dutch coast (Veen et al., 2012) and China, where cattle (*Bos taurus*) preferred grazing on incipient *L. flavus* mounds instead of equivalent areas from which the ants had been removed (Li et al., 2018). A high grazing intensity by cattle or sheep during the initial establishment of new grassland is likely to reduce the rate at which vigorous ant-hills appear. Wright (1990) recommends that a sheep grazing intensity of 500–700 sheep grazing days year⁻¹ hectare⁻¹ is likely to achieve the optimal balance between vegetation height and ant-hill establishment.

In mown pastures, *L. flavus* ant-hills do not establish and increase in size. Once they reach a certain size in a grazed pasture, mowing becomes impossible, so that scything or clipping on and around the ant-hills, with removal of the clippings, is necessary to maintain the characteristic grassland species composition and prevent the establishment of tall grassland.

L. flavus appears likely to provide 'resilience' (Isaac et al., 2018) to maintain animal and plant species characteristic of the surrounding grassland during periods when grazing is relaxed and the taller vegetation eliminates species from the surrounding grassland. The lack of regular grazing is important in places which are in rotational systems to promote the survival of arthropods characteristic of tall grasslands (Morris, 2000). It may, however, increase the abundance of tall grasses, such as *Brachypodium rupestre*, *B. pinnatum*, *Dactylis glomerata*, *Bromopsis erecta* (Hawes, 2015) or *Molinia caerulea*, at the expense of low-growing forbs. This is the main risk to a flourishing ant-hill population. These grass species, especially if allowed to fruit, can invade the mounds, spread rhizomatously, eliminate lower-growing species, and shade out the ant colonies. This reduces the value of the high temperature sites and ant-hill bare soil which seem so valuable for the oviposition of insects such as grasshoppers (Richards & Waloff, 1954) and certain butterflies, reducing environmental heterogeneity. These grasses colonize the ant-hills more slowly than the surrounding pasture. When shaded, the ants heap bare soil more rapidly (as confirmed experimentally by Blomqvist et al., 2000). If grazing resumes in time, for example because of the resumption of a rotational or 'mob' grazing scheme, ant-hills are likely to act as sources of those low-growing grassland species which have been largely eliminated from the pasture. Once regular grazing resumes, many plant species surviving on the tops of ant-hills are likely to recolonize the grassland between them.

Despite the high proportion of the grassland surface covered by these ant-hills in many National Nature Reserves, Sites of Special Scientific interest and local Nature Reserves in Britain, they are frequently ignored in management plans, despite their distinctive contribution to grassland ecology. The data in this paper from Aston Rowant about their heterogeneity, fluctuations in size and dynamics of their vegetation over 45 years suggest that they add an additional dimension to conservation, and that their importance increases with time.

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DATA AVAILABILITY STATEMENT

The ant-hill measurements and calculations are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.fqz612jrm> (King, 2020).

PEER REVIEW

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