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The Life and Death of Barn Beetles: Faunas from Manure and Stored Hay inside Farm Buildings in Northern Iceland

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Abstract:

1. Subfossil beetle remains from archaeological sites have proven invaluable for examining past living conditions, human activities and their impacts on landscapes and ecosystems.

2. In Iceland, specific economic practices (e.g. land management, natural resource exploitation) and major historical events (i.e. colonisation, economic intensification and commercialisation, urbanisation) have affected local environments and left recognisable traces in the beetle subfossil record.

3. Understanding the ecology of synanthropic beetles is crucial if they are to be employed in high-resolution reconstructions of past lifeways and their ecological impacts, yet, because buildings' interiors are rarely the object of systematic entomological research, the ecological requirements of many such species are poorly understood.

4. We conducted a survey of live and dead beetle faunas from habitats that have so far been largely neglected by entomological research: stable manure and stored hay inside farm buildings, two key facets of a northern European pastoral economy.

5. Our results clarify the ecological requirements of some under-studied synanthropic beetles and the processes by which their exoskeletons may become incorporated into the archaeological record, while also producing new records of exotic species recently introduced to Iceland.

6. This paper provides crucial guidance for the interpretation of archaeological beetle assemblages and highlights the potential of further investigations of indoor insect faunas for clarifying the causes, processes and ecological impacts of recent bio-invasions.

Keywords:

Synanthropic beetles, archaeoentomology, buildings' interiors, stable manure, stored hay, land management practices

1. Introduction

Beetles are common in archaeological sites and as a result of their very specific habitat requirements they offer a powerful means to reconstruct human activity and environmental changes over multi-century timescales (Elias, 2010). Thanks to a growing number of beetle subfossil studies in Europe and Scandinavia (Buckland & Buckland, 2006), and also increasingly from North America (e.g. Bain, 2001; Forbes *et al*., 2015), the Near East (e.g. Panagiotakopulu, 2001) and Eurasia (e.g. Obata *et al*., 2011; Reilly, 2012), we now have an appreciation of what conditions were like in ancient dwellings and food stores and we can better recognise activities such as manuring, leather production, trade and natural resource harvesting in the archaeological record. Importantly, the recovery of ancient remains of arthropod vectors of disease and stored good pests has also begun to clarify the biogeographical histories of harmful insects that were dispersed around the world as a result of human migrations and global trade (Forbes *et al*., 2013; King *et al*., 2014; Panagiotakopulu, 2004, 2014; Smith & Kenward, 2011), as well as the impact of these long-distance exchanges on local ecosystems (e.g. Bain & King, 2011; Panagiotakopulu, 2014; Whitehouse & Smith, 2010).

In Iceland – where archaeology provides a record of more than a thousand years of human-environment interactions – climatic, environmental, economic and political changes have shaped the island's biodiversity (Dugmore *et al*., 2005; Sadler & Skidmore, 1995). Major events of Icelandic history reflect key steps in the extension of a capitalist world system into the North Atlantic and the development of the European global hegemony (Wallerstein, 1974). These events include colonisation and the creation of a pastoral farming system based on introduced European domesticated species, the development of bulk commodities (wool and dried fish), economic intensification, gradual globalisation of commerce, and urbanisation. These developments produced ecological impacts that are visible in the Icelandic beetle fossil record as species' introductions, extirpations and range alterations (Buckland *et al*., 1991b; Forbes, 2013; Forbes *et al*., 2014; Vickers *et al*., 2011). On a smaller scale, beetle remains in old floor layers from turf buildings have revealed very detailed insights as to how both ordinary people and the elites lived through these major historical developments. For example, beetles are proxy indicators for grain imported from abroad and reveal details about the use of stable manure and domestic debris from buildings as fertiliser (Buckland *et al*., 1991a; 1992; Forbes *et al*., 2010; Forbes & Milek, 2014). Recent changes in the species make-up and structure of beetle communities in stored hay also reflect 19-20th-century developments such as the draining and re-seeding of hayfields (Buckland *et al*., 1991b; Forbes, 2013). These aspects of land management matter as they represent the potential to mitigate the impacts of climate change through local adaptation, in this case boosting yields compromised by a reduced growing season.

Archaeoentomology (the analysis of insect remains from archaeological sites) uses species' known ecological requirements to reconstruct past environments and infer human activity. The accuracy and precision of interpretations based on beetle subfossil assemblages are therefore to a large extent dependent on our understanding of the ecological requirements of modern species. However, thirty years of archaeoentomological research have shown that there are no direct modern parallels for beetle communities that lived in organic materials inside buildings that pre-date the modern world (i.e. prior to c. 1950 in Iceland), mostly due to changes in microhabitat availability and recent species introductions (Buckland *et al*., 1991b; Kenward & Allison, 1994; Smith, 2012). The complexity of archaeoentomological assemblage poses additional challenges to archaeoentomological interpretation. They typically include an autochthonous (originating from the sampled deposit) as well as an allochthonous (transported or 'background') component (Kenward, 1975; 1978) that need to be differentiated for the insect evidence to be correctly interpreted. To overcome these problems, studies of modern 'death assemblages' (groups of organisms that were not necessarily associated during their lives but were recovered together after death) have been compared to archaeological faunas (e.g. Hellqvist, 2004; Kenward *et al*., 2012; Osborne, 1983; Smith, 1996a; 1996b; 1998; 2000; Smith *et al*., 2005). In addition, multivariate statistics have been used to define 'indicator groups' of taxa on the basis of their recurrent associations in the archaeological record (Carrott & Kenward, 2001; Kenward & Carrott, 2006; Smith, 2012). These developments have refined archaeoentomological methods and allowed for a better identification of the nature of archaeological deposits, but as they have focused on species associations within death assemblages, they do not necessarily clarify the habitat requirements of living species.

In order to better understand insect species' ecological requirements, it may be better to focus on live faunas, as the materials and conditions with which they interact are readily measurable, unaltered by taphonomic processes or decay. Archaeoentomologists have often undertaken surveys of live beetles (e.g. Panagiotakopulu & Buchan, 2015), but seldom included detailed habitat descriptions and/or examined indoor communities. Specific work is necessary in the particular case of Iceland because at such high latitudes, some species may be more dependent on artificial habitats than they are in the more southern part of their range (e.g. in the British Isles). A few Icelandic barns and byres have been examined for their modern beetle faunas (in Eyjafjallasveit in the south and Reykir in the north – see Buckland *et al*., 1991b; Sadler & Dugmore, 1995), but more precise habitat descriptions are needed to clarify the range of conditions and materials required by particular species.

This paper presents a survey of live and dead beetles from farm buildings in northern Iceland. Our aims are (1) to refine our understanding of the ecological requirements of synanthropic beetle species that exploit indoor microhabitats such as stored hay and manure and (2) to examine the taphonomic processes affecting these beetles as they die and become incorporated (or not) into the archaeological record.

2. Materials and methods

2.1 Field methods

As the purpose of this study was to collect new contemporary beetle records and associated habitat data for archaeological interpretations, pitfall trapping and hand collecting from screened hay were the key methods employed. Various factors (e.g. population size, weather, trap spacing, habitat structure) are known to influence pitfall trap catches (Luff, 1975; Melbourne, 1999; Spence & Niemelä, 1994; Ward *et al*., 2001), but the method is useful for community richness and habitat assessments and has the advantage of being cheap and simple to operate (Southwood & Henderson, 2000). Seven different farm buildings used for housing animals and storing hay were selected for this study, primarily because of their accessibility and proximity to archaeological sites examined for insect remains (e.g. Forbes, 2013; Forbes & Milek, 2014; Forbes *et al*., 2010). The location of the sites is shown in Figure 1 and Table 1 provides descriptions of the buildings investigated. One building (Lyngbrekka) contained cows at the time of the study and so no traps were placed directly in the animal stalls.

Fieldwork was undertaken from 15th-23rd June (at Laugaland, Lyngbrekka, Mýrarkot, Staðarbakki and Vatn) and between 20-25th September (at Gerði and Spónsgerði). Pitfall traps (Fig. 2a) were used to capture live beetles in buildings used primarily for housing animals (sheep and cattle). The traps were made of plastic cups (10cm diameter, 14cm deep) half-filled with soapy water and sunk in the ground so that their lip was level with the surface. Each trap was set for c. 24 hours, then the captured insects were washed and stored in 70% ethanol. The most pitfall traps (53) were positioned in stable manure, some in stored hay (11) and some in bare earthen floors (7). As those placed in hay did not catch many insects, additional sampling was undertaken in this material. Between 5-10L of hay was sieved through a 4mm-mesh sieve and both the finer material that passed through the sieve and the coarser fraction that remained on the mesh were searched on a bright orange plastic sheet (Fig. 2b). Live and dead insects were collected using a pooter (aspirating device) before being washed and stored in 70% ethanol. The hay sampled for beetles came from diverse sources, including small and large hay stores, fresh and old hay. The size of the sampled hay accumulations and the age of the hay itself are both likely to have influenced the composition and state of the beetles found and the implications for this are considered in section 3.2. Habitat data (i.e. type of substrate, substrate moisture, light intensity, proximity of organic materials) was recorded for each trap and sampled location (Tables 2 and 3).

2.2 Laboratory methods

Beetles were identified using modern reference specimens from the insect collections at Náttúrufræðistofnun Íslands in Reykjavík, the Laurentian Forestry Centre's René Martineau Insectarium in Quebec City and the Osborne Insect Collection at the University of Edinburgh. In addition entomological publications were consulted (Bousquet, 1990; Joy, 1932; Palm, 1970; Strand & Vik, 1964; 1966; Tottenham, 1954). The taxonomy employed in this paper is based on Ólafsson (1991) and the nomenclature used for the Coleoptera follows Duff (2012).

2.3 Analytical methods

There are significant differences between the assemblages obtained by pitfall trapping and those produced by hand collecting. Most notably, all the beetles that came from pitfall traps were alive at the time of capture, while both live and dead beetles were recovered from screened hay. It is important to emphasise that pitfall traps can only sample living beetles that are active and their presence at the sampling location is likely to reflect the availability of suitable microhabitats in the trap's immediate vicinity (Southwood & Henderson, 2000). In contrast, hand collecting from screened hay allowed the recovery of assemblages more akin to archaeoentomological faunas. Most of the live beetles collected from screened hay may have actually lived there, but the dead ones may also include allochthonous elements – those incorporated from the sites of hay collection or as 'background fauna' that originated in other places and arrived either by chance or in search of food or shelter. These differences highlight the distinct ecological (and archaeological) significance of assemblages obtained by pitfall trapping versus hand collecting and the need to analyse them using different approaches.

2.3.1 Analysis of beetles captured by pitfall traps

Initially, the recovered taxa were grouped by their preferred habitats, based on our current knowledge of each taxon's ecological requirements in Iceland. Taxa were divided into two broad groups: (1) the non-synanthropic fauna – beetles able to complete their whole developmental cycle outdoors in Iceland, away from cultivated land and domestic animals, and (2) synanthropes – beetles that are either favoured by or completely dependent upon cultural habitats, either buildings or agricultural land. Synanthropic taxa were then separated into smaller ecological groups according to their preference for particular materials (i.e. animal waste, decaying vegetation, carrion) and conditions.

To facilitate comparisons between previous studies and new pitfall trap records, a method based on the visualisation of the microhabitat preferences of individual species was devised. The method captures semi-quantified measures of the range of materials and conditions associated with each species, using a diagram made up of five axes, each of which represents one measured ecological parameter (Fig. 3). The shapes of individual diagrams illustrate species habitat preferences and they can be visually grouped into classes for comparative purposes; they can, for example capture variation within and between different types of substrates and environmental conditions. Multivariate statistics were used to explore ecological relationships between synanthropic taxa (and their environment). This approach replicates aspects of the methodology devised by Carrott & Kenward (2001; Kenward & Carrott, 2006) to analyse British archaeoentomological assemblages. Detrended Correspondence Analysis revealed that the dataset was following a linear response model (Lepš & Šmilauer, 2003; ter Braak, 1995) so CANOCO 4.5 (ter Braak & Šmilauer, 2002) was used to conduct Principal Component Analysis (PCA). The results are presented so that the axis *x* represents the component (or environmental variable) that explains the most variation, and the axis *y*, the second component in importance. Spearman's rank-order correlation has also been used to identify pairs of co-occurent taxa on raw counts using SPSS v.23. This non-parametric test can identify correlations between pairs of variables (in this case, insect taxa) without requiring normally distributed data. A positive coefficient for each pair indicates that the values obtained for the two taxa tend to increase simultaneously, and a negative one, that values for one taxon tend to decrease as those for the other increase. Spearman's rank-order correlations are illustrated with constellation diagrams, where all positive and statistically significant relationships between pairs of taxa are indicated. The possible ecological significance of the groups of taxa defined by the results of multivariate statistical analysis is evaluated in terms of the materials and ecological parameters recorded for each trap.

2.3.2 Analysis of beetles collected from stored hay

Synanthropic beetle taxa from stored hay were classified according to their preferred habitat in Iceland (Gudleifsson, 2005; Larsson & Gígja, 1959; Ólafsson, 2008). In order to facilitate comparisons between different samples and types of assemblages (i.e. dead versus live), the data was compiled as bar charts showing the contribution of each ecologically-defined group of beetles to the total collection obtained for each sample.

3. Results

3.1 Beetles captured from pitfall traps

Pitfall traps captured 426 beetles from which 35 taxa have been identified (see table 4). Traps active in July (when air temperatures ranged between 12-19 °C) produced many more beetles (up to 15 beetles in 24hours) than those active in September (when air temperature ranged between 4-9 °C), none of which collected more than one beetle. This was probably a result of lower temperatures and their impacts on beetles' activity (Speight *et al*., 1999).

Most of the 35 taxa (26) are considered synanthropic in Iceland, and either confined to, or strongly favoured by, the interiors of buildings or other habitats created by human activity. The remainder include six non-synanthropic beetles – the ground beetles (fam. Carabidae) *Nebria rufescens* (Strøm) (Fig. 4a), *Patrobus septentrionis* Dejean and *Calathus melanocephalus* (Linnaeus) and the rove beetles (fam. Staphylinidae) *Quedius* (*Raphirus*) *fulvicollis* (Stephens), *Othius angustus* Stephens and *Bessobia excellens* (Kraatz) – all of which are considered part of the indigenous fauna of the country (Larsson, 1959). All of these prey on arthropods and other organisms, and have been captured in Icelandic pastures and hayfields (Gudleifsson, 2005; Forbes, 2008). They could have entered buildings opportunistically in search of the abundant prey to be found in accumulations of decaying plant matter and manure (e.g. see Skidmore, 1991). Two taxa (*Cercyon* sp. and *Atheta* sp.) could only be identified to genus. These genera include both synanthropic and non-synanthropic species in Iceland so without more precise identification little can be said about their habitat requirements.

Synanthropic beetles have been placed into ecological groups (Figure 5). Those that do not seem to have clear preferences for particular microhabitats in Iceland are grouped as 'eurytopic synanthropes'. This group is dominated by rove beetles but also includes the water scavenger beetle (fam. Hydrophilidae) *Cercyon analis* (Paykull) and the ant-like flower beetle (fam. Anthicidae) *Omonadus floralis* (L.). All these species are macropterous (potentially able to fly) and, apart from *Philonthus longicornis* Stephens, all have been recorded in compost and old hay in Iceland (Larsson & Gígja, 1959). The staphylinids *Bisnius cephalotes* (Gravenhorst) (Fig. 4b), *B. sordidus* (Gravenhorst), *Omalium excavatum* Stephens, *O. septentrionis* Thomson and *Aleochara sparsa* Heer, as well as the anthicid *Omonadus floralis* (Linnaeus), are also known to occur in manure In Iceland (Larsson & Gígja, 1959). Habitats in which these species have been recorded in the British Isles and mainland Europe also include organic matter from vegetation or animals, and most are also known to occur in carrion and/or nests (Koch, 1989; Lott & Anderson, 2011).

The seven specimens of *Philonthus longicornis* recovered from Lyngbrekka and Mýrarkot are the first records of this species in Iceland, suggesting that it is a very recent introduction and/or that the habitats in which the species occur in Iceland have been overlooked. *P. longicornis* is a predacious rove beetle whose natural range was Palaearctic, but it is now cosmopolitan thanks to its dispersal in trade goods (Klimaszewski *et al*., 2013). It is known to occur in diverse materials and substrates elsewhere in Europe, including litter, compost, manure and carrion (Lott & Anderson, 2011; Koch, 1989).

Three of the rove beetles identified are usually found in Iceland in foul rotting matter such as manure and carrion. Indeed, *Philonthus politus* (Gravenhorst) (Fig. 4c) and *Creophilus maxillosus* (Marsham) (Fig. 4d) prey on maggots breeding in dung, feeding grounds also favoured by the smaller beetle *Dimetrota atramentaria* (Gyllenhal) (Larsson & Gígja, 1959; Ólafsson, 2008). Elsewhere in the world, *C. maxillosus* is regarded as a carrion species since it preys on larvae and pupae feeding on corpses (Hinton, 1945; Byrd & Castner, 2009). In addition, both *P. politus* and *D. atramentaria* are commonly recorded in carrion and are occasionally found in rotting vegetation and fungi (Hinton, 1945; Koch, 1989; Lindroth *et al*., 1973).

The 'dry mouldy matter' group includes silken fungus beetles (fam. Cryptophagidae) and minute brown fungus beetles (fam. Latridiidae), all of which are mycetophagous (feeding on moulds, spores and hyphae). Only the predacious rove beetle *Xylodromus concinnus* (Marsham) has a different diet; it preys on other arthropods. All of these species are usually found indoor within old decaying hay in Iceland (Larsson & Gígja, 1959). In Scandinavia, most of these species are also known from tree hollows, rodents and birds' nests, as well as diverse types of decaying vegetal matter and fungi (Koch, 1989; Palm, 1951; 1959). This group also includes another first record for Iceland, *Monotoma picipes* Herbst. The species is found throughout Europe and has also been introduced to North America (Bousquet, 1990; Koch, 1989). The closely related *M. testacea* Motschulsky has been found twice in Iceland in recent times in decaying plant residues including old hay (Larsson & Gígja, 1959; Ólafsson, 2008). Both *Monotoma* species are associated with decaying organic matter, where they feed on fungi (Bousquet, 1990; Pakaluk & Ślipiński, 1993).

Two of the species captured by pitfall traps have only been recorded indoors in Iceland: the spider beetles (fam. Ptinidae) *Tipnus unicolor* (Piller & Mitterpacher) (Fig. 4e) and *Ptinus tectus* Boildieu. These beetles differ from other members of the group 'mouldy matter fauna' because they have a diverse diet and in Iceland they have been most frequently recorded in human habitations rather than barns and byres (Larsson, 1959; Larsson & Gígja, 1959; Ólafsson, 2008). Both species have poor dispersal capacity because they are brachypterous (and thus unable to fly) (Larsson & Gígja, 1959; Ólafsson, 2008). Elsewhere in Europe, these species occur in both rural and domestic built environments, birds' nests and old wood (Fowler, 1890; Howe, 1955; Koch, 1989; Palm, 1959).

By visually grouping similarly shaped diagrams together (Fig. 6), it is possible to differentiate five classes of preferred habitats: (1) damp stable manure, (2) moist stable manure, (3) dry hay, (4) moist hay and (5) the proximity of mixed organic materials. The majority of the species (19/25) were captured more often in stable manure, which is not surprising given that the smooth and clearly defined surface of this substrate was more effectively sampled with pitfall traps than stored hay. Principal component analysis suggests that not all the synanthropic taxa recovered respond to environmental variables in the same manner (Fig. 7a). The PCA plot differentiates two groups of taxa. Group A is composed of eight staphylinids and one hydrophilid. Six of those species are eurytopic in Iceland and three are usually found in association with foul rotting matter. Group B is dominated by species associated with mouldy vegetal matter, but also includes four eurytopic rove beetles. The constellation diagram based on the results of Spearman's rank-order correlation separates the synanthropic taxa in a similar manner (Fig. 8), but several species (most notably *Philonthus politus* and *Phyllodrepa floralis*) share links between the two groups. Although a certain separation may be assumed between taxa most commonly associated with manure and those associated with stored hay, the PCA plots for each sample (Fig. 7b-d) suggests a more complicated story, in which the substrate moisture and (perhaps to a lesser extent) the level of brightness also play a role.

3.2 Beetles hand collected from hay

A total of 124 beetles were recovered from screened hay and 21 taxa identified, of which only nine were also captured by pitfall traps. In some cases, the beetles were still alive at the time of capture, but more than half of the specimens recovered using this method were dead, and some disarticulated. There is significant variation in the numbers of beetles recovered from different samples of screened hay. Eight of them yielded less than five beetles and three produced more than fifteen specimens. Two samples (C and D) did not produce any beetles.

Nine of the beetles collected from stored hay belong to non-synanthropic taxa: the ground beetles *Notiophilus biguttatus* (Fabricius)*, Calathus melanocephalus* and *Trichocellus cognatus* (Gyllenhal), the pill beetle (fam. Byrrhidae) *Byrrhus fasciatus* (Forster) and the broad-nosed weevil (fam. Curculionidae, subfam. Entiminae) *Otiorhynchus nodosus* (O.F. Müller). All of these are considered part of the indigenous fauna of Iceland (Larsson, 1959), but they also have been recorded in synanthropic settings such as hayfields and pastures (Gudleifsson, 2005). All were dead at the time of their recovery, implying that they were probably transported from fields to barns along with the hay harvest and were not be able to flourish in interior habitats.

Each of the fourteen synanthropic beetle taxon was placed into an ecological group (Fig. 9). Eurytopic synanthropes in the hay are much less diverse than in samples collected from pitfall traps, as there are only two species, *Bisnius sordidus* and *Omalium excavatum.* Only one beetle associated with foul rotting matter was recovered, the dung beetle (fam. Scarabaeidae) *Aphodius lapponum* Gyllenhal, which was not captured by the pitfall traps. Although this species is normally encountered in the open (Larsson & Gígja, 1959), it is considered to be synanthropic in Iceland as it can only breed in the dung of larger mammals such as cattle and horses, which were unknown on the island prior to its colonisation by the Norse (Dugmore *et al.*, 2005).

The 'dry mouldy matter fauna' is dominant in samples from stored hay, both in terms of diversity (nine of fourteen synanthropic taxa) and quantity (more than 80% of the total specimens). *Monotoma picipes, Cryptophagus acutangulus* Gyllenhal *and C. scutellatus* Newman were not recovered even though they occurred in pitfall traps. Other silken fungus beetle and minute brown beetle taxa were found, including *C. scanicus* (Linnaeus), *Atomaria analis* Erichson, *Atomaria munda* Erichson and *Corticaria elongata* (Gyllenhal). All of these species are mycetophagous and occur in old hay in barns and byres in the country (Larsson & Gígja, 1959). A few spider beetles *Tipnus unicolor* were recovered from screened hay, as well as one specimen of the latridid *Cartodere nodifer* (Westwood). The first Icelandic specimens of the latter species were first captured in 1989 in Kópavogur, a township adjacent to Reykjavík, in mouldy seeds stuck between imported stone slabs. Subsequent records include specimens captured inside a house and an office, as well as others obtained outdoors, in a homefield and in a Sitka spruce and mountain birch woodland. Outside Iceland, *C. nodifer* has been recorded from stored food products, mouldy vegetation, nests and burrows (Hinton, 1941; 1945; Koch, 1989). Most of the Icelandic specimens came from within the vicinity of the capital, which suggests that the species was introduced very recently to southwest-Iceland, presumably in ships or planes' cargoes (see Kenis et al., 2007), before eventually making its way to northern Iceland.

Figure 10 shows differences between live and dead assemblages from stored hay, which was categorized into two broad groupings of 'fresh' hay with no signs of decay and compaction and 'old' hay where the hay was broken into short pieces, compacted and showing visible signs of mould or decay. Only synanthropic beetles were recovered alive in these samples. Apart from the spider beetle *Tipnus unicolor,* all the live specimens identified belong to taxa feeding in mouldy vegetal matter. In contrast, the dead beetles recovered are more taxonomically diverse and include non-synanthropic taxa, foul rotting matter fauna and a few eurytopic synanthropes in addition to the 'dry mouldy matter fauna'. The type of hay examined seems to have had an influence on the number of beetles present in each sample. Old hay from substantial hay stores (samples A, I, J & K) yielded the highest numbers of specimens, while none of the samples collected from old hay in feeding troughs (B, H & L) or fresh hay (C-G) produced more than five beetles.

4. Discussion

The records of beetle species and their associated habitat data presented in this paper develop our understanding of the ecological requirements of species commonly found in barns and byres in Iceland. Thus, despite restricted exposure times for the pitfall traps and variations in the timing of data collection that will have exerted an influence on the samples and their representation of synanthropic habitats, these data do provide us with ways to better understand subfossil assemblages. Most of the synanthropic beetles collected by pitfall traps occurred in materials and conditions that are in agreement with habitat descriptions provided in the Icelandic entomological literature, but there are anomalies that require closer examination. Six of the seven mould-feeder species collected by pitfall traps (*Latridius minutus* (gr.), *Cryptophagus acutangulus, C. denticulatus, C. distinguendus, C. scutellatus* and *Monotoma picipes*) were recovered more often in traps placed in stable manure than in stored hay (Fig. 6). However, this should not be seen as an indication that these species prefer manure as their habitat because of the higher number of traps placed in manure. In all but one case (trap 10 from Lyngbrekka), the sampled manure was a mixture of animal dung and straw. Therefore, it is likely that the mould-feeders were feeding off the straw-component of the manure rather than the animal dung. Of these six taxa, only *L. minutus* (gr.) was recovered in numbers large enough to allow a good insight into the range of conditions in which it can occur. It was captured in dark to bright locations, in dry to damp substrates and it was almost present as often in hay as in manure (Fig. 6). There is only one instance where it occurred more than one metre away from stored hay. This data suggests that although the species is associated with mouldy vegetal matter, it is tolerant of a wide range of conditions. The rove beetle *Bisnius cephalotes* was the most abundant taxon in the pitfall trap assemblage, totalling 89 specimens. Only ten of these were collected from traps that were not in stable manure, which is remarkable given the species' high dispersal capacity (Lindroth et al., 1973). This suggests that *B. cephalotes* prefers foul rotting matter such as animal waste to drier plant waste and may therefore be considered relatively stenotopic. Another large rove beetle, *Creophilus maxillosus,* is reported in the Icelandic literature as being most common in manure and carrion (Larsson, 1959; Larsson & Gígja, 1959). The species was obtained from two sites, Mýrarkot and Vatn, less than 1 km apart, and in a very restricted range of conditions (Fig. 6). Indeed, it was only found in particularly 'squalid' situations, in damp and foul-smelling urine-soaked stable manure within stalls for immature livestock (calves and lambs feeding on maternal milk). That *C. maxillosus* appears to prefer prey who feed on protein-rich dung is unsurprising, given that elsewhere in northern Europe, the species is most often encountered in carrion (Buckland & Buckland, 2006).

The five specimens of *Tipnus unicolor* recovered from pitfall traps in hay and manure are worthy of note, as this species is believed to be rare in modern Iceland and to occur mostly in old houses (Ólafsson, 2008). In addition to the records obtained in this study, 25 other specimens are known from an old sheephouse at Vatnsfjörður in northwest Iceland (Forbes, 2015), suggesting that the apparent rarity of this species in Iceland may result from a lack of entomological investigations in barns and byres. Owing to its poor locomotive capacities and its apparent inability to survive outside suitable habitats (e.g. buildings' interiors) in Iceland, it is likely that *T. unicolor* relies on humans for its dispersal. Therefore, its virtual absence from farm buildings investigated over 20 years ago for their insect faunas in Iceland (e.g. Buckland *et al.,* 1991b; Sadler & Dugmore, 1995) may simply signify that the species had not been carried to these particular buildings by the late 20th century.

The pitfall trap survey allowed the identification of species more strongly indicative of either foul rotting matter (e.g. *B. cephalotes, C. maxillosus*) or dry mouldy matter (e.g. *Xylodromus concinnus*). By examining possible ecological associations between such stenotopes and eurytopic species in the dataset, results of the PCA and Spearman's rank-order correlations permitted the recognition of two groups of taxa seemingly indicative of different types of materials and conditions. The first two axes of the PCA plot (Fig. 7a) and the constellation diagram (Fig. 8) suggest two clusters of taxa (Table 6). The first one (group A) includes species preferring rotting matter, such as animal waste, and several eurytopic species tolerant to foul conditions. The second one (group B) is almost exclusively composed of mould-feeders and predators associated with pure plant waste. The two groups may represent two communities, both formed of a suite of decomposer and predacious species: one (B) prefers foul rotting matter and the other (A), dry mouldy vegetation. These groups are not discrete however, with two taxa shared between them: *Philonthus politus* and *Phyllodrepa floralis*. This is unsurprising given that ecological habitats form a continuum and that the requirements of certain species overlap (Schowalter 2011), a pattern that has long been recognised by archaeoentomologists (e.g. Carrott & Kenward, 2001; Carrott & Kenward, 2006).

The results of the pitfall trap survey showed high variability in terms of species composition. We may speculate that this reflects the varying amounts of hay, manure, turf and wood present in the buildings. At Mýrarkot and Vatn, where only small amounts of stored hay were present, the entomological signal for mouldy plant material is hardly detectable. In the sheephouses at Spónsgerði and Staðarbakki, it is not the 'foul rotting matter fauna', but the 'dry mouldy matter fauna' that is dominant. As both buildings were partially built of turf, this may be seen as an indication that turf provided favourable conditions for mould-feeders. Similar observations have been made by Kenward *et al*. (2012) and Smith (1996a; 1996b) during investigations of insect faunas from roofing turf and thatch. The materials and conditions within the buildings in this study seem to have exerted a strong influence on the composition of synanthropic faunas and the relative abundance of different taxa, but it is important to stress that spatial (altitude, longitude, climate) and temporal (time and duration of investigation) factors, as well as variations in population densities from species to species (Schowalter, 2011), are also likely to have played a role.

Insects associated with manure and stored hay were present and active inside the buildings at the time of investigation. The live component of beetle assemblages obtained from screened old hay produced evidence for mould-feeders and their predators such as *Omalium excavatum, Xylodromus concinnus, Cryptophagus* spp., *Atomaria* spp., *Latridius minutus* (gr.) and *Corticaria elongata,* as well as indoor synanthropes such as *T. unicolor* and *Cartodere nodifer,* having been active in this material immediately before their capture*.* In contrast, screened material from fresh hay bales and bundles only produced five mould-feeders and three indoor synanthropes, which suggest that substantial ‘barn beetle’ communities had not colonised the habitats provided by freshly harvested fodder, presumably because it was unattractive due to a lack of suitable foods such as moulds and fungi. This, however, is in contrast with results of a similar study conducted at Conisbrough Parks Farms in the UK, where large numbers of mould-feeders were recovered from fresh hay bales stored in open Dutch barns (Smith, 1998).

The dead component of assemblages from screened hay from Gerði and Staðarbakki includes many mould-feeders, indicating that at least some of them died and remained where they had been feeding and breeding. Apart from eurytopic synanthropes, all the other taxa identified in these dead assemblages have most likely originated away from the stored hay. They may have been carried indoors with the hay harvest or casually entered the buildings, but it is also possible that they entered them in search of prey or shelter. These outdoor insects may have subsequently died indoors, either because they reached the natural end of their life or because of the absence of suitable food sources and environmental conditions. The dung beetle *Aphodius lapponum,* found in Staðarbakki, is attracted to fresh animal droppings, so it may have entered the building of its own accord. The faunas recovered from stored hay show that although communities actively associated with decaying hay microhabitats are almost exclusively composed of mould-feeders and their predators, death assemblages within the hay may be made up of a more ecologically diverse fauna and include non-synanthropic beetles that originated from hayfields. These death assemblages are much smaller than those analysed from a hay store in northern Iceland (Forbes & Milek, 2014) and hay bales and stores on British farms (Grinter, 2004; Smith, 1998; 2000), but they do share similarities with them. Modern death assemblages from other plant materials such as roofing thatch and leaf fodder have also been shown to contain similar faunas (Smith, 1996a; 1996b). This stresses the need for careful interpretation of archaeoentomological assemblages, as synanthropic faunas may sometimes be better indicators of ecological conditions rather than material types (cf. Smith, 1998, 2012).

It is important to keep in mind that there is a strong discrepancy between the time-frames represented by modern insect assemblages and those recovered from archaeological sites, the latter possibly incorporating remains that have accumulated over years or decades. Indeed, longer depositional (or sampling) periods augment the probability for rare and low-density species to be collected (Krebbs, 1994). Although this means that the beetle faunas discussed in this study cannot be directly compared with archaeoentomological assemblages, careful examination of the (dis)continuities between the live and dead component of these faunas provides crucial guidance for understanding the processes at play in the formation of death insect assemblages.

5. Conclusions

This study is the first Icelandic entomological survey to integrate both live and dead insect faunas in an attempt to illuminate the ecological requirements of non-harmful synanthropic taxa and the processes at play in the formation of archaeoentomological assemblages. By targeting undersurveyed habitats, it has been possible to clarify the range of conditions suitable for some species occurring indoors in Iceland. The diverse situations in which *Latridius minutus* (gr.) was captured reinforce current understanding of this species' ecological range, namely that it encompasses a wide range of conditions (Koch, 1989). That *Creophilus maxillosus* was only recorded in damp stable manure also corroborates earlier data on the preference of the species for predation in foul materials. Repeated captures of *Bisnius cephalotes* in damp animal waste suggests that this species prefers foul rotting matter and that in Iceland, the species may be less eurytopic than previously believed. The study also produced new records of *Tipnus unicolor* that show that this species is not simply restricted to old houses and may be more common in Iceland than 20th-century records indicate. This new data will allow for more accurate interpretations of the archaeological significance of these species.

This survey has identified predacious rove beetles associated with dung as well as mould-feeders tolerant to damp and foul conditions in stable manure. However, it is still unclear if death assemblages from manure are composed of a similar suite of species. Modern faunas from deep litter byre floors in the UK (Smith, 1998; 2000) have shown that this substrate may not always produce a strong entomological signal for foul rotting matter. This comparative work, however, focused on a single site and the results obtained may therefore be the exception rather than the norm. It is possible that, like the dead component of faunas identified from stored hay in buildings in the present study, the insects that died and became incorporated into the stable manure itself comprised both elements of the original community breeding in the manure and others that originated from hayfields and the buildings' surroundings. Our results suggest that stable manure in Iceland does support beetle species specifically associated with foul rotting matter. No such species were recovered from the stored hay. Distinguishing entomological signatures for stable manure versus purely vegetal decaying matter allows activities such as the clearing of animal waste from byres and its use as fertiliser to be more confidently recognised in the archaeological record, thereby enhancing our understanding of changing agricultural practices in both Iceland, and the wider North Atlantic region. For this reason, we recommend further examination of modern death insect assemblages from stable manure.

Records in this study of beetle species that were rarely or never previously encountered in Iceland serve as a reminder that care must be taken when comparing modern and archaeological insect communities. Although faunas living in ancient buildings may have been similar to modern ones in terms of their habitat preferences, they cannot be assumed to have been composed of the same suite of species. *Philonthus longicornis, Monotoma picipes, Cartodere nodifer* and *Thes bergrothi* (Fig. 4f) have apparently arrived in Iceland within the last 100 years, suggesting that the conditions for their successful introduction and dispersal from seaport towns to northern farms are recent. Over the course of the last century, Iceland has been transformed from a largely rural society into one that is prosperous, urbanised and closely integrated within a global market economy (Jónsson, 2004, Karlsson, 2000). It is probably no coincidence that more adventive species, some originating from beyond Europe (*C. nodifer,* see Horion, 1961), made their first appearance in Iceland at the same time. Future work on entomological faunas from modern farm buildings' interiors and recent archaeological sites may help elucidate the causes, timing and processes of exotic species' dispersal and the impact of these faunal invasions on local biodiversity.

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7. Contribution of authors

VF and AJD designed the project. VF conducted the fieldwork and the laboratory and statistical analyses. EO helped with the identification of specimens and the gathering of Icelandic beetle records and associated habitat data. VF wrote the original manuscript and all authors discussed the results and their implications and commented on/edited the paper at all stages.

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The Life and Death of Barn Beetles: Faunas from Manure and Stored Hay inside Farm Buildings in Northern Iceland

Véronique Forbes[a*], Andrew J. Dugmore[b] and Erling Ólafsson[c]

Table 1. List of study sites and description of the buildings investigated.

Site	Fieldwork dates	Building types	Building materials	Outdoor surroundings	Activity areas investigated	Elevation (m.a.s.l.)	Local weather and temperature during pitfall trapping
Gerði	22-23 September 2010	Barn (attached to a turf sheep house out of use since 2000)	Walls and roof: corrugated iron and wood. Earthen (partly wooden) floors	Dry grasslands, rhubarb garden	Hay store	168	Cloudy, 8 to 9°C
Laugaland	22-23 July (pitfall traps) and 25 September 2010 (hand collecting from hay)	Sheep house 1	Roof and Walls: corrugated iron and wood. Wooden slatted floor.	Grassland (pastures), bare ground	Animal stalls, hay stores	30	Cloudy with sunny intervals, 17 to 18°C
	22-23 July 2010	Sheep house 2	Roof and Walls: corrugated iron and wood. Earthen floor.	Grassland (pastures), bare ground	Animal stalls	30	Cloudy with sunny intervals, 17 to 18°C
Lyngbrekka	18-19 July (pitfall traps) and 20 September 2010 (hand collecting from hay)	Animal house	Walls: concrete and corrugated iron. Roof: corrugated iron. Concrete, earthen and slatted floors	Hayfields, pastures and cultivated fields	Animal stalls, hay stores	161	Cloudy with sunny intervals, 15 to 23°C (July)
Mýrarkot	15-16 July 2010	Animal house	Corrugated iron roof. Concrete walls. Concrete and slatted floors.	Dry grasslands, disturbed land (manure heap) hayfields and bare ground	Animal stalls, hay store	35	Sunny and windy, 12 to 15°C
Spónsgerði	21-22 September 2010	Sheep house	Roof: turf, wood, corrugated iron and wool. Walls: turf, corrugated iron and wood. Earthen floor.	Pastures, disturbed land (manure heap), bare ground	Animal Stalls, hay store	33	Cloudy, 4 to 7°C
Staðarbakki	20-21 July (pitfall traps) and 22 September 2010 (hand collecting from hay)	Sheep house	Corrugated iron roof. Walls: turf, stones and wood. Earthen floor.	Pastures, hayfields, heatland	Animal Stalls, hay store	323	Sunny and windy, 17 to 19°C (July)
Vatn	15-16 July 2010	Animal house	Corrugated iron roof. Concrete walls. Concrete and earthen floors.	Hayfields, pastures and bare ground	Animal Stalls, hay store	22	Sunny and windy, 13 to 16°C

Table 2. List and description of pitfall traps and associated habitat data. Ground moisture was assessed by sinking the probe of a moisture meter c. 10 cm below the earth (values obtained were displayed on a scale from 1 to 10) and by pressing a dry paper towel on the substrate's surface (1 to 3 and leaving no trace: dry, 4 to 7 and leaving minor traces: moist, 8 to 10 and leaving a clear wet trace: damp). Brightness was evaluated using a light meter that provided lux values at each trap location (≤10 lux : dark, 11 to 50 lux: medium, ≥ 51 lux bright). All brightness measurements were taken during daytime and as Icelandic summer nights are bright nearly 24h, it is assumed that light levels did not vary significantly from night to day. Organic materials were considered to be in proximity to traps if they were within a 1m radius.

Site	**Trap #**	**Substrate**			**Moisture**			**Brightness**			**Proximity of organic materials**				
		Earth	Manure	Hay	Dry	Moist	Damp	Dark	Medium	Bright	Manure	Old hay	Fresh hay	Turf	Wood
Laugaland	**1**	x			x					x		x			
	2	x				x				x		x			
	3	x			x			x				x		x	x
	4		x				x	x			x	x			x
	5		x			x		x			x	x			x
	6		x				x	x			x	x			x
	7		x				x	x			x	x			x
	8		x			x		x			x	x			x
	9		x				x	x			x	x			x
	10		x				x	x			x	x			x
	11		x			x		x			x	x			x
	12		x				x	x			x	x			x
	13		x				x	x			x	x			x
	14		x			x			x		x	x			x
	15		x				x	x			x	x			x
	16		x				x	x			x	x			x
	17		x				x	x			x	x			x
	18		x			x		x			x	x			x
Lyngbrekka	**1**	x		x	x			x				x			
	2	x		x	x			x				x			
	3	x		x	x			x				x			
	4	x			x				x		x	x			
	5			x	x				x			x			
	6	x	x			x			x		x	x			
	7	x	x			x			x		x	x			
	8	x	x			x			x		x	x			
	9	x					x	x			x	x			
	10		x				x	x			x				
Mýrarkot	**1**		x				x	x			x				
	2		x				x	x			x				
	3		x				x	x			x				
	4			x	x				x				x		
	5		x				x	x			x				
	6		x				x	x			x				
Spónsgerði	**1**		x			x		x			x	x			x
	2		x			x		x			x	x			x
	3		x			x		x			x	x			x
	4		x			x		x			x	x			x
	5		x			x		x			x	x			x
	6		x			x		x			x	x		x	x
	7		x			x		x			x	x		x	x
	8		x			x		x			x	x		x	x
	9		x			x		x			x	x		x	x
	10	x					x	x			x	x		x	x
	11	x				x		x			x	x		x	x
Staðarbakki	**1**		x			x		x			x	x		x	
	2		x			x		x			x	x		x	
	3		x				x	x			x	x		x	
	4		x				x	x			x	x			
	5		x			x			x		x	x			
	6		x			x				x	x	x		x	
	7		x				x	x			x	x			
	8		x			x		x			x	x			
	9		x				x	x			x	x			
	10		x				x	x			x	x		x	
	11		x			x		x			x	x		x	
	12		x			x				x	x	x		x	
	13			x	x					x		x			
	14			x	x					x		x			
	15			x	x					x		x			
Vatn	**1**		x				x	x			x	x			
	2		x				x	x			x	x			
	3			x	x				x			x			
	4		x				x	x			x	x			
	5		x				x	x			x	x			x
	6			x	x			x				x			
	7		x				x	x			x	x			
	8		x				x	x			x	x			
	9			x	x			x				x			
	10		x				x	x			x	x			
	11		x				x	x			x	x			

Table 3. List and description of samples collected from stored hay.

Site	Sample	Old vs fresh hay	Live vs. dead insects	Volume sieved (L)	Details
Gerði	**A**	old	both	10	Slightly moist hay debris on the floor a few cm away from a substantial amount (>2m cube) of stored hay
Laugaland	**B**	old	dead	10	Dry hay from a small amount of stored hay
	C	fresh	neither	10	Slightly moist hay taken from the upper surface of a hay bale
	D	fresh	neither	10	Moist hay taken from whithin a hay bale
Lyngbrekka	**E**	fresh	live	10	Dry new hay from a substantial amount (>2m cube) of stored hay
	F	fresh	live	10	Dry new hay from a substantial amount (>2m cube) of stored hay
Spónsgerði	**G**	fresh	live	10	Dry new hay from a substantial amount (>2m cube) of stored hay
	H	old	dead	10	Dry hay from a feeding trough
Staðarbakki	**I**	old	dead	10	Dry hay from the upper surface of a substantial amount (>2m cube) of stored hay
	J	old	dead	10	Moist hay from the floor surface a few cm away from a substantial amount (>2m cube) of stored hay
	K	old	dead	5	Dry hay from within a substantial amount (>2m cube) of stored hay
Vatn	**L**	old	live	10	Dry hay from a feeding trough

Table 4. List of identified beetles captured in pitfall traps.

	Laugaland																		**Lyngbrekka**									
Trap #	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
CARABIDAE																												
Nebria rufescens (Strøm)																												
Patrobus septentrionis Dejean																												
Calathus melanocephalus (Linnaeus)							1												1									
HYDROPHILIDAE																												
Cercyon analis (Paykull)	1															1	3	1										
Cercyon sp.																												
STAPHYLINIDAE																												
Philonthus politus (Linnaeus)								1		1		1				8	9	2					1					
Philonthus longicornis Stephens																							1	2				1
Bisnius cephalotes (Gravenhorst)	5	1	2	1	1	3	2				2	5	1			6	8	2							1			
Bisnius sordidus (Gravenhorst)	3			1	1	4	1	3	7	2		5	2	1	3	1	8			1		4	1					
Creophilus maxillosus (Linnaeus)																												
Quedius (Raphirus) fulvicollis (Stephens)																												
Othius angustus Stephens																												
Phyllodrepa floralis (Paykull)																												
Omalium excavatum Stephens													1									2		3	1	1		
Omalium rivulare (Paykull)																												
Omalium septentrionis Thomson																												
Xylodromus concinnus (Marsham)																			1			1	4	1				
Aleochara sparsa Heer					1																				1		1	
Oxypoda haemorrhoa (Mannerheim)																							1					
Alaobia trinotata (Kraatz)																						1		1				
Bessobia excellens (Kraatz)	1																											
Dimetrota atramentaria (Gyllenhal)	5				1		1	1		1	2			4	1		1											
Atheta sp.					2																	2	2	3				
PTINIDAE																												
Tipnus unicolor (Piller & Mitterpacher)																												
Ptinus tectus Boildieu			1																									
MONOTOMIDAE																												
Monotoma picipes Herbst																								1				
CRYPTOPHAGIDAE																												
Cryptophagus acutangulus Gyllenhal																												
Cryptophagus denticulatus Heer																			1					1				
Cryptophagus distinguendus Sturm																						1	1					
Cryptophagus scutellatus Newman																												
Cryptophagus sp.																						1						
Atomaria sp.																												
LATRIDIIDAE																												
Latridius minutus (gr.)	1				1	2	1			1				1		3	3	3	11			4	15	13	12	4		
Thes bergrothi (Reitter)																							1					
ANTHICIDAE																												
Omonadus floralis (Linnaeus)																												

Table 4. (continued)

	Mýrarkot						**Spónsgerði**										
Trap #	**1**	**2**	**3**	**4**	**5**	**6**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**
CARABIDAE																	
Nebria rufescens (Strøm)	1		1														
Patrobus septentrionis Dejean																	
Calathus melanocephalus (Linnaeus)			1														
HYDROPHILIDAE																	
Cercyon analis (Paykull)																	1
Cercyon sp.																	
STAPHYLINIDAE																	
Philonthus politus (Linnaeus)												1	1				
Philonthus longicornis Stephens	2					1											
Bisnius cephalotes (Gravenhorst)	3		2		1	2											
Bisnius sordidus (Gravenhorst)	3			5													
Creophilus maxillosus (Linnaeus)			3			2											
Quedius (Raphirus) fulvicollis (Stephens)																	
Othius angustus Stephens						1											
Phyllodrepa floralis (Paykull)																	
Omalium excavatum Stephens																	
Omalium rivulare (Paykull)																	
Omalium septentrionis Thomson																	
Xylodromus concinnus (Marsham)																	
Aleochara sparsa Heer							1										
Oxypoda haemorrhoa (Mannerheim)																	
Alaobia trinotata (Kraatz)																	
Bessobia excellens (Kraatz)																	
Dimetrota atramentaria (Gyllenhal)																	
Atheta sp.																	
PTINIDAE																	
Tipnus unicolor (Piller & Mitterpacher)																	
Ptinus tectus Boildieu																	
MONOTOMIDAE																	
Monotoma picipes Herbst																	
CRYPTOPHAGIDAE																	
Cryptophagus acutangulus Gyllenhal																	
Cryptophagus denticulatus Heer																	
Cryptophagus distinguendus Sturm																	
Cryptophagus scutellatus Newman												1	1				1
Cryptophagus sp.																	
Atomaria sp.																	1
LATRIDIIDAE																	
Latridius minutus (gr.)																	
Thes bergrothi (Reitter)																	
ANTHICIDAE																	
Omonadus floralis (Linnaeus)									1								

Table 4. (continued)

	Staðarbakki															Vatn										
Trap #	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**
CARABIDAE																										
Nebria rufescens (Strøm)	1									1		1				2									1	1
Patrobus septentrionis Dejean																										1
Calathus melanocephalus (Linnaeus)																				2		3	1			
HYDROPHILIDAE																										
Cercyon analis (Paykull)																				2						1
Cercyon sp.																				1						
STAPHYLINIDAE																										
Philonthus politus (Linnaeus)																						1				
Philonthus longicornis Stephens																										
Bisnius cephalotes (Gravenhorst)						1										1			2	5	1	8	8		5	10
Bisnius sordidus (Gravenhorst)		1	1						2											1		1				
Creophilus maxillosus (Linnaeus)																						10	1		9	2
Quedius (Raphirus) fulvicollis (Stephens)						1			1																	
Othius angustus Stephens																										
Phyllodrepa floralis (Paykull)			1												1							1			1	
Omalium excavatum Stephens																										1
Omalium rivulare (Paykull)												1											1			1
Omalium septentrionis Thomson						1			1																	
Xylodromus concinnus (Marsham)																										
Aleochara sparsa Heer																1			5	2		2			1	
Oxypoda haemorrhoa (Mannerheim)																										
Alaobia trinotata (Kraatz)																								1		
Bessobia excellens (Kraatz)																										
Dimetrota atramentaria (Gyllenhal)																				1	1		1			1
Atheta sp.									1																	
PTINIDAE																										
Tipnus unicolor (Piller & Mitterpacher)		1						1							3											
Ptinus tectus Boildieu																										
MONOTOMIDAE																										
Monotoma picipes Herbst																										
CRYPTOPHAGIDAE																										
Cryptophagus acutangulus Gyllenhal							1																			
Cryptophagus denticulatus Heer			1		1			1																		
Cryptophagus distinguendus Sturm		1			1			1																		
Cryptophagus scutellatus Newman							1																			
Cryptophagus sp.																										
Atomaria sp.																										
LATRIDIIDAE																										
Latridius minutus (gr.)					1								1	1								1		1		
Thes bergrothi (Reitter)																										
ANTHICIDAE																										
Omonadus floralis (Linnaeus)																										

Table 5. List of identified beetles hand collected from screened hay. Italicized numbers indicate beetles that were dead at the moment of their recovery.

	Gerði	**Laugaland**			**Lyngbrekka**		**Spónsgerði**		**Staðarbakki**			**Vatn**
Sample #	**A**	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**J**	**K**	**L**
CARABIDAE												
Notiophilus biguttatus (Fabricius)									*1*			
Calathus melanocephalus (Linnaeus)	*2*							*1*	*1*			
Trichocellus cognatus (Gyllenhal)	*1*											
STAPHYLINIDAE												
Bisnius sordidus (Gravenhorst)											*1*	
Staphylininae indet.	*1*	*1*										
Omalium excavatum Stephens										*1*		
Xylodromus concinnus (Marsham)	*3*						1		*2*	*5*		
Tachinus corticinus Gravenhorst	*1*											
SCARABAEIDAE												
Aphodius lapponum Gyllenhal									*1*		*1*	
BYRRHIDAE												
Byrrhus fasciatus (Forster)	*1*											
PTINIDAE												
Tipnus unicolor (Piller & Mitterpacher)	*5*						2	*1*				
CRYPTOPHAGIDAE												
Cryptophagus denticulatus Heer	*1*											
Cryptophagus distinguendus Sturm	6 + *2*									*1*		
Cryptophagus scanicus (Linnaeus)					1							
Atomaria analis Erichson	2											
Atomaria munda Erichson	1											
LATRIDIIDAE												
Lathridius minutus (gr.) (Linnaeus)	37					3			*10*	*12*	*1*	3
Cartodere nodifer (Westwood)							1					
Thes bergrothi (Reitter)									*4*	*2*	*1*	
Corticaria elongata (Gyllenhal)	*2*											
CURCULIONIDAE												
Otiorhynchus nodosus (O. F. Müller)								*1*				

Table 6. Grouping of synanthropic taxa based on the results of the Principal Component Analysis (Fig. 7) and the value of Spearman's rank-order correlations (Fig. 8).

Group A	**Group B**
Cercyon analis (Paykull)	*Philonthus longicornis* Stephens
Bisnius cephalotes (Gravenhorst)	*Omalium excavatum* Stephens
Bisnius sordidus (Gravenhorst)	*Xylodromus concinnus* (Marsham)
Creophilus maxillosus (Marsham)	*Oxypoda haemorrhoa* (Mannerheim)
Omalium rivulare (Paykull)	*Alaobia trinotata* (Kraatz)
Aleochara sparsa Heer	*Monotoma picipes* Motschulsky
Dimetrota atramentaria (Gyllenhal)	*Cryptophagus distinguendus* Sturm
	Cryptophagus denticulatus Heer
	Cryptophagus sp.
	Latridius minutus (gr.)Linnaeus)
	Thes bergrothi (Reitter)
Shared taxa	
Philonthus politus (Linnaeus)	
Phyllodrepa floralis (Paykull)	

The Life and Death of Barn Beetles: Faunas from Manure and Stored Hay inside Farm Buildings in Northern Iceland

Véronique Forbes[a*], Andrew J. Dugmore[b] and Erling Ólafsson[c]

Figure legends

Figure 1. Map of Iceland showing the location of study sites.

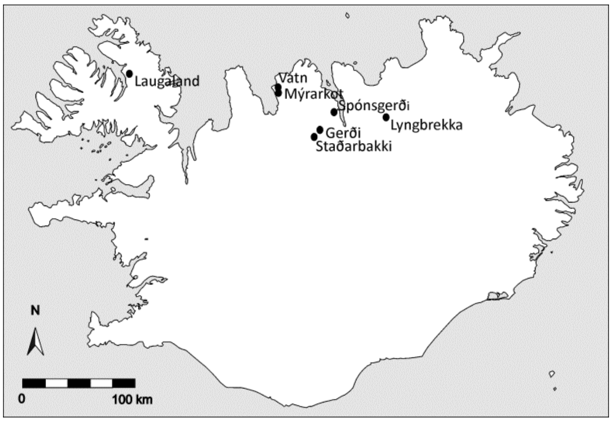


Figure 2. Sampling techniques used as part of this study: a) a pitfall trap placed in stable manure at Vatn (circled in white); b) searching through screened hay at Spónsgerði.

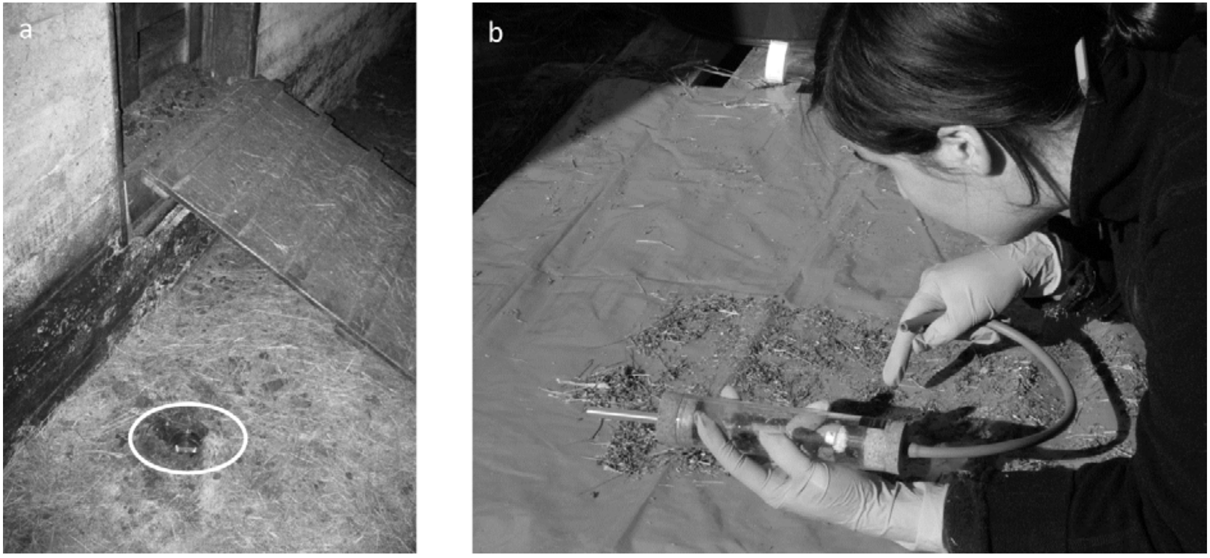
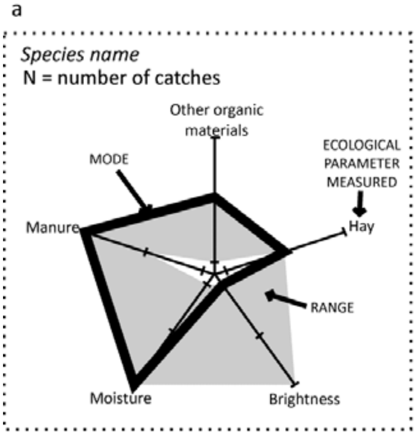


Figure 3. a) Hypothetical 'flavour diagram', with each axis representing one measured ecological parameter (b). A full black line shows the mode for each ecological parameter, while the grey area represents the whole range of conditions in which the species occurred. This one could be read as such: 'this species has been captured *n* times, most often in traps placed in damp manure in dark locations, close to stored hay and other organic materials such as wood or turf. It has not been captured from traps placed in hay, but was encountered in bright to dark locations, and from moist to damp substrates'.



b

Ecological parameters	Signification of scoring values
Proximity of manure	0: no stable manure near the trap 1: stable manure present near the trap 2: trap placed in stable manure
Proximity of hay	0: no hay near the trap 1: hay present near the trap 2: trap placed in hay
Proximity of other organic materials	0: no organic materials other than hay or manure near the trap 1: turf or wood present near the trap 2: both turf and wood present near the trap
Moisture	0: substrate dry 1: substrate moist 2: substrate damp
Brightness	0: trap location dark (10 lux or less) 1: trap location moderately bright (between 11 and 50 lux) 2: trap location bright (51 or more lux)

Figure 4. Photographs of some of the beetles collected as part of this study: a) *Nebria rufescens* from Vatn, b) *Bisnius cephalotes* from Vatn, c) *Philonthus politus* from Laugaland, d) *Creophilus maxillosus* from Vatn, e) *Tipnus unicolor* from Staðarbakki and f) *Thes bergrothi* from Staðarbakki.

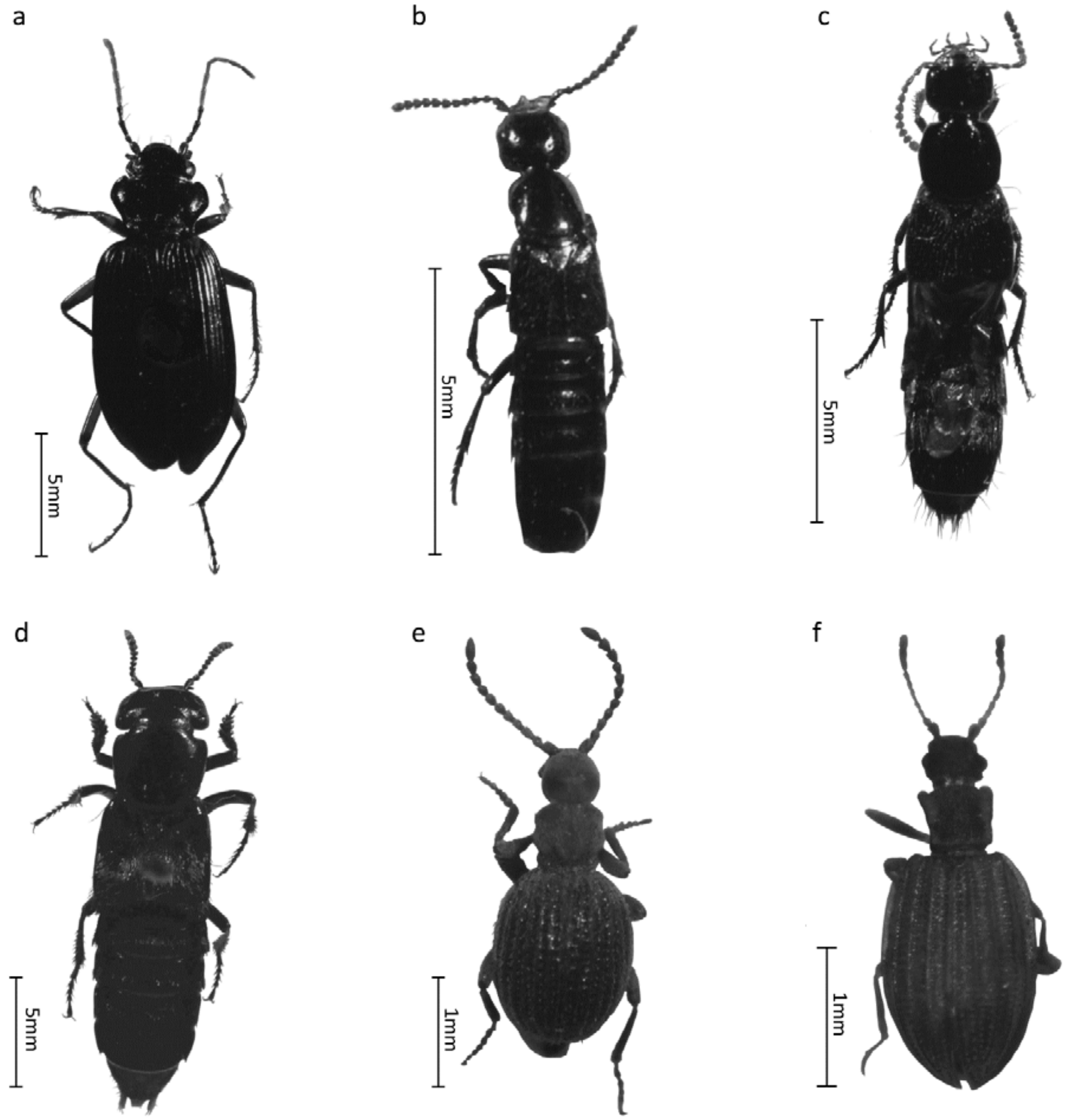


Figure 5. Tentative ecological grouping of synanthropic beetle taxa captured by pitfall traps based on information about their ecological requirements provided in the entomological literature on Icelandic beetles (Buckland et al., 1991b; Buckland & Buckland, 2006; Larsson, 1959; Larsson & Gígja, 1959; Sadler & Dugmore, 1995) and unpublished habitat data compiled from labels on specimens in the insect collection at Náttúrufræðistofnun Íslands (Ólafsson, 2008).

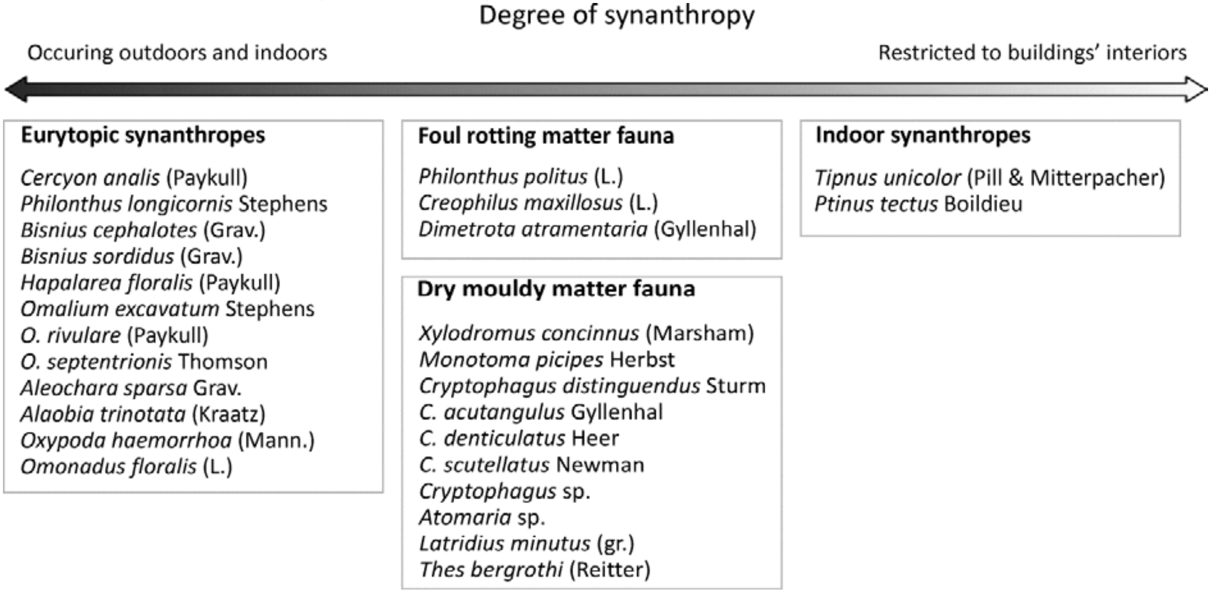


Figure 6. 'Flavour diagrams' drawn for each synanthropic beetle species captured by pitfalls traps. Similar diagrams were grouped together, allowing for each species to be classified according to the type of substrate and conditions in which it was the most often recorded. Note that these diagrams do not represent the whole range of ecological conditions in which these species occur in northern Iceland, but the range of situations in which they were captured during the present study. Taxa that could not be identified to species (*Cryptophagus* sp. and *Atomaria* sp). are not included.

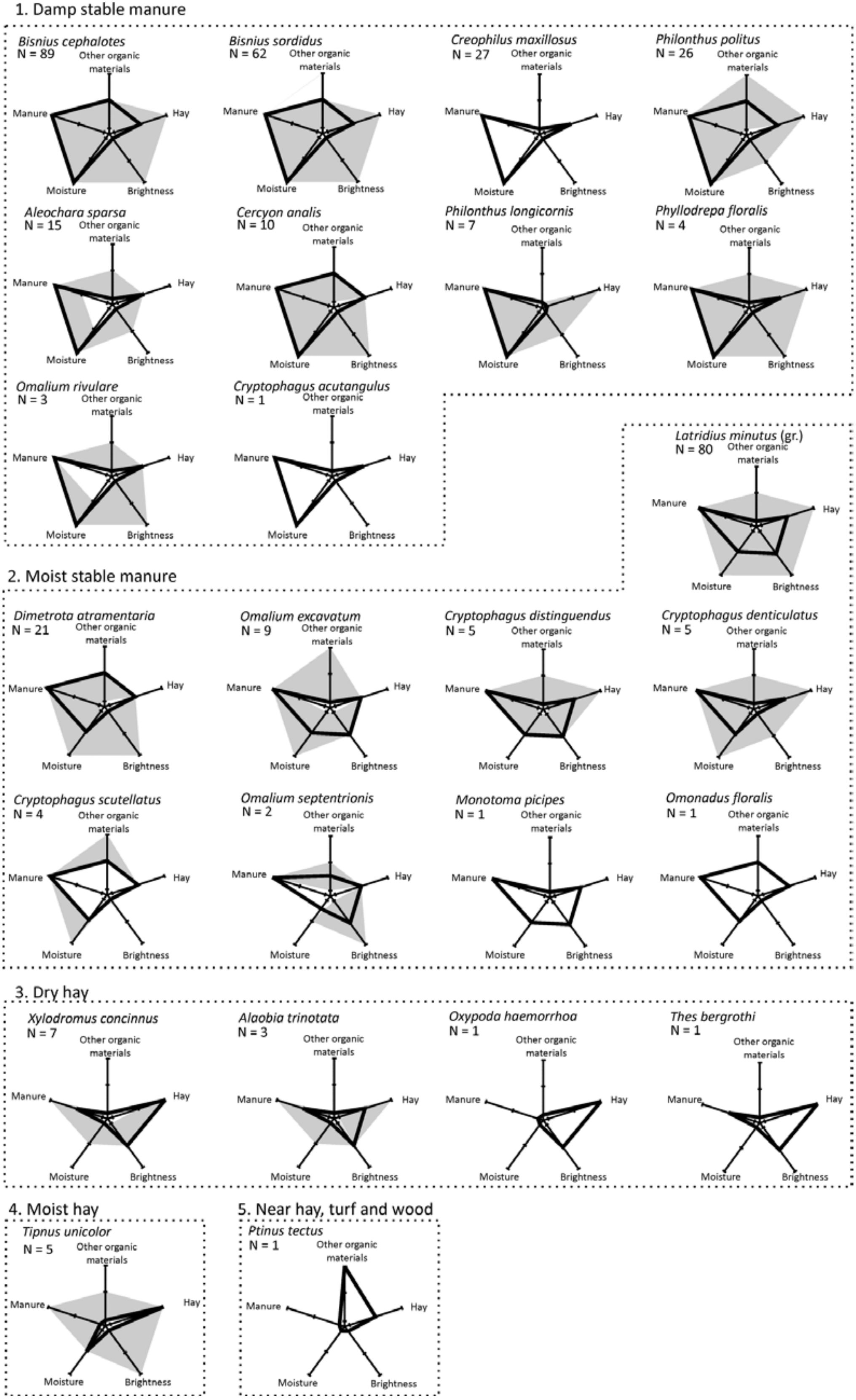


Figure 7. Principal Component Analysis conducted on raw counts of synanthropic beetles captured by pitfall traps: a) PCA plot of scores obtained for each taxon; b) PCA plot of scores obtained for each sample, with legend indicating the substrate in which each pitfall trap was placed; c) PCA plot of scores obtained for each sample, with legend indicating the moisture level of the substrate in which the pitfall trap was placed; d) PCA plot of scores obtained for each sample, with legend indicating the brightness level at each trap's location. Axis 1 accounts for 39% of the variance within the dataset and axis 2 for 27.2%. Traps that did not capture any synanthropic beetles were excluded from the analysis.

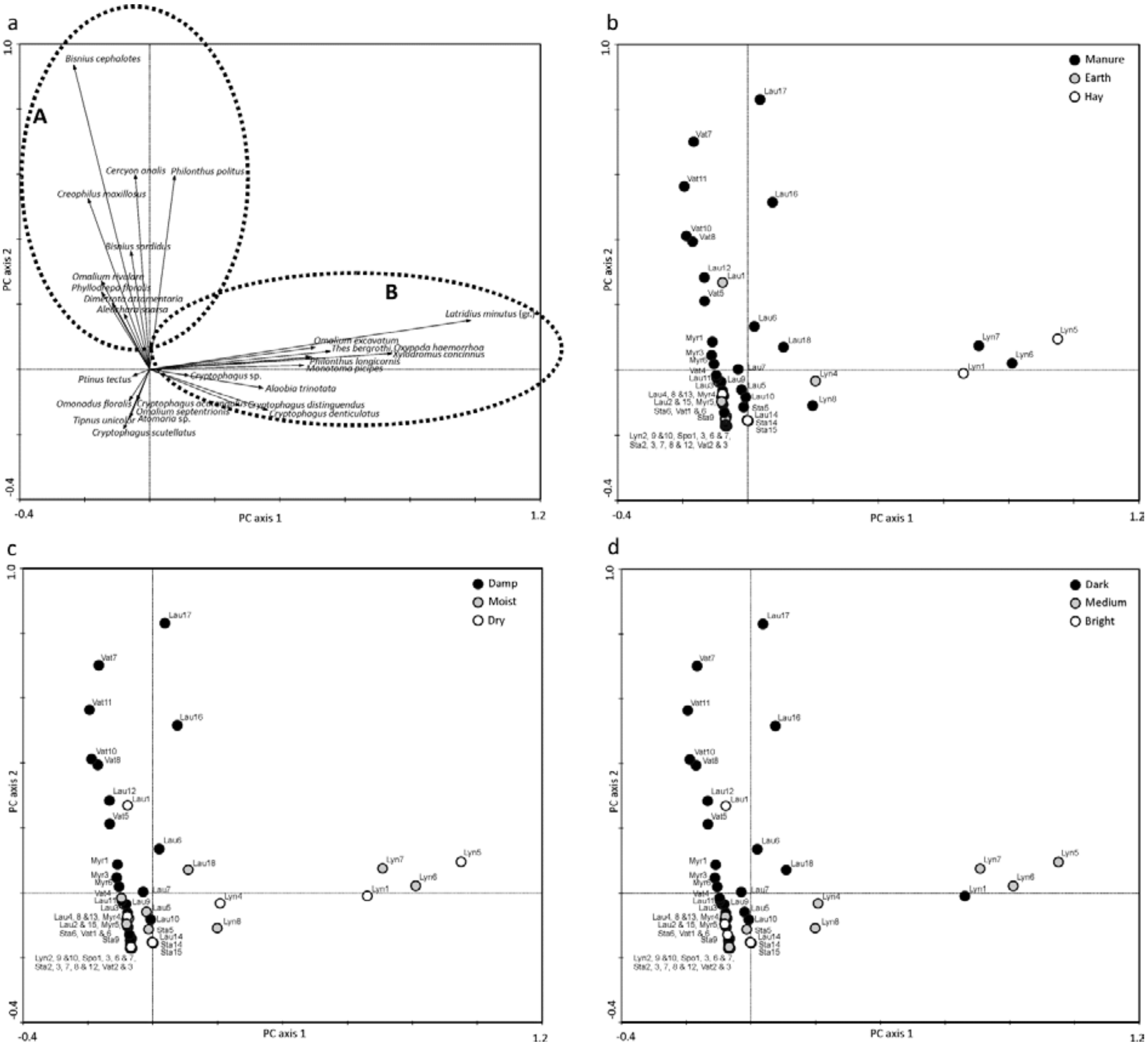


Figure 8. Constellation diagram showing statistically significant relationships between synanthropic beetle taxa captured by pitfall traps based on values of Spearman's rank-order correlations.

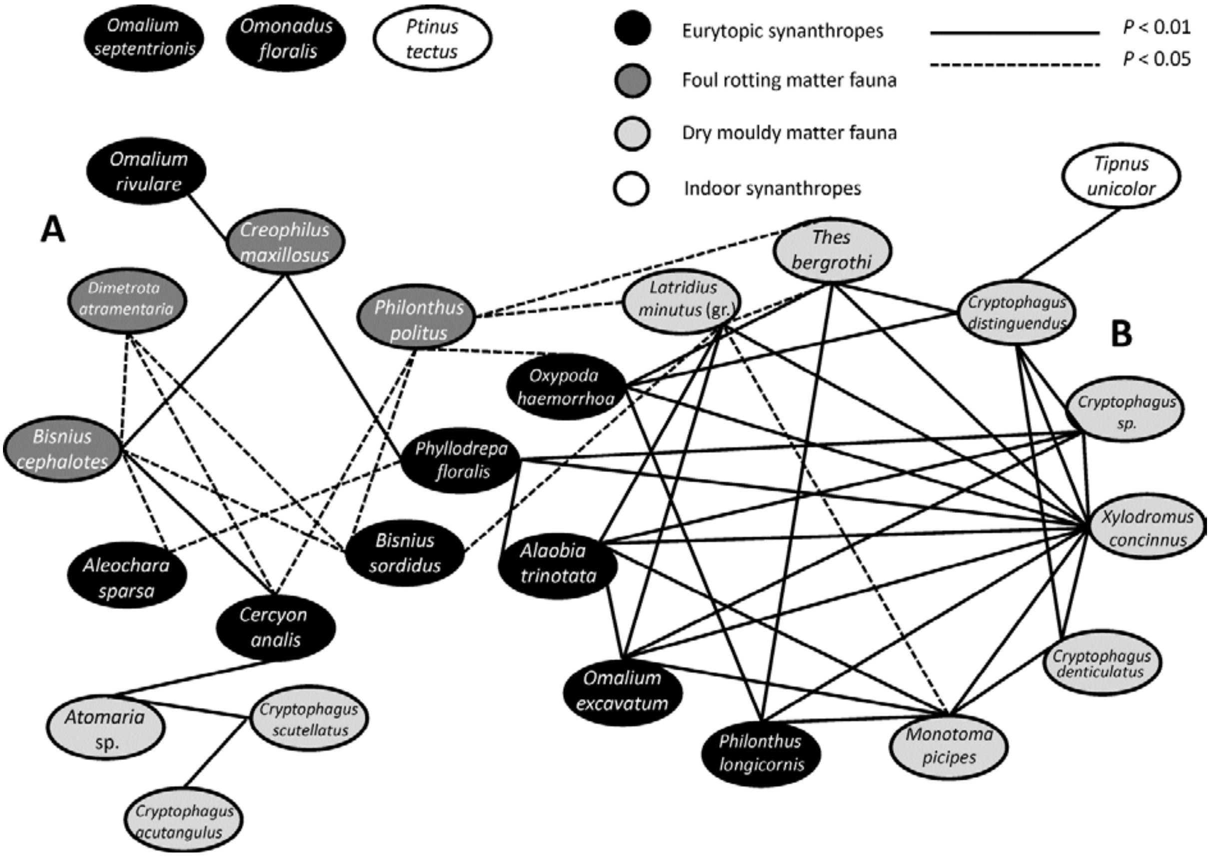


Figure 9. Tentative ecological grouping of synanthropic beetle taxa collected from screened hay based on information about their ecological requirements provided in the entomological literature on Icelandic beetles (Buckland et al., 1991b; Buckland & Buckland, 2006; Larsson, 1959; Larsson & Gígja, 1959; Sadler & Dugmore, 1995) and unpublished habitat data compiled from labels on specimens in the insect collection at Náttúrufræðistofnun Íslands (Ólafsson, 2008).

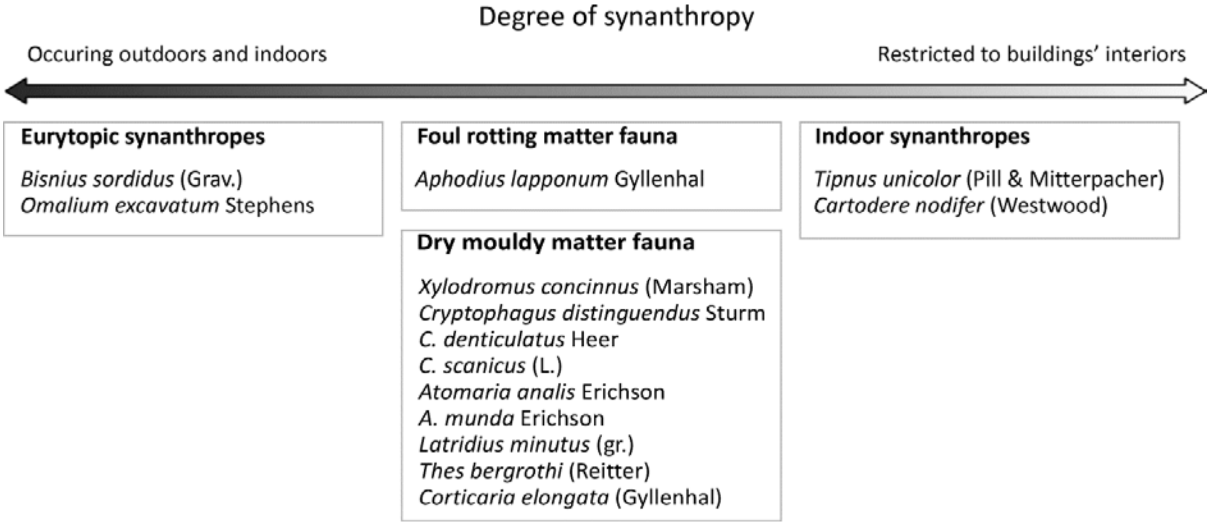


Figure 10. Bar chart comparing beetle assemblages obtained from screened hay.