Survey on the terrestrial invertebrate fauna of Surtsey with special emphasis on 2007–2021

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ABSTRACT
This paper summarises the results of standardised studies on the colonisation and succession of terrestrial invertebrate communities on Surtsey during 2007–2021, continuing from the previously published results from 2002–2006. Sampling has been carried out annually in mid-July using pitfall traps placed in permanent plots, supported by a Malaise trap in the gull colony and manual collection in various habitats. The aim has been to follow changes in the terrestrial invertebrate fauna and provide evaluation of species establishment in relation to habitat succession. In total, 410 species or species-equivalent taxa have been identified on Surtsey since the beginning of research there in 1965. Of these, 198 were regarded as settled, 33 of uncertain status and 179 not settled. Species composition and community structure were analysed by TWINSPAN and DCA ordination of material from 30 permanent plots. The results showed clear faunal differences between the well vegetated gull colony, the sand-filled lava areas, and the northern spit. The gull colony represented the most diverse habitat in terms of both specimens and species, strongly influenced by nutrient input from the breeding birds. Dipterans and hymenopterans represented the greatest diversity and specimen abundance, while staphylinid beetles and spiders were among the most successful colonisers. The succession of the terrestrial invertebrate communities followed the gradual formation of organic soil and denser vegetation cover, showing slow but steady change. This research was of great importance for understanding the colonisation of terrestrial invertebrate species and the development of their communities on newly formed volcanic islands.

INTRODUCTION
A submarine eruption started off the south coast of Iceland in November 1963, eventually lasting until June 1967 and leading to the formation of a new island that soon rose above the ocean surface (Þórarinsson 1968). As the eruption progressed, scientists gradually reached the conclusion that the island being formed had a good change to last. The eruption, and an island building up from the ocean bottom 130 m below sea level, provided a remarkable opportunity for geological studies. Biologists also recognised it as a unique chance to study how a sterile, isolated landmass would become invaded and colonised by living organisms. To ensure that the colonisation and succession of flora and fauna would remain as undisturbed by humans as possible, the island was protected by law in 1965 and reserved exclusively for scientific research, with media granted occasional access to document and communicate the ongoing succession of life on Surtsey (Svavarsdóttir & Walker 2009).

Surtsey is the southernmost offshore island of Iceland, located 32 km off the south coast and 4.8 km from the nearest small island of the Vestmannaeyjar archipelago. From the very beginning, the island has been continuously shaped by coastal erosion, with, heavy surf and severe winter storms gradually reducing its size. In 2019, the area of the island was estimated 1.2 km^2 (Óskarsson *et al.* 2020), remaining from the maximum area of 2.7 km^2 when the eruption stopped in 1967 (Jakobsson *et al.* 2000).

Surtsey´s volcanic surface can be divided into three main types (Fig. 1). Firstly, the consolidated palagonite tuff core formed from two central tephra craters, partly mantled by mobile ash that is actively reworked by wind erosion (Óskarsson *et al.* 2020). Secondly, a southern basaltic lava field, continuously eroded by open-ocean surf, especially during winter storms, forming steep sea cliffs. Thirdly, a northern boulder-based spit, built by wave driven transport of cliff material from the south, which remains highly unstable and is still periodically submerged during winter storm tides.

There have been fast and dramatic changes in vegetation cover and succession of plant communities for terrestrial invertebrates to colonise (Friðriksson 1994, Magnússon *et al.* 2009, 2014). The pace of ecological succession changed when seagulls started to breed and form a colony in the centre of the lava field in 1985 (Friðriksson 1994, Magnússon & Ólafsson 2003, Petersen 2009). Until then, plant succession was slow and relatively stable (Baldursson & Ingadottir 2007). The fertilising effect of the breeding gulls (Leblans *et al.* 2014), along with their import of nesting materials from neighbouring islands, marked a turning point in the succession of both flora (Magnússon & Magnússon 2000) and the terrestrial invertebrate fauna (Ólafsson & Ingimarsdóttir 2009). New plant species were recorded regularly thereafter, some of which did not persist for long. By 2021, 79 species of vascular plants had been recorded on the island, 66 of which were confirmed alive that year (Magnússon *et al.* 2023). Several plant species are rare and appear unable to sustain viable populations on the island. Consequently, they contribute minimally to the plant community composition and have little influence on the settlements of invertebrate species (Magnússon *et al.* 2023).

Organic soil is gradually being formed which is the essential foundation for colonisation of soil invertebrates and maintaining the humidity required by most species (Magnússon & Magnússon 2000, Sigurdsson & Leblans 2020, Möckel & Sigurdsson 2025). Sparsely vegetated lava surfaces and sand plains are generally too dry for invertebrate communities to form and develop. These substrates are porous and dry quickly on sunny days (Sigurdsson 2009, Sigurdsson & Stefánsdóttir 2015).

The terrestrial invertebrate survey on Surtsey was initiated as early as 1965, under the direction of Prof. Carl H. Lindroth and his team (Lindroth *et al.* 1973). The first author of this article, Erling Ólafsson, first visited the island in 1970 for a summer long stay to prepare for Lindroth´s fifth expedition to the island that summer. Lindroth´s final visit to Surtsey took place two years later. From then on, the first author grabbed the baton and secured the continuation of the studies. Summer long studies by author were repeated in 1971, and by biology student Jón Eldon in 1972, followed by the first author´s visits in 1974, 1976, 1981 and 1984. A gap in his research followed until 2002. Since that time, the island has been visited annually for terrestrial invertebrate monitoring, in connection with other terrestrial ecology research.

Results of terrestrial invertebrate studies up to 2006 have been reported by several authors in multiple publications. References are made here to the most important works. As mentioned earlier, Lindroth´s original project was followed by his student Ólafsson (1978, 1982). H. Bödvarsson (1982) presented the results of his collembolan studies, Gjelstrup (2000) reported on soil mites and collembolans collected in 1995, and Sigurdardóttir (2000) published her collembolan studies from the same year. Ólafsson´s studies have been carried out annually since 2002, with assistance from M. Ingimarsdóttir from 2003 to 2006. Their 2002–2006 results were published in Ólafsson and Ingimarsdóttir (2009), including a comprehensive species list covering all recorded terrestrial invertebrate taxa with assessments of species status (settled, unsettled or uncertain) and habitat-based presentations derived from DCA ordinations of pitfall trap samples.

In this paper the emphasis is on results from the standardised studies of the colonisation of terrestrial invertebrates, and on how their communities have formed and developed across different habitats during 2007–2021, in continuation of the earlier five years series from 2002–2006. In 2015, M. Alfredsson (second author) joined the project and took over the research after 2020, when the first author retired after 50 years of service.

For this publication, new species recorded during 2007–2021 have been added to the list, and all species statuses have been revised. The paper further provides updated analyses of terrestrial invertebrate community succession across habitats, derived from four successive five-year datasets covering the period 2002–2021.

METHODS

In 2002 the re-initiated terrestrial invertebrate research program was standardised. The work focused on: 1) collecting invertebrates in permanent research plots previously established for botanical studies using pitfall traps; 2) sweep netting in vegetation and across sparsely vegetated surfaces; and 3) manual searches beneath lava stones, driftwood and carcasses on the ground. This collecting program has been repeated annually since 2002, and sampling has been carried out each year over continuous four-day period in mid-July. In 2008, a Malaise trap was first installed in the gull colony to obtain better information on that most important habitat.

These standardised data collection methods were meant to give comparable results as the studies progressed, to indicate the succession of the terrestrial invertebrate fauna, to track new settlers, and to document how communities form and evolve.

Weather conditions prior to and during fieldwork can influence sampling efficiency; for example, rainy or windy days may prevent sweep netting and reduce the accessibility of invertebrates sheltering in vegetation or soil. As a result, short sampling periods can be affected by such variability.

Figure 1. Locations of the 30 permanent terrestrial invertebrate pitfall trapping sites on Surtsey 2002–2021. Dense vegetation appears in green colour showing the gull breeding colony in a Worldview 2 image from 8 August 2021 (Source: Esri, Maxar, Earthstar Geographics, and the GIS User Community).

Pitfall trapping

In 2002, pitfall traps were placed in 21 square plots (10 x 10 m) used by botanists to monitor vegetation succession and biomass in different habitats (Fig. 1). One plot, located at the northern foothills of the palagonite hills (R25), which no longer is used in the botanical studies due to its unstable surface, has continued to be included in this study. Three additional trap sites, not associated with the permanent plots, were established in 2002 to detect potential human effects. They are traps R27 and R28. adjacent to the research hut and trap R26 at the edge of the helicopter platform (Fig. 1). No trapping was conducted on the hard tuff surfaces on the hills where pitfall traps cannot be installed effectively.

In 2005, two new plots were added on the northern spit (R29 and R30), followed by a third in 2015 (R37). In 2008, two additional plots (R31 and R32) were established in an AA-lava flow, an area with very slow vegetation succession. A total of 30 traps have been operated for varying length of time up to 2021 (Fig. 1).

To summarise, five categories of trap sites were defined: 1) bare and sand-filled lava with an active breeding colony of large gulls; 2) sand-filled lava without breeding gulls; 3) mostly bare lava outside the gull colony; 4) the sandy northern spit, periodically under overflowing conditions during wintertime; and 5) areas possibly influenced by human activity around the research hut (Fig. 1).

Each pitfall trap consisted of a plastic container with 6.3 cm diameter opening and depth of 6.5 cm, filled up to one quarter of its volume with 4% formaldehyde as well as a drop of soap to break the surface tension. The trap was covered with a round plastic lid to prevent rain from entering and was kept approximately 4 cm above the surface using 6 inches nails. Within the gull colony the traps were shielded with wire mesh screens to protected them from curious gulls. To minimise the impact on the fauna within the permanent plots, a single trap was placed near the centre of each plot during each field visit and left running for approximately 70 hours (Fig. 2).

Figure 2. A pitfall trap in Plot 22. Photo Erling Ólafsson.

Malaise trap

Malaise traps are designed to capture flying insects and operate automatically once deployed. On Surtsey, this device was first set up in 2008 and has been operated continuously since then. It was located within the oldest part of the gull colony, at a fixed position next to plot R3 (Fig. 1), set up for approximately 70 hours, weather permitting (Fig. 3). Operation of the Malaise trap can be restricted by adverse weather conditions, particularly heavy rainfall and strong wind.

Figure 3. The Malaise trap in oldest part of gull colony. Photo Erling Ólafsson.

Manual sampling

Manual collecting was performed to sample invertebrates that might escape the trapping methods. This was mainly based on sweep netting conducted in vegetation in the gull colony and areas of lush vegetation elsewhere, for instance from lyme grass stands (*Leymus arenarius*) and sea sandwort (*Honckenya peploides*) on the northern spit and inside the larger crater, Surtungur. Secondly, direct picking was performed where conditions allowed, from beneath lava stones and driftwood, carcasses and among roots of plants. Thirdly, on top of the eastern palagonite tuff crater, Austurbunki, the ruins of a lighthouse were regularly checked as newly windblown insects often accumulate there, both inside and around cracks emitting hot steam.

Storage of material

Specimens collected by pitfall traps were fixed in formaldehyde (4%) on site and subsequently preserved in 80% ethanol for long-term storage. Malaise trap specimens were collected directly into ethanol. Most manually collected specimens were also placed directly in ethanol, except for lepidopterans and coleopterans, which were pinned; A small number of dipteran and hymenopteran specimens were likewise pinned. All research material is housed in the scientific collections of the Natural Science Institute of Iceland.

Identifications

Identifications of the collected material were carried out in the laboratory. Most insect orders were determined to species level except for certain families within the Diptera and Hymenoptera, for which taxonomic expertise is limited, (e.g., Sciaridae and Cecidomyiidae within Diptera, several families or species groups within Hymenoptera, and aphids and coccoids within Hemiptera). In such cases, specimens were assigned to unnamed morphospecies or grouped at the genus level and listed accordingly to obtain an approximate estimate of species diversity. Springtails (Collembola) and mites (Acari) were treated in the same manner as in Ólafsson and Ingimarsdóttir (2009), and new specimens were extracted, counted and stored.

Data analysis

The assessment of terrestrial invertebrate communities is based on data obtained from pitfall traps placed in permanent plots across multiple locations on Surtsey between 2002 and 2021. Species in individual samples were identified and specimens counted, giving numerical values allowing neutral comparison of invertebrate faunas under different environmental conditions. The data were analysed using, firstly, Two-Way Indicator Species Analysis (TWINSPAN), secondly, Detrended Correspondence Analysis (DCA) in PC-ORD version 6.08 (McCune and Mefford 2011).

A data matrix of 30 samples, including 160 arthropod species or species equivalent taxa was used for analysis. The dataset also included an unidentified Pseudococcidae species, presumably with species status. Species groups comprising more than one species, such as Aphididae, were omitted, as were all Colembola and Acari, except for the bdellid species *Neomolgus littoralis*, a habitat describing species on the northern spit. Prior to analysis, species abundances data were standardised by trap days and number of years and finally log(x+1) transformed. Rare species were downweighted.

TWINSPAN was run with user defined cut levels of 0, 0.2, 0.5, 1.0, and 2.0 to define pseudo-species categories. Axis scores were generated using pseudocanonical correspondence analysis. The resulting classification was used to identify distinct arthropod assemblages and their indicator species.

For the analysis of pitfall trap data, DECORANA ordination (Hill 1979) was used to assess similarities between sampling plots. As the four-day annual samples were regarded too small for meaningful ordination, five-year data sets were combined to trace successional changes over time. Accordingly, the material from 2002–2021 was divided into four data sets prior to analysis (2002–2006, 2007–2011, 2012–2016, and 2017–2021). The small annual samples are sometimes affected by unfavourable weather during the sampling days. The impact of a single defective sample among five years should therefore be reduced. Species and taxa treated equivalent to species were included, and the number of individuals captured was standardised as catch per day (24 hours). Rare species, and those of minor significance in the plot-fauna were down weighted to avoid unrealistic influence on the results. Rare species are not necessarily important elements in describing the functional composition of the plot fauna, as they may represent unsettled, randomly windborne stragglers.

RESULTS

The species list

A revised species list (1965–2021) was compiled, including all terrestrial Arthropoda, Mollusca and Annelida i.e. including revised earlier data together with new additions from 2007–2021 (Supplement S1). In the new list, seven species from previous version have been omitted, species originally found

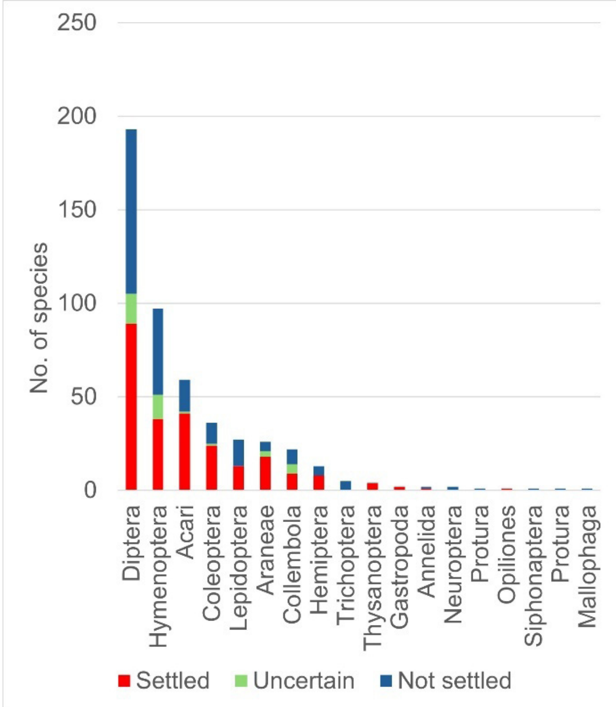

Figure 4. Terrestrial invertebrates, orders and higher taxa, collected on Surtsey during the 2002–2021 survey, no. of species and status evaluations; red: settled; green: status uncertain; blue: not settled. For further information on status evaliations reference is made to Appendix 1.

dead in drift material on the shore during the early years and not rediscovered since. The updated species list comprises 410 species or species equivalent taxa, including 136 new records from 2007–2021.

Species were evaluated as either settled, unsettled or of uncertain status (Fig. 4). With new data some of the previous evaluations have changed. The annual standardised samplings have provided the basis for these evaluations. In many cases, there is little or no doubt about stable settlement, species collected every year, often in considerable numbers. Many species are not easily detected in the field yet were collected in certain years and habitat conditions suggest they should be regarded as settled. In total, 198 species are considered settled. Thirty-three species are currently of uncertain status, but continued annual sampling may confirm settlement for many of them. The remaining 179 species are certainly, or most likely, not settled, although some of them may deserve reclassification to the uncertain category (Fig. 4).

TWINSPAN results

The TWINSPAN resulted in a clear first division of the 30 plots into two groups (Fig. 5). Ten plots

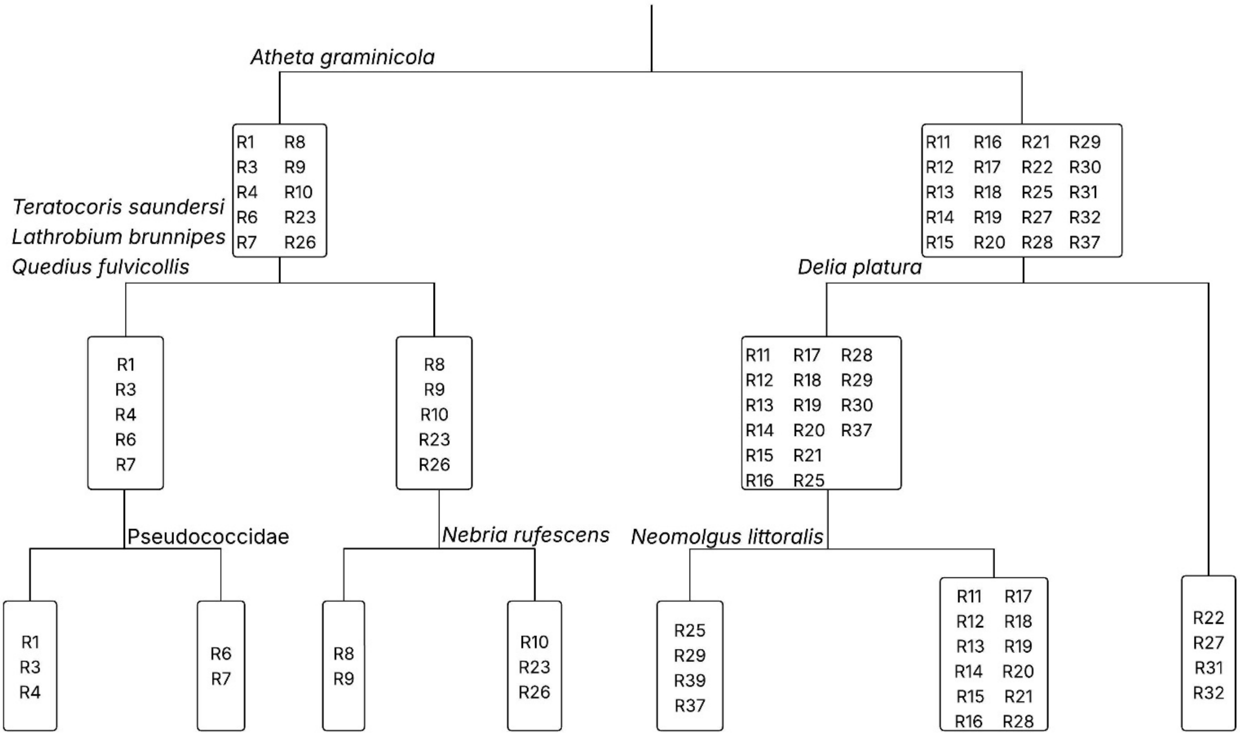

Figure 5. TWINSPAN results from 30 pitfall trap plots on Surtsey 2002–2021 with terrestrial invertebrate species directing divisions. Rxx stands for the trap number on Fig. 1.

fell within the gull colony that began to develop in 1986 in the centre of the lava field south of the main craters. The presence of the breeding gulls, together with their nutrient rich droppings and food remains, led to a quick succession of the vegetation cover and the development of luxuriant plant growth. The remaining twenty plots are located on less vegetated sand-filled lava and the sandy surface of the northern spit, areas largely unaffected by breeding gulls, except perhaps to minor degree in recent years. This division is directed by the staphylinid beetle, *Atheta graminicola*, common within the colony but absent on the less vegetated dry sandy grounds.

A subdivision within the gull colony separates plots located in the oldest part of the colony (R1, R3, R4, R6, R7), characterised by dominating grasses leaving other plants limited possibilities to grow, and marginal plots (R8, R9, R10, R23, R26) still under marked succession where grasses have not taken over completely. The species primarily responsible for this division are the hemipteran bug *Teratocorix saundersi* and the staphylinid beetles *Lathrobius brunnipes* and *Quedius fulvicollis*, which are associated with the more developed side. It is worth mentioning that an unidentified pseuducoccid species, expected to feed on grass roots, separates two plots within the oldest part dominated by the grasses *Festuca richardsonii* (R6, R7) and *Poa pratensis* and *Leymus arenarius* (R1, R3, R4) all of which are omnipotent in that area. The other branch also subdivides. The first group (R8, R9) comprises two plots that, given the ongoing succession, will likely converge with the most advanced plots. The second subgroup represents true marginal plots (R10, R23, R26), characterised by more open surface and diverse flora. The relatively recently established carabid beetle *Nebria rufescens*

Figure 6. The carabid beetle *Nebria rufescens*, a relatively new settler on Surtsey. Photo Erling Ólafsson.

Figure 7. The dbellid mite *Neomolgus littoralis*, characteristic for the bolder beaches of northern spit. Photo Erling Ólafsson.

(Fig. 6), which prefers open surface for its quick movements, is responsible for this division. In fact, one of these plots (R26) lies beyond the colony boundaries, it is located at the edge of the helicopter platform near the research hut. Gulls tend to bathe in temporary rainwater pools on the concrete platform, leading to rich fertilisation round the edges.

The remaining 20 plots are all situated on sandy grounds, spread widely over the island, mostly unaffected by breeding gulls (Fig. 5). A second split, driven by the common anthomyiid fly *Delia platura*, whose larvae develop on plant roots, groups 16 plots together while separating four plots (R22, R27, R31, R32) from the rest. Three of these plots are situated in lava that gulls appear to regard as future breeding grounds. The fourth plot (R27) is quite anomalous. It is sheltered under a terrace at the research hut and was originally established to assess possible effects of the hut and human activity. This assemblage of four plots is stabilised in the Twinspan graph. The other branch splits convincingly. The low-lying spit on the northern side of the island is extremely unstable and is regularly submerged by seawater during fierce winter storms. In autumn, this area is also affected by a large grey seal (*Halichoerus grypus*) rookery, which contributes notable amounts of marine-derived nutrients to the northern spit (Magnússon *et al*. 2020). A cluster of four coastal plots (R25, R29, R30, R37) is caused by the halophilic bdellid mite *Neomolgus littoralis* (Fig. 7).

DCA-ordination

The results of the DCA ordination revealed substantial variation in community structure (Fig. 8). Axis 1 had a gradient length of 3.11 standard deviation (SD) units and an eigenvalue of 0.645, indicating strong species turnover and supporting the use of a unimodal ordination method. Axes 2 and 3 had gradient lengths of 2.34 and 1.98 SD units, respectively, with corresponding eigenvalues 0.208 and 0.110.

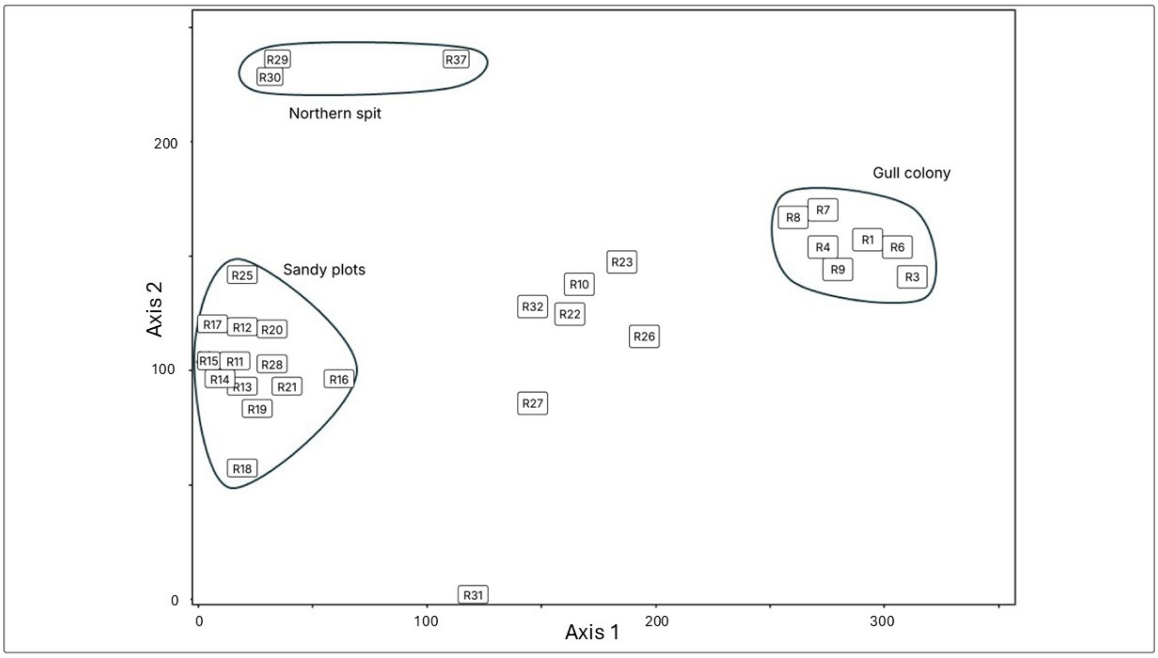

Figure 8. DCA-ordination results from permanent pitfall trap plots on Surtsey 2002–2021. Encircled upper left: northern low spit (3 plots); lower left: sandy ground (13 plots); far right: gull colony (7 plots); outside circles: marginal plots near gull colony (R10, R22, R23), human effect study traps near hut (R26, R27), recent plots in AA-lava (R31, R32). See Fig. 1 for locations.

The DCA ordination diagram shows a clear separation of plots and great variation along Axis 1 (Fig. 8). Three clusters of plots will be considered specially. On the right side are plots within the oldest part of the gull colony and on the left side two clusters of plots on less affected sandy grounds, firstly on sand-filled lava, secondly plots on the northern spit. The decided cluster of plots on sand-filled lava indicates a stable situation in a habitat with limited vegetation succession. In the middle of the diagram are plots some of which with uncertain future. There are two marginal plots in the gull colony (R10, R23) expected by time to move further towards the left side. To mention, R10 will fall into the ocean within few years. Two of the plots established to trace possible human effects around the hut are located there in the diagram, a plot at the helicopter platform (R26) affected by gulls attracted by incidental rain pools on the platform is grouped with the gull colony marginal plots. The second plot under the terrace at the hut (R27) shows that the location is affected by human activity. A third plot (R28) on the opposite side 6m away from the hut shows that human effect round the hut does not reach that far, the plot being placed with other sand-filled lava plots on the left side of Fig. 8.

Pitfall traps results

There are three main types of habitats worth considering, gull colony (8 plots), sandy plots outside the gull colony (12 plots) and the low northern spit (3 plots) (Table 1). The remaining seven plots stand out and are not easily grouped with the others. The catches from all traps within each habitat were combined, giving the results presented in Table 1 where the higher taxa are summarised. These are raw counts, the differences in trap numbers and sampling duration have not been accounted for. As expected, the superiority of the well vegetated gull colony is obvious considering number of specimens and species, with ca. 35.700 specimens of at least 140 species. In the sandy areas outside the gull colony, vegetation cover is limited, with little or no vegetational succession, and there the surface is unstable and regularly on the move with blowing winds. The fauna on the northern spit does not establish so easily as most winters the low-lying surface is overflooded in harsh storms. The results on species basis are shown for each habitat in Supplements S2–4.

Table 1. Terrestrial Invertebrate, orders and higher taxa, collected on Surtsey during the 2002–2021 survey with no. of specimens and species.

	Gull colony plots 8 traps/20 years		**Sandy plots outside gull colony 12 traps/20 years**		**Spit plots 3 traps/17, 16, 7 years**	
Higer taxa	**No of specimens**	**No. of species**	**No of specimens**	**No. of species**	**No of specimens**	**No. of species**
Collembola	11.726	Uncertain	1.146	Uncertain	679	Uncertain
Hemiptera	941	6	224	3	281	1
Thysanoptera	232	4	3.015	2	175	1
Lepidoptera	6	2	13	4	2	2
Coleoptera	2.490	27	1.524	9	47	3
Hymenoptera	312	26	11	7	3	2
Diptera	1.063	60	2.885	43	373	22
Araneae	2.394	13	1.282	8	229	4
Opiliones	2	1	1	1		
Acari	16.486	Uncertain	10.345	Uncertain	2.169	Uncertain
Enchytridae	16	Uncertain	6	Uncertain	4	Uncertain
Gastropoda	8	1				
Nematoda	71	Uncertain	4		7	Uncertain
Total:	**35.747**	**140**	**20.456**	**77**	**3.969**	**35**

Malaise trap results

Flying insects account for the bulk of collected specimens in the Malaise trap (Table 2). Bugs crawling up the tent sheet to the top and into the collecting jar (*cf.* Hemiptera, Acari, Araneae, Coleoptera) are of minor importance. As the activity of flying insects is dependent on weather conditions which can be either excellent, unfavourable or sometimes impossible, running the Malaise trap for only four days gives results that are rarely comparable between years (Fig. 9).

The combined fourteen-year catch provides a clear indication of the composition and character of the flying insects fauna within the gull colony (Table 2), including both species composition and a rough indication of species populations and their importance. The total number of species equivalent taxa is 196 (Acari omitted), representing the absolute minimum number of species. In total 32.756 specimens were collected, with annual totals ranging from 601 to 5,083, and an annual average of specimens of 2,340 (Supplement S5). Species of the order Diptera dominated the fauna in both specimen count and species richness, followed by the Hymenoptera. Hemipterans ranked third in specimen number, largely due to unidentified aphids (Table 2).

Table 2. Total catch during 2008–2021 by a Malaise trap on Surtsey. Orders and other high taxa, no. of specimens and species caught.

Higer taxa	No. of specimens	No. of species
Diptera	28.809	107
Hymenoptera	1.754	62
Hemiptera	1.725	3
Acari	275	Uncertain
Lepidoptera	119	9
Araneae	40	5
Coleoptera	26	8
Trichoptera	4	1
Thysanoptera	4	1
Total:	**32.756**	**196**

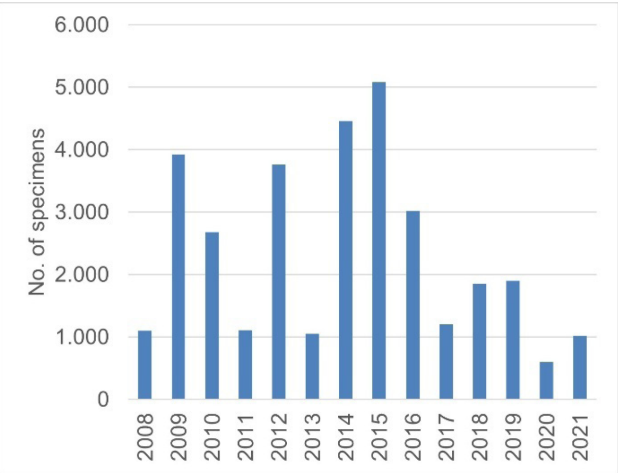

Figure 9. Yearly catches during 2008–2021 (no. of specimens) by a Malaise trap on Surtsey.

DISCUSSION

Since its formation, Surtsey has provided scientists with exceptional opportunities to study how an isolated, barren and inorganic landmass becomes colonised by life. Similar events have been documented in Indonesia, where explosive eruptions on the volcanic island Anak Krakatau destroyed large parts of the island and eliminated its ecosystem. Subsequent recolonisation followed (New 2015). As Anak Krakatau lies in the Asian tropics, the circumstances differ markedly from those of subarctic Surtsey in the North-Atlantic, which is both more isolated and strictly protected.

The terrestrial invertebrate project on Surtsey was initiated in 1965, about a year and a half after the eruption that formed the island began far off the south coast of Iceland, while volcanic activity was still ongoing (Þórarinsson 1968). Colonisation and successional development of the terrestrial fauna was slow during the initial decades but gradually stabilised. A major milestone was reached in 1986 when several pairs of lesser black-backed gulls (*Larus fuscus*) joined the already breeding European herring gulls (*L. argentatus*) to establish a breeding colony on the lava field along the southern side of the island (Petersen 2009). Gull colonisation was a successful, and the number of breeding pairs increased gradually in the years that followed. As the island lacked sufficient nesting material for the expanding colony, the gulls initially transported some from the mainland or neighbouring islands. They also brought food from the ocean to feed their chicks, enriching the soil with food remains and droppings (Magnússon & Magnússon 2000, Sigurdsson & Leblans 2020). This nutrient input had a substantial fertilising effect that benefitted the vegetation and improved the conditions for invertebrate colonisation.

Dispersal of terrestrial invertebrates has been accounted for in a previous publication, wind-borne, sea-drifted and bird-assisted transport (Ólafsson & Ingimarsdóttir 2009). The influx of wind-borne invertebrates, arriving from other islands of the archipelago, from mainland Iceland, and even from distant Europe, was regularly witnessed in the earliest years, when the possibilities for colonisation were extremely limited (Lindroth *et al.* 1973, Ólafsson & Ingimarsdóttir 2009). Such influxes happen regularly with favourable winds, sometimes clearly indicated by the species compositions of samples. In 2005 and 2009, several species originating from Iceland's mainland wetlands were caught, species with no possibility of establishing populations on the island due to the absence of wetlands.

The terrestrial invertebrate faunas of different habitats

The invertebrate fauna within the gull colony has received particular attention in this study. As described earlier, data were collected not only through pitfall trapping and sweep netting, as in other habitats, but also by the use of a Malaise trap. The vegetation in the colony is continuously developing, with the succession still ongoing and the vegetated area gradually expanding (Magnússon *et al.* 2023). The invertebrate fauna shows similar pattern, new settlers continue to be recorded, and their establishment is monitored through the annual surveys.

The character of the invertebrate fauna within the colony is best appreciated by examining the species list in Supplement S2. Among ground-living coleopterans, the staphylinids are dominating, not surprisingly as many are excellent flyers and readily dispersed to islands by favourable winds (Hansen *et al.* 2018). Twenty species of staphylinids have been recorded in the colony, *Atheta fungi* and *A. graminicola* being the far most numerous ones. *Oxypoda haemorrhoa* should also be noted. Seven of these species were also caught by the Malaise trap but in low numbers. One of the most common staphylinid species in Iceland, *Atheta atramentaria*, only a single specimen was extracted from the pitfall material. In the early 1970s, influxes of this species carried by northerly winds were regularly observed, as the beetles are active fliers under calm weather conditions (Ólafsson 1978). In contrast to the pitfall samples, *A. atramentaria* was the species most frequently captured by the Malaise trap. It depends

Figure 10. The carabid beetle *Amara quenseli*, an early settler on Surtsey prefering sandy habitats with low vegetation cover. Photo Erling Ólafsson.

on the presence of livestock feces in order to establish a population (Larsson & Gígja 1959). These beetles are generally active fliers that locate their preferred food while flying, rather than on the ground. This may explain the difference in capture efficiency between the Malaise trap and the pitfall traps for this species, which is not regarded as a potential coloniser of Surtsey.

Five species of carabid beetles were recorded in the colony, all caught in low numbers except for *Amara quenseli*. This species, however, is restricted to the marginal areas of the colony as its preferred habitat is the surrounding sandy ground (Fig. 10).

A surprisingly high numbers of hymenopteran species (and species equivalents) were trapped in the colony, a total of 73. The Malaise trap was much more efficient than the pitfall traps with 62 species caught compared with 27 by the latter. Fifteen species were caught by both methods, while 12 recorded only from pitfall traps. The pitfall samples were dominated by small hymenopteran species, primarily parasitoids of aphids or secondary parasitoids.

Aphids are important hosts for parasitic hymenopterans in the gull colony, with a total of 2,354 specimens captured across all traps, and they were also collected in considerable numbers by sweep netting. Unfortunately, the aphids have not been identified to species level.

An interesting agromyzid dipteran *Taumatomyia glabra* was recorded on Surtsey, the first records of this species for Iceland (Fig. 11). It´s larvae feed on aphids that suck plant roots (Nartshuk & Andersson 2012). A braconid species, *Monoctonus caricis*, was the most abundant parasitic wasp, with 317

Figure 11. An agromyzid dipteran, *Thaumatomyia glabra*, which larvae feed on root sucking aphids. First Icelandic records on Surtsey. Photo Erling Ólafsson.

individuals caught in the Malaise trap and 67 in the pitfall traps, another example of a parasite on aphids (Lindroth *et al.* 1973). The second most numerous species was the eulopid *Chrysocharis pallipes* (326 specimens), with all but three specimens collected by Malaise trap. This parasitoid is known to utilize leaf-mining larvae as hosts (Lindroth *et al*. 1973*)*, such as species within the dipteran family Agromyzidae. Ichneumonidae is by far the most diverse family of hymenopterans in the colony with 34 morphospecies listed plus additional ones collected by sweep netting. Unfortunately, many of the hymenopteran morphospecies remain unnamed.

Dipterans are the most species-rich group in the Icelandic terrestrial invertebrate fauna (Ólafsson 1991), a pattern that is reflected in the Surtsey fauna. Although pitfall traps are designed to capture ground-active, often flightless invertebrates, many flying insects are also active on the ground and therefore frequently caught. Anthomyiidae flies were the most numerous of dipterans in the colony, with many species supposed to lay their eggs among plant roots (Baba *et al*. 2019). This was reflected by the pitfall catches, where females dominated over males, whereas the opposite pattern was found in the Malaise trap samples. Another factor that influenced the pitfall catches was the use of lids placed over the traps to protect them from rainfall, flies tended to seek shelter under the lids, which increased their likelihood of being captured.

As expected, Dipteran species dominate in the colony both in species richness and number of specimens. The total number of species trapped was 110. The Malaise trap captured 106 species, whereas 60 were collected by pitfall traps, with only four species obtained exclusively by pitfall trapping (sweep net results are here not considered). As noted above, anthomyiid species were particularly numerous, 17 species were caught by the Malaise trap, 14 of which were also obtained by pitfall traps, indicating that females entered the vegetation cover to oviposit in the soil.

The saltwater chironomid *Halocladius variabilis*, whose larvae develop in marine coastal water (Hrafnsdottir 2005), was collected in the greatest numbers (5,847 individuals), nearly all by the Malaise trap, and it was also collected in additional numbers by sweep netting. Five other species exceeded one thousand specimens: *Rhamphomyia simplex* (2,806), *Leia fascipennis* (2,577), *Dilophus femoratus* (2,025), *Botanophila fugax* (1,596), and *Dolichopus plumipes* (1,318). Many other species were caught in hundreds of specimens.

Spiders, typical ground-dwelling invertebrates, proved to be both diverse and numerous in the colony. A total of 14 linyphiid species were recorded. There were few samples from the Malaise trap and of little significance. The most numerous species were *Erigone arctica* (1,077), *Allomengea scopigera* (421) and *Savignya frontata* (230). Unidentified juveniles were also common (602). Two species of the family Lycosidae were present in the colony, *Pardosa sphagnicola* and *P. palustris* (Fig. 12), the former being encountered more frequently.

Although collembolans and mites obtained during the new research period were not identified to species or potential species level, they were extracted from the trap samples and counted. In total, 11,726 collembolans and 16,486 mites were counted. These

Figure 12. A lycosid spider, *Pardosa palustris* on Surtsey, a female with an egg sack releasing the newly hatched young. Photo Erling Ólafsson.

numbers indicate that soil invertebrates are far more abundant in the gull colony than in other habitats on the island, which is consistent with the substantially greater development of organic soil in that area compared with the sandy plots. Similar results have been reported for soil nematodes inside and outside the gull colony on Surtsey (Ilieva-Makulec *et al.* 2015). Comparative data from the sandy plots are presented later. Further information on other, less prominent species groups is provided in Supplement S2.

A considerable part of the island´s surface outside the gull colony consists of sand-filled lava, where several species of vascular plants grow, although the overall vegetation cover remains very low (Magnússon *et al.* 2023). Consequently, invertebrates have little shelter to seek, as the surface is unstable, sand grains are constantly shifted by wind and become hot and dry under sunny conditions. Consequently, this habitat is unstable and largely inhospitable, suitable only for the lesser part of the invertebrate fauna. The succession of this habitat has been slow over the years, and the fauna appears to have remained unchanged in recent years. The research has been based primarily on pitfall trapping in 12 sandy plots, and to a lesser degree on sweep netting and direct manual collection. Examination of the species list and abundance data in Supplement S3 illustrates the overall composition of the invertebrate fauna under these conditions. The dipteran family Anthomyiidae was particularly notable, with several species presumed to have root-feeding larvae (Baba *et al*. 2019), and no other species group was as diverse. The most abundant species *Botanophila fugax* and *Delia setigera* dominate, followed by *D. fabricii* and *D. platura* and lastly *D. angustifrons*, *D. echinata* and *Lasiomma picipes*. Of other dipteran groups, only the chironomid *Halocladius variabilis* was collected in notable numbers, as in the gull colony. However, this species is blown in from the Surtsey coastline where its larvae develop in marine salt water and is therefore not representative of habitats other than coastal ones. The thripid species *Thrips vulgatissimus* was the invertebrate caught in the greatest numbers. It is a sap-sucking insect on Surtsey associated with sea sandwort (Lindroth *et al*. 1973), the dominant plant in this habitat. This is also the proper habitat for the carabid beetle *Amara quenseli* which prefers open sandy surfaces with limited plant cover (Larsson & Gígja, 1959). Three linyphiid spiders were also characteristic of this environment. *Erigone arctica* was a generalist species abundant both here and in the gull colony, whereas *Meioneta nigripes* and *Islandiana princeps,* were largely confined to this habitat.

Compared with the gull colony, the numbers of caught invertebrates were much less in the sand-filled lava than in the densely vegetated colony where organic soil is forming. A total of 1,146 collembolans and 10,345 mites were counted, the latter number consisting mostly of tiny juveniles. Further information on other less important species groups is provided in Supplement S3.

The conditions on the northern spit adjacent to the northern slopes of the tephra craters, make it difficult for terrestrial invertebrates to settle. The elevation is only few meters above sea level, and the plain is inevitably flooded during winter storms at high tide, with the surface repeatedly eroded and sediment and driftwood washed back and forth. The soil is saline and unsuitable for most terrestrial invertebrates, only species adapted to such oceanic influences were able to persist. As a result, the invertebrate fauna was poor and unstable. The beach vegetation is adapted to these conditions (Magnússon *et al.* 2023), although still subject to considerable erosion. Windborne flying insects tended to gather in the vegetation and were best surveyed by sweep netting.

Three pitfall traps on the spit (R29, R30, R37) were operated for fewer seasons than those in gull colony and the sand-filled lava, and the raw counts are therefore not fully comparable. They nevertheless provided a useful indication of the character of the fauna. Sea sandwort is the dominating plant on the spit (Magnússon *et al.* 2023) and it was heavily parasitised by the thripid *Thrips vulgatissimus* and by aphids, presumably *Acyrthosiphon auctum* (Ólafsson 1982). Coleopterans were less important there, with few species recorded, although *Amara quenseli* was almost always present. The staphylinid *Micralymma marinum*, typically found on Icelandic mainland beaches (Larsson & Gígja 1959), was caught once in a trap located close to the shoreline, most likely after being washed ashore.

As expected, the marine-associated chironomid *Halocladius variabilis* was trapped in numbers on the spit, along with a single specimen of *Telmatogeton japonicus*, another species whose marine larvae develop among algal vegetation on wet rocks (Hrafnsdottir 2005). As in the sand-filled lava anthomyiid dipterans were regular in the vegetation of the spit, particularly within the lyme grass stands where they may breed; *Botanophila fugax* was the most abundant species, *Delia angustifrons*, *D. setigera* and *D. platura* also occurred in notable numbers. Linyphiid spiders were common, with *Erigone arctica* dominating, as it did throughout the island. Finally, the conspicuous predatory bdellid mite *Neomolgus littoralis*, characteristic of coastal beach habitats (Atyeo & Tuxen 1962), was also recorded. The fauna of the northern spit resembled that of the higher sand-filled lava, though it was less diverse due to the unstable conditions, and included several species typically associated with beach habitats. Further information on other less important species groups is provided in Appendix 4.

The terrestrial invertebrate orders and equivalent categories

Actively flying species were the most numerous in the insect fauna, as they can easily be windborne from mainland Iceland and neighbouring islands in the archipelago. The insect orders Diptera and Hymenoptera are the most diverse on mainland Iceland (Ólafsson 1991), which was also reflected in the island fauna. Each species has specific requirements to establish on the island, including access to suitable habitats and resources. This helps explain the high number of species not to have settled, even though some of them were regularly blown to the island.

Approximately half of the dipteran species recorded were regarded as permanent settlers. Many species within the order require aquatic or semi-aquatic habitats for larval development, such as lakes, streams, bogs or wet soil, and were therefore automatically excluded. For example, 20 chironomid species were listed, but only three of them were considered settled, two of which have larval stages in salt water (Hrafnsdottir 2005). Similarly, the three recorded simuliid species all require running water for developing (Nielsen *et al*. 1954) and were therefore not regarded as colonised. These groups illustrate dipterans that were unable to establish viable populations on the island.

All hymenopteran species recorded, except one, were parasitic wasps specialised on specific hosts such as lepidopteran or dipteran larvae, aphids and spiders. This explains the high number of species classified as not settled or of uncertain status compared with those regarded as settled. The bumblebee *Bombus lucorum*, was represented by a single queen, demonstrating the ability of this large and heavy hymenopteran to disperse relatively long distances across open ocean. It was however, not considered to have settled.

Many coleopteran species are not easily dispersed across open ocean but have nevertheless reached Surtsey and are regarded as permanent settlers. Many staphylinid species are excellent fliers and can be carried long distances by wind (Hansen *et al.* 2018). This was regularly observed during the earliest research years, when staphylinids were seen swarming over lava rocks along the north facing shore (pers. obs.). A total of 26 species of staphylinid beetles, about 35% of the Icelandic fauna, have been recorded on Surtsey, of which 18 were regarded settlers.

Many lepidopterans are readily carried by wind across the open sea, not only from mainland Iceland but also from more distant parts of Europe. Almost all species are specialised plant feeders, dependent on a single or a few closely related host plants. The existing flora on Surtsey therefore limits the colonisation possibilities for many lepidopterans. Approximately half of the recorded species (13 of 27) were considered to have settled. Of the remaining 14 species, eight were assumed to have been windborne from Europe, one of which, *Plutella xylostella*, is a classic opportunist whose larvae have been found on Surtsey feeding on northern rock-cress (*Arabidopsis petraea*), a Brassicaceae species.

The number of hemipteran species presented here, 13 in total, represents a minimum estimate, as several aphid species were not identified. Two aphid species were named, one commonly found on sea sandwort on the spit, and a second dependent on downy birch (*Betula pubescens*) which has not colonised Surtsey (Magnússon *et al.* 2023), which therefore cannot be regarded as a potential settler. The coccoids collected might all belong to a single species, except for *Arctorthezia cataphracta*, which was found in a tuft of grass washed ashore in an early year (Ólafsson 1978). The remaining specimens might belong to a newly described species (Gerő *et al.* 2025). Of the remaining seven hemipteran species, five are without doubt colonised, while two were of uncertain status.

Five species of windborne caddisflies were found, all with aquatic larval stages (Gíslason 1978), making colonisation impossible. All four Thysanoptera species recorded had colonised the island with little doubt. Two neuropteran species were recorded, one windborne from mainland Iceland and the other a regular immigrant to Iceland from Europe. A single siphonapteran species was found in 1967 (Lindroth *et al.* 1973), most likely carried to the island by an unknown bird. No signs of colonisation have been observed since.

All birds on the island are no doubt infested with feather lice, making the birds themselves their true "islands" rather than Surtsey itself. Consequently, these parasites are not of direct relevance to this project. Nevertheless, a single record has been published, a feather louse collected from an unnamed bird in 1967. The species (*Eidmanniella pustulosa)* had not been previously recorded from Iceland at the time but is a known parasite of the northern gannet (*Morus bassanus*) (Lindroth *et al*. 1973).

Spiders have been surprisingly successful both in reaching the island and in establishing populations there. The survey documented 26 species, of which 18 are thought to have settled successfully, three were possibly settled and five were considered unlikely to have done so. Juvenile spiders are known to spin silk thread that are caught by the wind, allowing them to become airborne and be carried long distances (Bell *et al*. 2005). The species found only rarely were not regarded as settled.

A single opilionid species, *Mitopus morio*, was first discovered on the island in 2019 and has since been found annually in increasing numbers. It is a very common species throughout Iceland (Agnarsson 1998) and was most likely transported to the island by birds.

Two species of land snails were found, both of which were regarded as settled. They require humid conditions, which they obtain beneath lava stones and within the uppermost soil layer, and they become more evident during rainfall. They were probably carried to Surtsey by birds transporting nesting material.

Enchytraeid annelids were found in soil, beneath driftwood and in gull nests. Although not identified to species, the material appears to include several distinct forms and are thus likely represent more than one species. A single lumbricid specimen was found in a soil sample taken from a dry sand dune formed by lyme grass (Sigurdardóttir 2000). This was highly unexpected and most likely a casual occurrence. The species had been recorded earlier on Heimaey (Lindroth *et al.*1973).

Future work

It is well understood that the terrestrial invertebrates are not easily monitored through short-term annual fieldwork. Effective monitoring of the tiny invertebrates on Surtsey requires extensive knowledge on the island´s fauna, as well as the Icelandic fauna in general, in addition to long-term experience in fieldwork and specimen processing. The single four-day annual visits in mid-July provide only limited insight. Many invertebrate species have restricted periods of adult activity, the stage in which they are typically identifiable. Some species are active throughout the summer, whereas others occur only in early, mid or late summer. Ideally, three visits, in June, July and August, would be recommended. Such frequency is, however, unrealistic due to limited funding, the logistical challenges of accessing the island, and lack of specialised expertise both in the field and in the laboratory.

This research has been maintained for over half a century during the early phases of the island's primary succession. The ecological succession on the island remains an active and ongoing process. For this reason, it is of great importance that this project continues into the future. Surtsey has offered a unique opportunity for investigations of this kind on northern latitudes.

As noted above, certain important taxonomic groups have been largely overlooked to date. Additional specialist expertise is needed to address them adequately. Soil invertebrates such as collembolans and mites are extremely important components of the ecosystem, and it is hoped that qualified specialists on these groups will engage in the future. The same need applies to aphids, coccoids and several unresolved hymenopteran taxa.

A comprehensive description of the island´s ecosystems, integrating terrestrial invertebrates, vegetation and birdlife, would also be highly desirable, and would best be achieved through a collaborative effort among all specialists involved in Surtsey research.

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