

## LETTER OPEN ACCESS

# Putative ‘Dispersal Adaptations’ Do Not Explain the Colonisation of a Volcanic Island by Vascular Plants, but Birds Can

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## ABSTRACT

Dispersal syndromes based on traits assumed to be adaptations for specific dispersal mechanisms are routinely assigned to flowering plants. Using the colonisation record from a volcanic island formed in 1963, we assess whether dispersal syndromes predict which species establish on newly formed land. We evaluated the long-distance dispersal (LDD) syndromes of the 78 plant species using three European classification systems. Syndrome assignments were inconsistent between classifications (coinciding for  $\leq 13\%$  of species). Two systems showed no evidence that LDD syndromes conferred a colonisation advantage. The third classification suggested wind syndromes were favoured, but only assigned a minority of colonisers to LDD syndromes. ‘Unassisted’ species assumed to lack dispersal adaptations were dominant. However, empirical evidence supports endozoochory via aquatic birds for 62 colonisers. This suggests bird-dispersal is a major driver of colonisation for dry-fruited plants, and underscores the need for new approaches to plant dispersal that account for overlooked plant–animal interactions.

## 1 | Introduction

For decades, it has been widely accepted that vascular plants have ‘dispersal syndromes’ diagnosed by readily identifiable morphological traits assumed to promote dispersal by specific mechanisms (van der Pijl 1969; Howe and Smallwood 1982; Lososov et al. 2023). This perspective has shaped functional trait-based ecology, influencing how we model plant migration and species distributions (Tamme et al. 2014; Lososov et al. 2023). For example, the ‘endozoochory syndrome’ applies

to plants with fleshy fruits, presumed to disperse seeds via gut passage. Empirical studies have shown that dispersal by vertebrates provides longer dispersal distances than abiotic mechanisms (Bullock et al. 2017). Therefore, if dispersal syndromes do not reliably predict real-world plant dispersal by birds, the use of trait-based approaches to infer plant movement and responses to global change may need reconsideration.

Various authors have expressed unease about the extent to which dispersal syndromes explain empirical data on dispersal

Pawel Wasowicz and Andy J. Green made equal contributions.

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mechanisms (see González-Varo et al. 2024 for synthesis), and many dispersal events over evolutionary time scales fail to match the syndrome-based expectations (Nogales et al. 2012). In particular, emerging evidence indicates that aquatic birds such as gulls, shorebirds and geese defy the syndrome paradigm and are major dispersal vectors of dry-fruited plants from the abiotic syndromes, especially via endozoochory (Green et al. 2022, 2023). The same is true for endozoochory and epizoochory by large herbivores (Pakeman et al. 2002; Albert et al. 2015). To date, no study has tested whether dispersal syndromes predict plant colonisation at the scale of a newly formed island—an invaluable task to confirm that syndromes are valid tools for modelling species movements in rapidly changing environments.

Few sites provide a better setting to test the dispersal syndrome paradigm than Surtsey. Located over 30 km off Iceland's southern coast, the island emerged in November 1963 (Þórarinnsson 1968) and has been strictly protected and closely monitored. Annual expeditions, beginning in May 1964 (Einarsson 1963), have generated a comprehensive dataset of plant species colonising Surtsey and their precise initial location. Surtsey offers a rare opportunity to document plant arrival, establishment and expansion and therefore for testing whether dispersal syndromes explain colonisation events over the timeframe of a single human generation. If morphological syndromes reliably predict long-distance dispersal (LDD), we would expect species with traits linked to LDD syndromes to be overrepresented among colonisers, while species lacking such 'adaptations' should rarely establish. We would also expect the precise location of plant colonisations to match the predicted vector (e.g., a species with a sea dispersal syndrome should colonise the shoreline). If, instead, colonisation patterns contradict the syndromes, then a reassessment of how we classify and predict dispersal mechanisms is required.

We tested three key assumptions of the dispersal syndrome paradigm. (1) That plant species can be objectively assigned to a specific syndrome, such that three existing syndrome classifications for the Icelandic flora largely agree on which species belong to which syndromes. (2) That syndromes predict which species successfully colonise over long distances. If syndromes have predictive power, Icelandic species with LDD syndromes should be overrepresented among species colonising Surtsey. If they are not, then colonisation must be explained by alternative dispersal mechanisms. (3) That the location of colonisation events within Surtsey aligns with syndrome-based expectations. If syndromes accurately reflect dispersal constraints, species assigned to wind, sea, or animal dispersal syndromes should be spatially structured in accordance with their predicted dispersal pathways. Finally, we consider whether empirical evidence for plant dispersal by birds explains the colonisation of Surtsey better than morphological dispersal syndromes.

## 2 | Materials and Methods

### 2.1 | Study Site

Surtsey is the southernmost and youngest island of the Vestmannaeyjar archipelago, located 32 km off the southern coast of Iceland. Formed by volcanic eruptions from 1963 to 1967, the island reached a maximum area of 2.65 km<sup>2</sup> and an

elevation of 174 m above sea level by the end of the eruption period (Magnússon et al. 2020). Subsequently, continuous marine erosion reduced its area by over 50%, leaving about 1.24 km<sup>2</sup> in 2019.

Two large palagonite cones and their craters dominate the island's central part, while lava fields extend across the southern part. A spit in the north formed from accumulated lava and coastal sediments. Intense marine abrasion has shaped high cliffs along most of the shoreline, except in the north and north-east (Magnússon et al. 2022, see also Figure 3). The substrate primarily consists of volcanic tephra and sand derived from it, creating a highly permeable surface that lacks organic soil, although colonisation by birds and seals has contributed to soil formation (Magnússon et al. 2020).

Surtsey experiences a windy maritime climate moderated by the surrounding ocean, which cools the island in summer and warms it in winter. Monthly mean temperatures remain above freezing (ranging from about 3.2°C in December to 11.3°C in August), and wind speeds exceed 20 m/s on roughly 30 days each year. Annual precipitation averages around 1000 mm, with the driest period in summer and the wettest in October (Petersen and Jónsson 2020). The growing season is exceptionally long for Iceland, with daily mean temperatures above 4°C often persisting from mid-April to November (Magnússon et al. 2020). Low-pressure systems from the south frequently bring strong southeasterly and easterly winds, while prevailing winds tend to be easterly (east-northeasterly to east-southeasterly) and north-northeasterly (Petersen and Jónsson 2020).

### 2.2 | Data Collection

Botanical observations on Surtsey began in May 1964 (Fridriksson 1987), six months after the first eruption, and have been conducted every year since. Currently, scientific expeditions take place in mid-July, an optimal time to study plant colonisation. From the beginning, strict measures were implemented to minimise the risk of researchers unintentionally introducing plant seeds to the island.

In the early years, every plant growing on the island was carefully marked—at first with wooden poles—then numbered and mapped on coordinate paper (Wasowicz et al. 2020). Later, the exact locations of the first colonising plants of each species were recorded more precisely with GPS technology. In some cases, multiple initial locations were documented when several independent colonisations occurred in the same year, or when populations went extinct and subsequently recolonised, either through new arrivals or, less likely, from locally persistent seeds.

The data used in this study come from both published sources (Wasowicz et al. 2020) and unpublished records, including over a decade of the authors' personal observations.

### 2.3 | Species Lists and Dispersal Syndromes

We compared three independently developed dispersal syndrome classifications for European flora:

1. Baseflor—Index botanique, écologique et chorologique de la flore de France (Julve 1998),
2. EuDiS—A database of dispersal syndromes for the native European flora (Vargas et al. 2023) and
3. SDDM—Seed Dispersal Distance Classes and Dispersal Modes for the European Flora (Lososová et al. 2023).

For Icelandic species, we followed the most recent vascular plant checklist (Wasowicz 2020) and applied these three classification systems to determine each species' dispersal syndrome(s).

## 2.4 | Aquatic Birds and Evidence of Endozoochory for Plant Species Recorded on Surtsey

Birds have been recorded on Surtsey from the beginning, and seabirds have bred there since 1970 (Petersen 2009). At least 17 bird species have bred on the island, including four gulls, two shorebirds and greylag geese *Anser anser*. Gulls are important plant vectors (Martín-Vélez, van Leeuwen, et al. 2021) and have established a large colony in the south of the island (dominated by *Larus fuscus* and *L. marinus*), beginning in 1986. The distribution of this and other bird colonies (gulls and/or fulmars) on Surtsey was mapped in 2024 using a Trimble T100 Tablet. The position of the biggest gull colony coincided with that documented previously (Magnússon et al. 2020). Like the other birds, gulls move readily between Surtsey, the mainland and the inhabited island of Vestmannaeyjar. Frequent observations of chicken and lamb bones in the gull colony indicate that gulls sometimes feed on urban waste.

To assess endozoochory (the dispersal of intact seeds via gut passage), we examined seed contents from three sources:

1. Limited sampling on Surtsey (July 2023): We collected 116 samples of faeces and regurgitated pellets from gulls (*Larus* spp., mainly *L. fuscus*), geese and ravens during fieldwork on Surtsey (18–20 July 2023). No *Empetrum nigrum* seeds were recorded, but gull faeces with seeds were recorded in 2024 and 2025 (since no berries were produced on Surtsey, this demonstrates dispersal from elsewhere).
2. Wider sampling in Iceland (August 2023): We gathered 358 faecal samples from Anatidae, gulls and shorebirds at multiple locations in Iceland from 8 to 15 August 2023.
3. Literature review: We surveyed published records of endozoochory by aquatic birds in Iceland and elsewhere in Europe.

Given the limited research on avian endozoochory of dry-fruited plants (Green et al. 2022), many dispersal interactions are likely undocumented. Because diaspore traits are often phylogenetically conserved (Liu et al. 2014; Chacón et al. 2017), we also considered evidence of endozoochory for congeneric species when evaluating potential dispersal mechanisms for plants present on Surtsey.

## 2.5 | Data Analysis

### 2.5.1 | Permutation Tests

All plant species recorded on Surtsey also occur on mainland Iceland. To compare actual colonisation events on Surtsey with expected patterns based on allocated dispersal syndromes, we began by refining the EuDiS, Baseflor and SDDM classification lists. For each list, we retained only native and naturalised Icelandic species (the 'donor area') and treated *Taraxacum* sp. and *Hieracium* sp. as a single species each. We then identified the dispersal syndromes of each plant species that successfully colonised Surtsey.

We focused on four syndromes traditionally associated with long-distance dispersal (LDD)—anemochory (wind), endozoochory (ingestion by animals), epizoochory (attachment to animal surfaces) and thalassochory (sea dispersal; exclusive to EuDiS following Heleno and Vargas 2015). All remaining syndromes were grouped into an 'other' category, which also included 'un-specialised' in EuDiS. Species absent from a classification were excluded from that classification's analysis.

To assess whether the proportion of each dispersal syndrome on Surtsey differs from that expected in the broader Icelandic flora (i.e., the donor area), we performed a permutation test. We compared observed and expected frequencies of dispersal syndromes using a chi-squared statistic, running 10,000 permutations. Standardised residuals were calculated to identify departures from the expected frequencies, with residuals exceeding |1.96| considered statistically significant (Haberman 1973). All analyses were conducted in R 4.4.2 (R Core Team 2024) using the *dplyr* 1.1.4 package (Wickham et al. 2025).

### 2.5.2 | Kernel Density Estimation

To evaluate spatiotemporal patterns of colonisation events, we applied Kernel Density Estimation (KDE) using the *kde2d* function from the *MASS* (Venables and Ripley 2002) package in R. Our input data consisted of georeferenced colonisation points (longitude, latitude) for each species, along with the year of colonisation. We divided the dataset into two temporal subsets: records from before 1986 (the year the gull colony was established; Magnússon et al. 2022) and records from 1986 onward.

For both subsets, **kde2d** was run on a 100×100 grid, using a bounding box based on the overall range of longitude and latitude values across all records. We then converted the resulting KDE surfaces into raster format using the **raster** package (Hijmans 2025), allowing for direct comparison of colonisation intensity between the two time periods.

### 2.5.3 | Elevation-Distance Index

To explore how elevation and proximity to the shoreline jointly influence colonisation patterns—and how these patterns may

relate to dispersal syndromes and bird colony locations—we developed a scaled Elevation-Distance Index (EDI). This index combines altitude and distance from the shore into a single measure:

$$\text{EDI} = \frac{e \times d}{10,000}$$

where  $e$  is elevation (m) and  $d$  is the minimum distance to the shoreline (m). Higher EDI values thus indicate areas that are both elevated and far from the coast, whereas lower EDI values represent locations nearer sea level, closer to the shore, or both—areas more likely to be reached via thalassochory. We calculated elevation and distance-to-shoreline layers in QGIS (QGIS 2024) using available topographic data for Surtsey (see Table S5 for data).

### 2.5.4 | Temporal Trends in Dispersal Syndromes

To test whether the proportional representation of dispersal syndromes among colonising species changed over time, we fitted generalised linear models (GLMs) with a binomial error structure and a logit link function using the `glm` function from the base R stats package (R Core Team 2024). For each classification system (EuDiS, Baseflor, SDDM), we calculated the proportion of colonisation events attributed to each syndrome per year and modelled this proportion as a function of year. Only syndromes represented in at least two different years were included in the analysis.

## 3 | Results

### 3.1 | Colonising Species on Surtsey

A total of 78 vascular plant species have been recorded on Surtsey since 1965 (Table S1). Across all three dispersal syndrome classifications, only a minority of these species was assigned to long-distance dispersal (LDD) categories (only 24%–41% of the recorded species).

Under the EuDiS classification, ‘unspecialised’ species constituted the majority of the colonisers (Figure 1, Table S2), followed by anemochorous species (wind-dispersed, 20%) and thalassochorous species (sea-dispersed, 10%), with other syndromes at lower frequencies. In contrast, the Baseflor classification assigned almost 30% of colonisers to barochory (gravity), 23% to anemochory and 17% to epizoochory. Finally, the SDDM classification placed 67% of Surtseyan species in ‘local non-specific dispersal’ (LNSD, with no dispersal vector), with anemochory again the second most frequent category (~22%), and other syndromes occurring much less often.

### 3.2 | A Mismatch Between Alternative Syndrome Classifications

We observed a strong mismatch among the three alternative dispersal syndrome classifications for Surtseyan species. At the syndrome level, anemochory and endozoochory showed relatively

consistent values, whereas most other syndromes exhibited marked discrepancies (Figure 1, Table S1,S2). At the species level, the mismatch level was very high and reached 89.74% between EuDiS and Baseflor, 88.46% between EuDiS and SDDM, and 84.62% between SDDM and Baseflor. However, if barochory (Baseflor) and LNSD (SDDM) and ‘unspecialised’ (EuDiS) were treated as equivalent, the mismatch was somewhat lower: 69.23% between EuDiS and Baseflor, 43.59% between EuDiS and SDDM and 60.26% between SDDM and Baseflor. Only seven species had consistent classifications across all three systems: *E. nigrum* (endozoochory), *Epilobium collinum*, *E. palustre*, *Leontodon autumnalis*, *Taraxacum* sp., *Tussilago farfara* (all anemochory), plus *Luzula multiflora* and *L. spicata* (both myrmecochory, i.e., ant-dispersed, although there are no ants on Surtsey).

### 3.3 | Do LDD Syndromes Favour Colonisation of Surtsey?

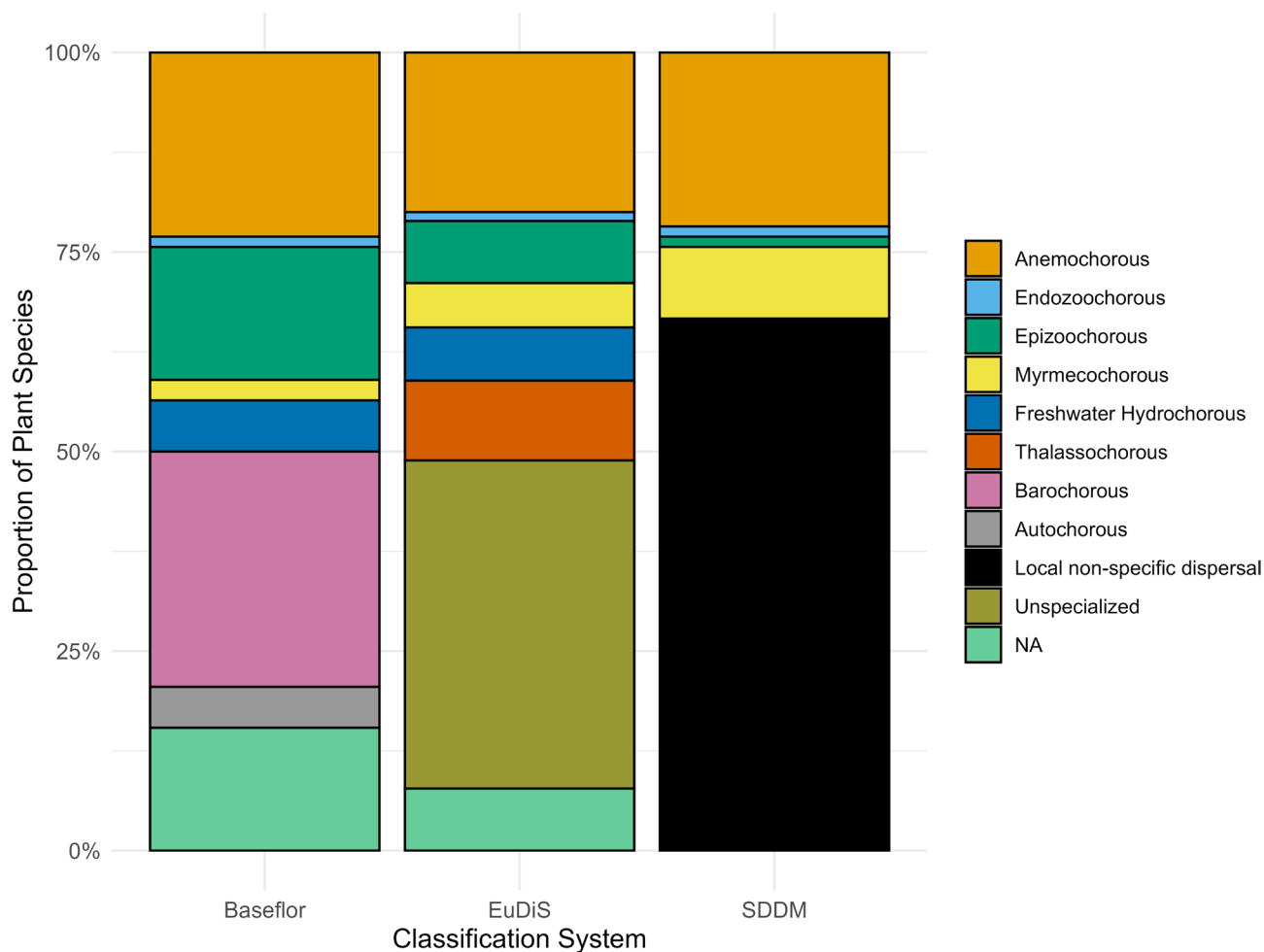
To test whether LDD syndromes are overrepresented among colonisers, we compared dispersal syndrome frequencies on Surtsey with those for the Icelandic flora. Only the EuDiS classification showed a statistically significant difference in syndrome frequencies ( $\chi^2 = 19.54$ ,  $df = 4$ ,  $p = 0.0025$ ), driven by the significant overrepresentation of anemochorous species on Surtsey (Table S3). For Baseflor and SDDM, the observed Surtseyan syndromes did not differ from expectations based on random sampling from the Icelandic flora: Baseflor ( $\chi^2 = 3.91$ ,  $df = 3$ ,  $p = 0.26$ ), SDDM ( $\chi^2 = 2.42$ ,  $df = 3$ ,  $p = 0.50$ ).

### 3.4 | Spatio-Temporal Patterns of Surtsey Colonisation

Following the island’s formation, Elevation Distance Index (EDI) values (the products of altitude and distance to the shoreline) for colonisation events were initially low but rose rapidly, peaking in the late 1970s (Figure 2). No new colonisation events were recorded for 6 years thereafter. Beginning in 1986, EDI values started to decline and later stabilised at intermediate levels (Figure 2).

Analysing all colonisation events revealed that, before the establishment of the gull colony in 1986, plants arrived at a rate of approximately 2.5 species per year, distributed fairly evenly across the island (Figure 3a), although the northern spit emerged as a hotspot, likely reflecting the relatively flat coastal habitat there, suitable for colonisation by sea dispersal. After gulls began nesting on Surtsey in 1986, colonisation accelerated to around 3.5 species per year and became spatially concentrated in the area occupied by the largest bird colony (Figure 3b). Overall, of the 18 colonisation events of nine species that were allocated a thalassochory syndrome under EuDiS, 12 had an EDI value  $< 0.5$ , consistent with arrival by sea (Figure 2).

GLM analysis revealed no statistically significant temporal trends in the proportional representation of dispersal syndromes in the Baseflor and SDDM classifications. In the EuDiS classification, one syndrome—thalassochory—showed a significant decline over time ( $\beta = -0.0499$ ,  $SE = 0.0220$ ,  $p = 0.0232$ ) (Table S4).



**FIGURE 1** | Proportional representation of dispersal syndromes for plants colonising Surtsey across three classification systems: EuDiS, Baseflor and SDDM. Each bar shows the relative proportion of plant species assigned to different dispersal syndromes within a given classification system. Only syndromes for which at least one species was assigned in a given system are represented. NA, Not available (i.e., unclassified species).

### 3.5 | Endozoochory Evidence

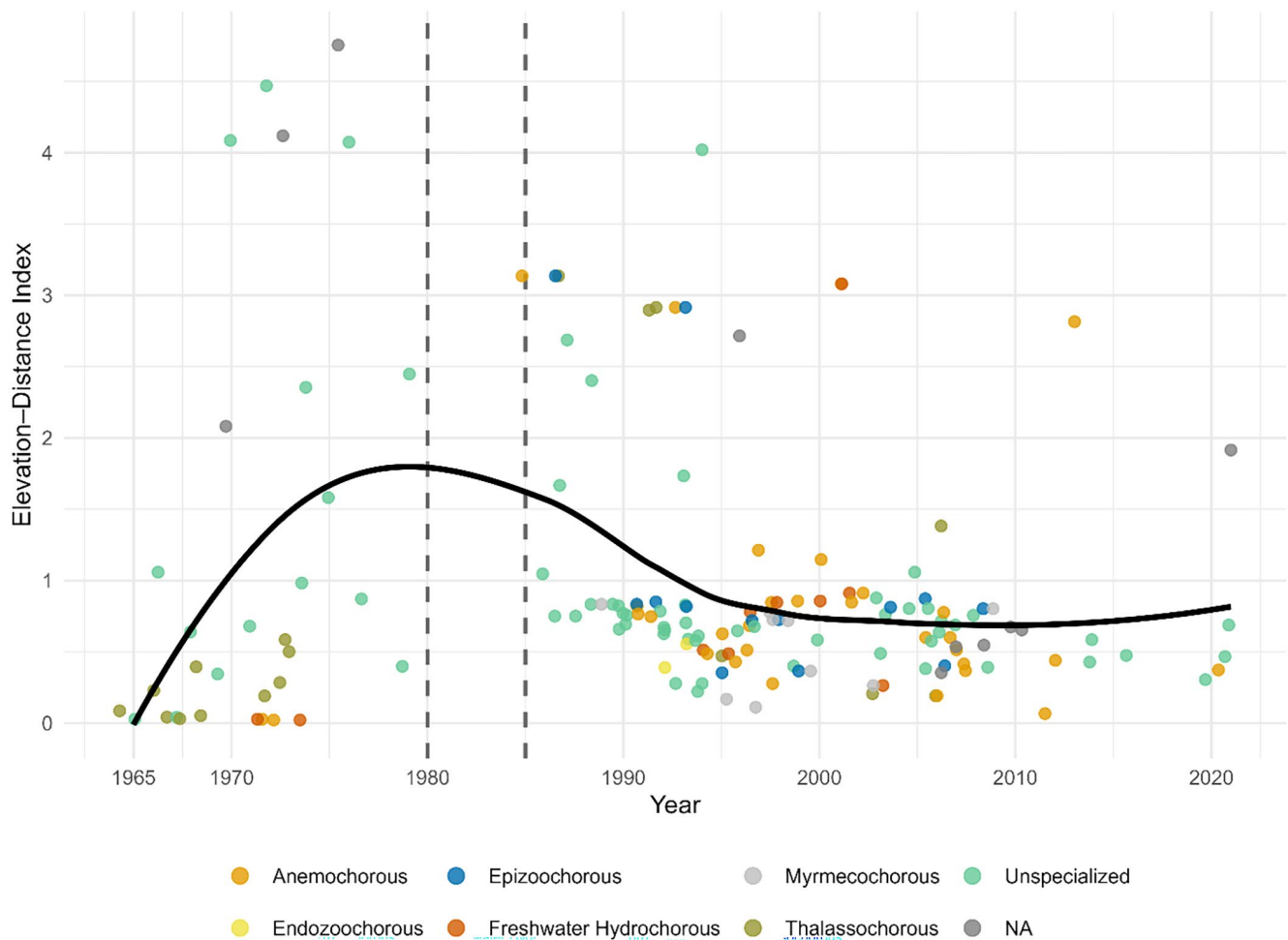
Despite only one of the 78 colonising species being allocated an ‘endozoochory syndrome,’ observational evidence supports an endozoochory mechanism for 62 of these species. This includes direct proof from egesta sampling on Surtsey for nine plant species. For 41 species, there is documented endozoochory in Europe by aquatic birds at the species level (often corroborated by multiple sources) (Table S1, Figures 4, S1). For an additional 21 species, evidence exists at the genus level, leaving only 16 species with no direct avian endozoochory records. Furthermore, many plants dispersed by ungulates are also dispersed by aquatic birds (Green et al. 2022), and for four of these 16 species, there is evidence of ungulate endozoochory (Table S1).

When this avian endozoochory evidence is compared with the three different syndrome classifications, the majority of taxa in each syndrome appear capable of dispersal via ingestion by aquatic birds (Figure 4). This suggests that observed colonisation patterns are more consistent with endozoochory by avifauna than with traditional syndrome assignments.

## 4 | Discussion

Our findings challenge the uncritical assumption that classical dispersal syndromes reliably predict the movement mechanisms driving dispersal. Rather than supporting expectations based on putative morphological adaptations, colonisation of Surtsey appears dominated by avian dispersal, especially endozoochory of species that lack an allocated zoochory syndrome. Indeed, the proportion of species allocated LDD syndromes (zoochory, wind, or sea) showed little or no deviation from what would be expected by chance. By contrast, the timing and spatial distribution of new arrivals point strongly to bird-mediated dispersal—especially in the area of Surtsey’s primary gull colony—and to the role of endozoochory in many species identified as ‘non-zoochorous’ in three databases. Direct observational data on gut passage of seeds by gulls and other aquatic birds provide a close match to Surtsey’s colonisation record, in contrast to the poor performance of LDD syndromes.

The source populations for seeds that were dispersed to Surtsey in initial colonisations are unknown. However, in a study of other Vestmannaeyjar islands, only 30 of Surtsey’s species were

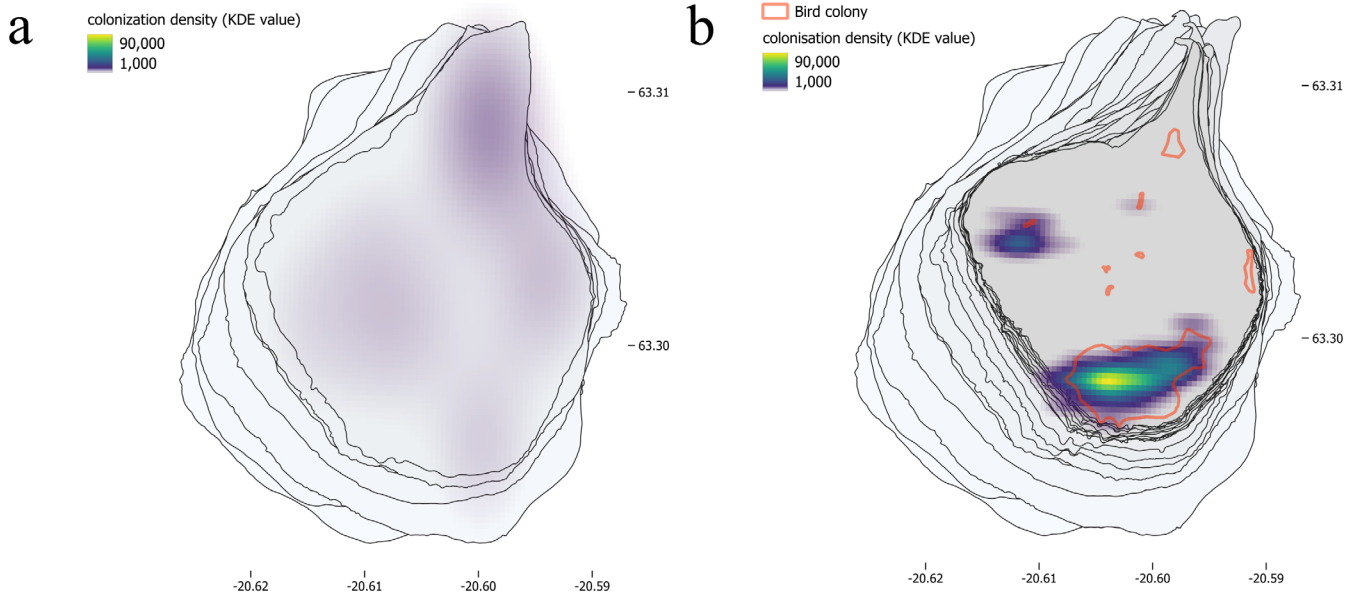


**FIGURE 2** | Variation in the elevation distance index (EDI) of plant colonisations over time, represented by individual data points (jittered by 0.5 years to improve visibility) and a smoothed trend line (Loess curve). The plot shows the timing of colonisation events on Surtsey (points), EUDIS dispersal syndrome (colours), and a six-year period between 1979 and 1986 (marked by dotted lines) when no new colonisation events were recorded during annual surveys. There are 138 colonisation events for 78 species because of extinctions, recolonisations and multiple colonisation events in the same year. Higher EDI values indicate areas that are both elevated and far from the coast, whereas lower EDI values represent locations nearer sea level, closer to the shore, or both. NA, Species not classified in EUDIS.

recorded (Magnússon et al. 2014), suggesting that the Icelandic mainland is a major source of propagules. Iceland is also well connected to the British and Irish Isles by bird movements, and gut contents of Surtsey snow buntings (*Plectrophenax nivalis*) suggested they may have brought seeds directly from there (Fridriksson and Sigurdsson 1968).

Among the three classifications tested, EuDiS performed better: it was the only system to include a thalassochoy category that aligns with some early coastline colonisations, and its anemochory class was the only LDD syndrome overrepresented on Surtsey. Nevertheless, our endozoochory evidence indicates that even these ‘anemochorous’ or ‘thalassochoyous’ species were likely transported by birds in many instances. Previous studies relating plant biogeography to EuDiS syndromes have had mixed results. Some LDD syndromes were positively correlated with broader distributions within the Canary Islands and some other archipelagos (Arjona et al. 2018), but some were negatively correlated with the estimated rate of spread within the alien range for European plants introduced elsewhere (Moyano et al. 2022).

Syndromes are assigned based on traits widely assumed to be adaptations for specific dispersal mechanisms, and only a fleshy fruit is recognised as an adaptation for endozoochory, despite the potential for more cryptic adaptations to the sensory systems and digestive processes of avian vectors (Costea et al. 2019; Green et al. 2023; Kreitschitz et al. 2025). It is further assumed that plants with zoochory syndromes are strictly dependent on animals for their dispersal, whilst other plants are not (Mendes et al. 2024). However, the extensive mismatch we detected between different syndrome classifications itself brings them into question. Strong inconsistencies of different syndrome classifications for the same plant species suggest that assigning syndromes based on diaspore traits is highly subjective, undermining assumptions that syndromes can provide a reliable indication of actual mechanisms. A further example of subjectivity is that *Cochlearia officinalis* was proposed to be epizoochorous and the first bird-dispersed coloniser of Surtsey by Magnússon et al. (2014), owing to the viewpoint that this species has sticky seeds. However, this species is not considered epizoochorous in any of the three syndrome classifications we analysed. The poor performance



**FIGURE 3** | Density of colonisation events before (a) and after (b) the establishment of the gull colony in 1986, visualised using Kernel Density Estimation (KDE). The KDE maps depict the relative likelihood of colonisation events across Surtsey. In panel (b), bird colony locations in 2024 are highlighted, with the evolving coastline from 1967 to 2024 shown in the background. The largest gull colony was established in 1986.

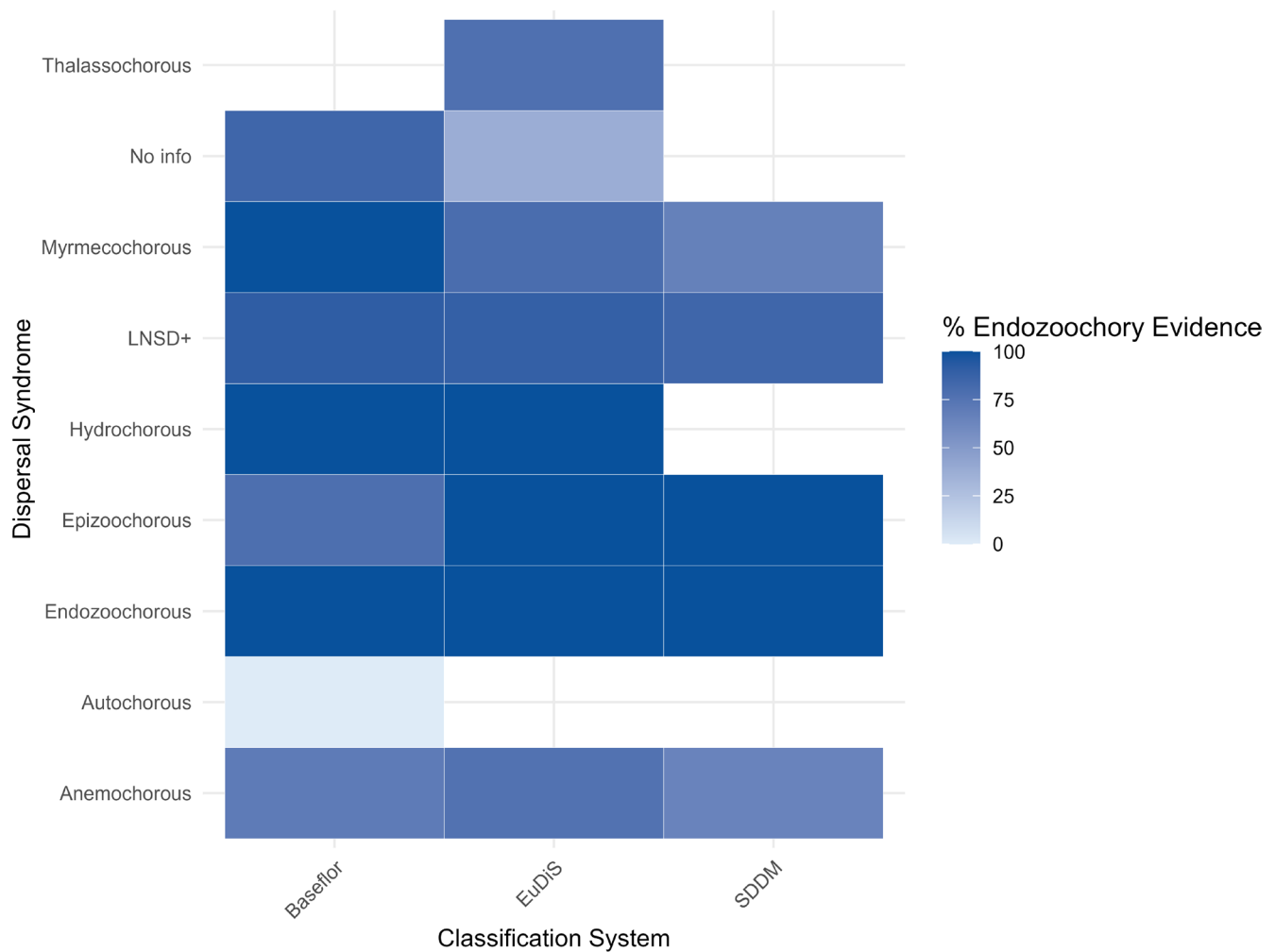
of syndromes in explaining colonisation of Surtsey, and the inconsistencies between classifications, further suggest that these traits may not always represent the adaptations for specific dispersal mechanisms they are presumed to be, and there may be alternative adaptive explanations (e.g., see Petersen and Kellogg 2022 for alternative functions of ‘epizoochory traits’). Experiments are needed to better understand the spatial or temporal scales and contexts under which such diaspore traits have value for dispersal. The dominance of species classified as ‘unassisted’, LNSD or ‘unspecialised’ because they are considered to lack diagnostic traits suggests they may have overlooked dispersal strategies and adaptations, highlighting a decoupling between syndrome classifications and actual dispersal mechanisms involving birds and other vertebrates (Pakeman et al. 2002; Albert et al. 2015; Green et al. 2022; González-Varo et al. 2024).

In a rapidly changing world, plants depend critically on animal vectors to adjust their distributions (Viana 2017; Nuñez et al. 2023), and our study indicates that empirical evidence about avian endozoochory can provide a better indication of the ability of plants to colonise offshore islands than do allocated syndromes. Many studies outside tropical forests assume that plant dispersal is accurately reflected by morphological syndromes (Lososová et al. 2023; Gao et al. 2024), and their results may not be reliable. Currently, the dominant view is that ‘the distinction between biotically and abiotically-dispersed fruits or seeds is uncontroversial’ (Howe 2016). Because fleshy-fruited plants commonly have larger seeds and are dominant in tropical plant communities, syndrome-based analyses often predict that larger seeds—and tropical species—are dispersed over longer distances (Thomson et al. 2011; Chen et al. 2019). In contrast, we have strong evidence for long-distance dispersal and endozoochory of numerous small-seeded plants in the sub-arctic. This is consistent with the larger global range sizes of vascular plants with smaller seeds and the lack of evidence that classical

LDD syndromes increase range size (Alzate and Onstein 2022). Under global warming, temperatures are increasing much faster at extreme (subarctic) latitudes than the global average (Post et al. 2018), and the role of birds as vectors is likely to be vital to facilitate the redistribution of plants in response to these changes.

Plant syndromes are widely envisaged as fixed categories typically assigned for a whole species from the inspection of a small number of herbarium specimens or based on subjective ‘expert opinion’. In contrast, as is widely recognised for animals (Côte et al. 2017), dispersal in a given plant species likely responds to spatial and temporal variation that acts through selection on multiple traits, leading to intraspecific diversity in dispersal strategies whose frequency responds readily to habitat variation and ecological change. New dispersal strategies can readily appear in a given species in response to changes in selection pressures. Indeed, selection can act quickly on plant traits such as seed size, plant height, or fruit morphology to change the balance between, for example, local and long-distance dispersal, or between abiotic dispersal and endozoochory (Cheptou et al. 2008; Williams et al. 2016; Skaïen and Arcese 2020).

Research into avian endozoochory has focussed primarily on frugivorous birds (Beckman and Sullivan 2023), promoted by scientists’ greater research attention into colourful, conspicuous fleshy fruits (Adamo et al. 2021). However, only 8% of European angiosperms are fleshy fruited (Heleno and Vargas 2015), and many dry-fruited plants with small seeds also disperse by birds (as well as herbivorous mammals, Pakeman et al. 2002). Surtsey provides a relatively dry hostile environment unsuitable for fleshy-fruited plants with high moisture requirements. Establishment is difficult on subarctic volcanic islands, where local extinctions and recolonisations are common. Likewise, fleshy fruits are less likely in arid ecosystems owing to the limited availability of water (Vander Wall and Moore 2016).



**FIGURE 4** | Endozoochory evidence (species or genus level) across different syndromes and classification systems. The heatmap represents the percentage of Surtsey colonisation records for which endozoochory evidence was present within a specific dispersal syndrome and classification system (EuDiS, Baseflor, SDDM). Darker blue shades indicate a higher proportion of records with endozoochory evidence, while lighter shades represent lower proportions. The LNSD+ row includes ‘Local non-specific’ for SDDM, ‘Unspecialised’ for EuDiS and ‘Barochorous’ for Baseflor. ‘No info’ refers to plant species not included in the respective syndrome classification.

*Empetrum nigrum*, the only species to colonise Surtsey that has an endozoochory syndrome, has never been seen to produce fruit there, and is much less abundant than many dry-fruited plants that can disperse by avian gut passage. As well as the plants that have colonised Surtsey successfully, birds have also brought seeds of other dry-fruited plants that have failed to colonise, as demonstrated by analysis of the gut contents of migrant snow buntings on the island (Fridriksson and Sigurdsson 1968). Birds have also likely contributed to the colonisation of the widespread bryophytes on Surtsey (Wilkinson et al. 2017; Ingimundardóttir et al. 2022).

Given their abundance (Petersen 2009), high mobility (Martín-Vélez, van Leeuwen, et al. 2021) and our empirical endozoochory data from the island, gulls are likely to be the most important vectors for plant dispersal to Surtsey. We also found empirical support for a role for the shorebirds that visit the island regularly and for the greylag geese that have bred there since 2002. Crucially, different kinds of aquatic birds tend to disperse seeds from similar sets of plant species (Martín-Vélez, Lovas-Kiss,

et al. 2021; Sebastián-González et al. 2020), so we did not restrict ourselves to the bird species dominant in Surtsey when identifying empirical evidence for endozoochory of Surtseyan plants.

The role of regurgitation of seeds by gulls in bringing plants to Surtsey was recognised by Fridriksson (1987). These seeds may often be in or on their prey (e.g., other birds or fish) when ingested (Martín-Vélez, Lovas-Kiss, et al. 2021; Green et al. 2023). It was previously noted that the arrival of new plant species has been concentrated in the area of the main gull colony but, as well as bringing seeds, their guano has likely facilitated the colonisation of many species unable to grow on bare volcanic soil (Magnússon and Magnússon 2000; Magnússon et al. 2020), thus increasing the opportunities for dispersed propagules to become established over time. The use of green plant material by gulls and other birds in nest construction has also provided an additional mechanism for the spread of plant species within the island, and evidence from elsewhere suggests this mechanism may potentially have had some role in the initial colonisation (Morton and Hogg 1989; Parnikoza et al. 2012). Previous

assumptions that aquatic birds disperse seeds mainly by epizoochory have been repeatedly debunked (Green et al. 2023; Green and Wilkinson 2024), and this mechanism has likely had a minor role in colonisation of Surtsey compared to endozoochory.

## 5 | Conclusions

Our study challenges the long-standing assumption that morphological dispersal syndromes reliably predict plant colonisation. Instead, we demonstrate that avian (endo)zoochory is a major force that fuels plant dispersal to a volcanic island, even for species without a zoochory syndrome. Our results revealed a critical flaw in existing predictive models, which assume that dispersal can be inferred from plant morphology alone. Moving forward, we suggest that ecological research should prioritise direct empirical evidence of dispersal processes rather than relying on subjective syndrome-based classifications. In order to accurately predict plant responses to environmental change, subjective assumptions based on plant morphological traits should be replaced with mechanistic understanding of plant–animal interactions. Intensive field studies have provided important and unexpected insights into how plants actually disperse to a volcanic island. To understand plant dispersal and colonisation mechanisms on islands, classical syndromes are inadequate and fail to reflect the complexities of plant dispersal strategies. Avian endozoochory of dry-fruited plants with small seeds is a hugely important but understudied process. More research is required into these key plant–animal interactions. Frugivory is not important in all terrestrial habitats where birds are the dominant seed vectors.

### Author Contributions

Conceptualisation: P.W., A.J.G. Developing methods: P.W., A.J.G., Á.L.-K. Conducting the research: P.W., A.J.G., N.S., Á.L.-K. Data analysis: P.W., A.J.G., N.S., Á.L.-K. Data interpretation: P.W., A.J.G., Á.L.-K. Preparation of figures and tables: P.W. Writing: P.W., A.J.G.

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### Conflicts of Interest

The authors declare no conflicts of interest.

### Data Availability Statement

Data and R code supporting the findings of this study are available on Zenodo (<https://zenodo.org/records/17235139>).

### Peer Review

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.70234>.

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### Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** ele70234-sup-0001-DataS1.pdf. **Table S5:** Spatial data used during the study.