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Research article

Dispersal rather than climate and local environment constrains non-marine snail fauna in west Greenland

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The biota of North Atlantic islands evokes intriguing questions on its evolution, colonisation routes, and an equilibrium between dispersal limitation and climatic/habitat constraints. While good data on non-marine snails exist for most of the islands, the data for Greenland were observed mainly between 1850 and 1900. The recorded species have been described as Greenland endemics, but this conclusion has never been fully questioned based on evidence. It can be assumed that these passively dispersing invertebrates are in fact of North American origin, due to the shortest distance to the mainland across the Davis Strait. To answer these questions, we collected the snail fauna at 72 sites of five locations across west Greenland. Our sampling revealed a very species-poor fauna, consisting of two aquatic and four terrestrial snail species. Based on mitochondrial and nuclear DNA sequences, the phylogenetic reconstruction and haplotype analysis showed that these taxa are either North American (all aquatic) or European (all terrestrial) in origin. None of them appeared to be endemic to Greenland and they were not even genetically distinct from the mainland populations. At both the macro and habitat scale, the Greenland snail fauna was found to be only a small fraction of the mainland species pool based on climate mapping and analysis of habitat requirements. While it appears to be limited mainly by dispersal, a detailed analysis of bird migration routes and intensity could not explain a puzzling difference in the biogeographical origin of the aquatic and terrestrial components. Terrestrial snails mimic the pattern seen in non-flying beetles, while the aquatic that of some flying insects. The results are a strong reminder that simple linear distance does not make a barrier, and that the barrier permeability can differ even within a group sharing the same dispersal mode and potential.

Keywords: biogeography, climate, gastropods, migration, North Atlantic, taxonomy

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Introduction

The biodiversity of oceanic islands has long fascinated biologists, with these biotas quite literally being one of the foundations for modern evolutionary thought (Whittaker et al. 2023). While most of such work has been done in subtropical to tropical locales, the development of unique biotas has also been studied on sub-Antarctic island archipelagos like Campbell, Kerguelen and South Georgia (Carlquist 1974). The North Atlantic also has islands and archipelagos in Newfoundland, Jan Mayen, Iceland, Greenland and the Faroes. While the former represents a land-bridge island which was connected to the North American mainland as recently as 8000 years ago (Liverman 2008), the remainder have never been connected to the mainland or have been separated since the start of the Tertiary. They vary in their geology from ancient continental cratons to recent volcanics, with closest biotic source pools varying from North America to Europe. Thus, there has been enough time and there exists enough potential environmental and historical biogeographic variation to allow for evolution of unique faunas.

By far the largest of the North Atlantic islands is Greenland, where a number of endemic invertebrates have been described. However , no fossil evidence exists to validate long-term lineage persistence for any group (Böcher 1997), with the validity of the 17 beetle and fly endemics reported by Bergersen (1995) being largely challenged (Sadler 1998). The three freshwater snail endemics reported from west Greenland also appear to represent a single biological entity – *Ladislavella catascopium* from North America (Vinarski et al. 2017).

Only four terrestrial gastropod species have been reported from Greenland – all originally described as endemics, i.e. *Euconulus fabricii*, *Oxyloma groenlandica*, *Vertigo hoppii* and *Vitrina angelicae*. Given their poor active dispersal abilities and small minimum-viable habitat requirements (Nekola 2014), could these actually represent endemic lineages? Or are these populations conspecific with other widespread arctic species? Is the Greenland fauna really this depauperate? What is the relative frequency of endemic, North American and European elements in the fauna? And what likely dispersal vectors brought these species to the region?

Here we aim to address these issues. Our data is based on de novo terrestrial gastropod assemblage samples collected in 2022 across the west Greenland coast from Nuuk to Disko Island. Since this fauna had never been observed using modern methods, and not at all within the last century, we wished to determine its true makeup. Following field work we empirically validated the taxonomic status of each encountered entity using DNA sequence data. To explain the mechanisms which have helped generate its species pool, we attempted to identify potential sources with the most analogous climates. We then compiled gastropod species lists from these areas and documented their presence from across the North Atlantic. Using modern climate niche envelopes already generated for 49 Holarctic species within the genera *Euconulus, Pupilla* and *Vertigo* (Nekola et al. 2022) and *Perpolita* (Saito et al. 2024) we also determined the presence of appropriate potential climate across the region for each. From this we estimated the potential faunal makeup and strength of the various oceanic barriers isolating the west Greenland fauna from its closest mainland climate analogues. Lastly, we also considered the relative importance of potential passive dispersal vectors which allow these barriers to be crossed, in particular bird migration from both eastern North America and western Europe.

Methods

Field sampling and processing of samples

We sampled 72 terrestrial and freshwater gastropod sites across west Greenland in August 2022 between 69°16′–64°10′N and 53°39′–50°38′W. These occurred in five general locations: Kangerlussuaq, Sisimiut, Ilulissat, Qeqertarsuaq and Nuuk (Fig. 1). We limited sampling to these areas because they encompassed all previous reported locations for the known species and are accessible by commercial airplane or boat service. Comparison with the Iceland fauna was made possible via our own quantitative data from 79 sites collected from 2016–2024 using the same sampling methodology. Although we have also surveyed the Faroe Islands, our observations combined with those of previous reports (Solhøy 1981) documents that because of its warmer Gulf Stream-influenced climate, its fauna is not boreal but rather temperate Atlantic European. As such we have not included these data and have not considered this archipellago as a stepping stone for boreal species across the North Atlantic.

At each site we documented terrestrial gastropod faunas following the protocols of Nekola (2010), in which ~ 0.1 ha areas were searched by eye for larger shells and accompanied by litter sampling of ~ 1 m² from appropriate microsites for smaller taxa. Retained ~ 0.5 l leaf litter fractions were passed through a standard mesh screen series and all shells and shell fragments were removed. These were identified and the number of individuals per species was counted. Freshwater gastropods were hand collected by washing sediment and aquatic vegetation through a 0.8 mm mesh metal strainer. Live individuals were either preserved in 96% ethanol or allowed to desiccate at room temperature. Initial nomenclature was based on Vinarski et al. (2017), Lorencová et al. (2021) and Nekola and Horsák (2022), with modifications based on DNA sequence analyses.

Phylogenetic analyses

DNA sequence analysis was used to verify taxonomic status and biogeographical affinity of all encountered Greenland gastropod species. Specimens were chosen to cover the entire Greenland and North Atlantic ranges of each species. The list of all analysed populations is presented in Table 1 and the Supporting information. DNA from each specimen was isolated, subjected to PCR amplification and Sanger sequencing

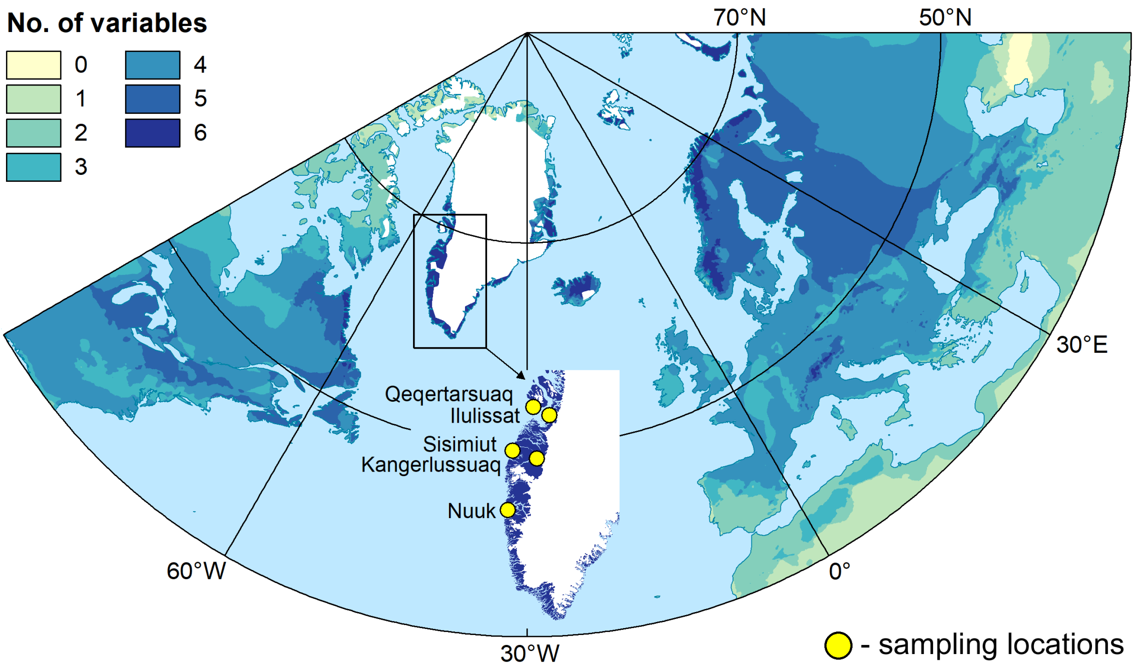

Figure 1. Location of studied areas and their climatic analogy across North Atlantic. Similarity to the climate of west Greenland is expressed as the number of climate variables whose values are within the range recorded across the sampling sites.

using a genus-specific combination of mtDNA (Cytochrome Oxidase Subunit I – COI, 16S ribosomal RNA, Cytochrome B – CytB) and nDNA (ITS1 and ITS2 of the nuclear ribosomal RNA complex) markers based upon amplification success and previously published data (Nekola et al. 2015, Lorencová et al. 2021). Protocols follow Horsáková et al. (2019). Generated sequence traces were assembled using Geneious ver. 8.0.2 (Biomatter Ltd.) and uploaded in GenBank (Supporting information).

Phylogenetic analyses were conducted separately on mtDNA and nDNA constructs. Tree reconstructions were based on maximum likelihood (ML) and Bayesian inference (BI). We report support values only for nodes > 70 (ML) and posterior probabilities of > 95 (BI). To visualize population-level similarity we constructed TCS haplotype networks and calculated their location in the ordination space created using principal coordinates analyses (PCoA) of the matrix of genetic p-distances. This analysis was limited to mtDNA markers because of lownDNA differentiation of ITS1+2 within species (Lorencová et al. 2021). These analyses were conducted as described in Horsáková et al. (2022).

We did not analyse *Ladislavella catascopium* as Vinarski et al. (2017) had already conducted these analyses on Greenland and North Atlantic populations. Because we were unable to locate *Euconulus fulvus* populations in the field, its genetic affinities could not be directly verified. However, a shell collected by J. Møller in the Qassinnguaq valley 20 km ESE of Nuuk in 1923 and deposited in Malacology Collection at the Academy of Natural Sciences at Drexel University (ANSP #139962), was digitally imaged and examined in terms of morphological taxonomically valid characters.

Species source pools

Following determination of the actual west Greenland gastropod fauna, we then compared it to other North Atlantic faunas. Compilation of the Iceland fauna was accomplished through reports in Kerney and Cameron (1979) and Welter-Schultes (2012), and our 2016–2024 field work (Horsák and

Table 1. List of recorded gastropod species at 72 sites across five locations in west Greenland (Fig. 1). An asterisk indicates the locations from which one population each was used for genetic analyses. Kanger. = Kangerlussuaq.

Terrestrial, n = 60	Locations	Sites	Nuuk	Kanger.	Sisimut	Ilulisat	Disko
Oxyloma elegans	1	1	0	0	1*	0	0
Vertigo hoppii	5	36	4*	3*	13	7*	9*
Vitrina pellucida	2	7	3*	0	0	0	4*
Vacant	5	24	2	10	9	3	0
Aquatic, n = 12							
Gyraulus parvus s.s.	2	3	0	2*	0	1*	0
Ladislavella catascopium	2	5	0	4	1	0	0
Vacant	5	5	1	1	1	1	1

Horsáková unpubl.). The mainland Scandinavian fauna was determined from these above texts as well as Waldén (2007) and our 2016–2019 field work from 94 sites (Horsák and Horsáková unpubl.). Data regarding the eastern Canada fauna is based on 48 sites collected in 2006 along the north side of the Gulf of St Lawrence from Godbout to Havre-St-Pierre and interior in the vicinity of Schefferville (Nekola 2014). These data were extended to include any additional species reported by Welter-Schultes (2012) for western Scandinavia and Pilsbry (1948) for Atlantic Canada. Clarke (1981) was the primary source to compile the list of Atlantic Canada freshwater Gastropods, while Glöer (2019) was used for eastern Scandinavia and Iceland. The resulting species lists for both terrestrial and freshwater species are presented in the Supporting information.

Climatic comparisons and potential species pools

We mapped the similarity of the west Greenland climate to other terrestrial areas across the North Atlantic using six WorldClim variables (Hijmans et al. 2005): temperature seasonality (BIO 4), mean temperature of warmest quarter (BIO 10), mean temperature of coldest quarter (BIO 11), precipitation seasonality (BIO 15), precipitation of warmest quarter (BIO 18) and precipitation of coldest quarter (BIO 19). For each we calculated the range present across west Greenland and then determined all other terrestrial areas across the North Atlantic which shared this range. A final composite map was then drawn showing climatic similarity to west Greenland, ranging from 6 (all variables fell within the west Greenland ranges) to 0 (none fell within the west Greenland range).

To document which boreal species within the genera *Euconulus*, *Perpolita*, *Pupilla* and *Vertigo* are capable of living in west Greenland, we projected their characteristic climate envelopes – based on genetically validated occurrence records – into the modern landscape (Nekola et al. 2022, Saito et al. 2024). We then recorded those taxa in which the climate of west Greenland was deemed suitable. Modelling and projection details are found in Nekola et al. (2022).

Migratory birds

We compiled a comprehensive list of bird species recorded in Greenland based on Boertmann (1994) and Lepage (2023). The list was filtered to include only species classified by Boertmann (1994) as commonly occurring in Greenland, i.e. those recorded in thousands of individuals and usually breeding in the region. The distribution of each species was then determined both for terrestrial areas east (Iceland, Faroe Islands, British Isles, Eurasia) and west (east coast of Canada, including the Baffin Island, Newfoundland, Labrador) of Greenland. Determination of migration direction for each species was established using Boertmann (1994), Cramp (1998), and recent online databases: Sullivan (2009), Birds of the World (2022), Franks et al. (2022), Smith et al. (2022), Lepage (2023) and BirdLife International (2023). Using these sources, we also determined whether migration to Greenland was confirmed by direct observation of banded individuals from North America, Europe, or both. Because bird species that feed on molluscs might have a higher probability of being passive dispersal vectors either through unintentional exozoochory or endozoochory (Wada et al. 2012, Simonová et al. 2016, Saito et al. 2023), we also reviewed Cramp (1998) and Birds of the World (2022) to determine whether each species is known to forage on terrestrial or aquatic molluscs, or both. Species were also classified by their breeding location in aquatic or terrestrial habitats, or both.

From these data we calculated the proportion of species migrating to west Greenland from the east (Europe) or west (North America) across three groups: all birds; only species that feed on molluscs; only species with confirmed band recoveries. Species reported to migrate in both directions were included in both eastern and western groups. For each of these subsets we separately tested for differences between those that breed preferentially in terrestrial versus aquatic habitats using the exact binomial test.

Results

Taxonomic status of west Greenland non-marine molluscs

Vertigo hoppii (Møller 1842) was described from west Greenland and has typically been synonymized under *Vertigo modesta* (Say 1824). However, mtDNA and nDNA sequence document (Fig. 2a) that it is conspecific with *Vertigo arctica* (Wallenberg 1858) which is known from Iceland, Scotland, and Scandinavia south to the Tatras and Alps (Welter-Schultes 2012). Because it has priority, all of these populations should be referred to as *V. hoppii*.

Oxyloma groenlandica (Møller 1842) was initially presented as a *nomen nudum* by Beck, but officially described five years later by Møller. The type locality is listed as Kuksuk. It was later reported as being widely spread in Iceland (Pilsbry 1948). The 1954 report from Chittenango Falls, New York (FMNH 235490; Hubricht 1985) is highly suspect as represents only empty shells with all subsequent relocation attempts having failed (R. Rundell, pers. comm.). Both mtDNA and nDNA sequence demonstrate that Greenland and Iceland material is referrable to *Oxyloma elegans* (Risso 1826), which ranges across Europe south to Italy (Fig. 2b). Material possessing very similar shells from the arctic tundra at Churchill, Manitoba have been identified by Nekola (2014) as *Oxyloma verrilli* and in fact do represent a different species which may be synonymous with *Oxyloma haydeni* or *Oxyloma hawkinsi*. It is unknown whether the type-location *O. verrilli* from the eastern Gulf of St Lawrence represents this or some other genetic race.

Vitrina angelicae (Beck 1837) was described from isothermal springs near Nuuk. Pilsbry (1948) noted that it appeared indistinguishable from *Vitrina limpida*. Given the priority of *V. angelicae*, recent treatments (Turgeon et al.

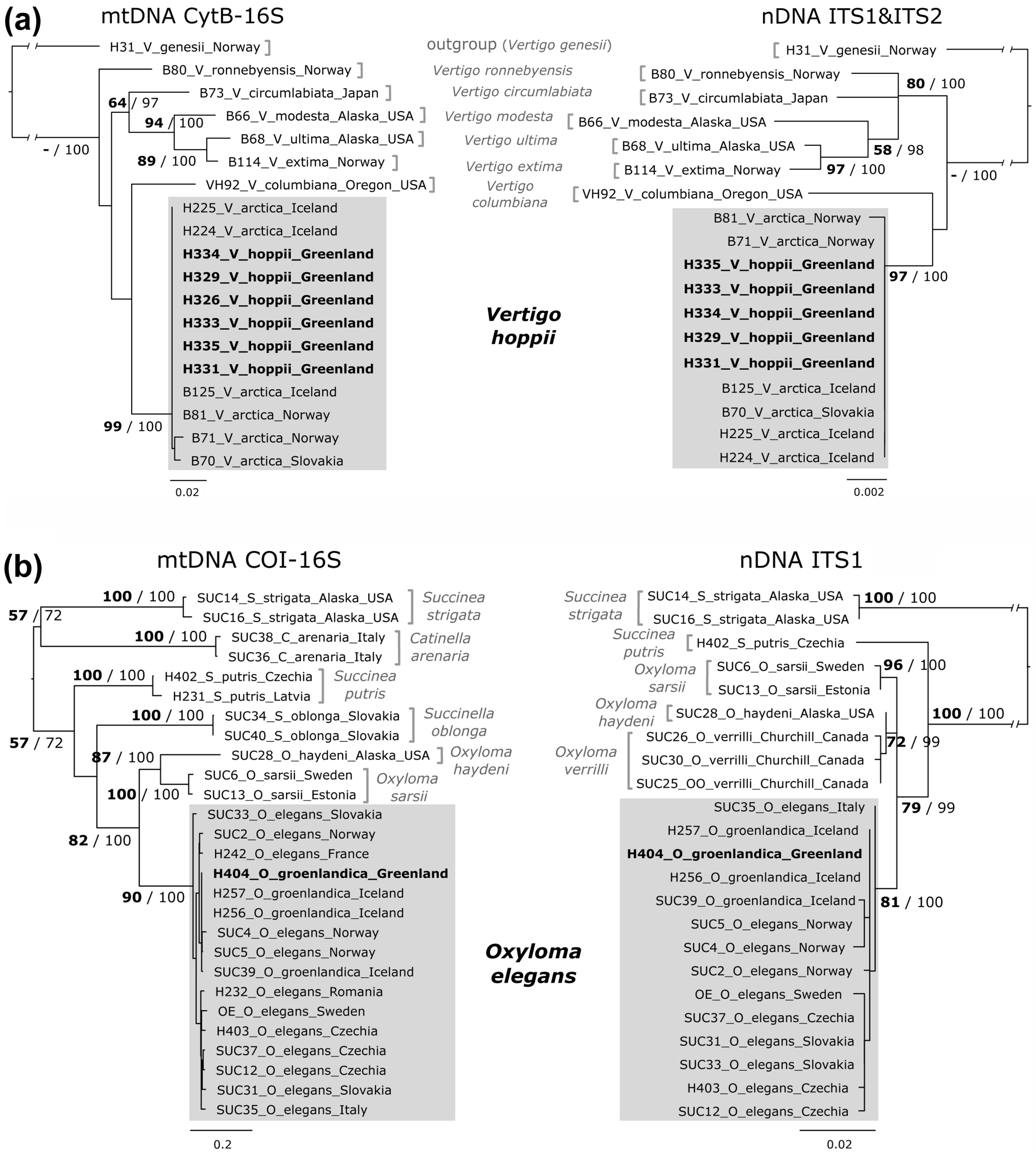

Figure 2. Phylogenetic trees based on Maximum likelihood (ML) for land snails of the genus *Vertigo* (a) and geographically relevant representatives of Succineidae (b), including populations of these taxa found in Greenland (Table 1). Only ML trees are shown as the topologies were almost identical with those based on Bayesian inference (BI). ML bootstrap values are shown by the respective nodes, followed by BI posterior probabilities. When two markers were available for mtDNA/nDNA, they were concatenated prior to analysis. All resulting trees are midpoint-rooted. All populations from Greenland belong to European species based on both mtDNA and nDNA analyses. Individual codes at the tree tips match those in the Supporting information.

1998) have transferred these North American populations to this *nomen*. However, mtDNA and nDNA sequence for *Vitrina* across the global Holarctic (B. Pfarrer, pers. comm.) demonstrate the presence of only a single species: *Vitrina pellucida* (Müller 1774). Haplotype analysis shows that the Greenland material is of European rather than North American stock (Fig. 3a).

Euconulus fabricii (Beck 1837) was described simply from Greenland. Soós and Schlesch (1924) and Pilsbry (1948) both relegated this taxon to a junior synonym of *Euconulus fulvus* (Müller 1774). Even though we were unable to locate any populations to genetically confirm this act, we fully support it: and comparing the digital image of ANSP 139962 to the diagnostic shell features provided in Horsáková et al. (2020) clearly shows this Nuuk-area shell to represent European *E. fulvus fulvus* given its more slowly expanding whorls and high spire.

Planorbis arcticus Møller 1842 (Møller 1842) was described from Narsaq in southern Greenland and also recently reported from Narsarsuaq (Vinarski et al. 2017). mtDNA and nDNA sequence both show that west Greenland populations are conspecific with Holarctic *Gyraulus parvus*, and are contained within North American subpopulation (Fig. 3b). By contrast, populations from Iceland represent its European race.

Additionaly, three endemic lymnaeid species had been described from west Greenland: *Limnaea holboellii*, *L. pingelii*, *L. vahlii*. All of these have previously been shown – using both mtDNA and nDNA sequence (Vinarski et al. 2017) – to be synonyms of the North American *Ladislavella catascopium*.

West Greenland gastropod assemblages

Based on these genetic assessments, three terrestrial and two freshwater aquatic gastropods were observed across the 72 sample sites (Table 1). While gastropods were observed in all five general locations, 40% of terrestrial (24) and 42% of aquatic (5) sample sites harboured none. *Vertigo hoppii* was the only species recorded at all five locations and it occurred at ~ 60% (36) of study sites, mostly in high abundance. In contrast, *Oxyloma elegans* was found at only a single site near Sisimiut. Terrestrial species were mostly observed in leaf litter accumulations under dense willow scrub small streams or in herb-rich spring-discharge areas with *Angelica officinalis*. Aquatic species were found on stones on the shores of large lakes (*Ladislavella catascopium*) and in vegetation-rich littoral zones of shallow lakes or pools (*Gyraulus parvus*).

West Greenland species pool in relation to biogeography, climate and ecology

Of the 55 land snail species known from western Scandinavia, 23 occur in Iceland (Fig. 4a, Supporting information). As shown above, four of these are found in west Greenland. Thus the ~ 1000 km ocean barrier to Iceland was permeable to ~40% of the western Scandinavian fauna, while the ~ 1100 km ocean and ice barrier to west Greenland was permeable to ~ 20% of the Iceland fauna. There are 34 land snail species known from the parts of Atlantic Canada most climatically similar to west Greenland (Fig. 4a, Supporting information). None of these occur in Greenland (or any of the other boreal North Atlantic islands), although three (*Columella columella, Vitrina pellucida, Zoogenetes harpa*) extend west across boreal North America through Beringia and Europe to western Scandinavia (Supporting information). The 300–800 km Davis Strait/Labrador Sea thus appears to represent a total barrier to movement.

The biogeographic affinities of the freshwater gastropod fauna differ, however (Fig. 4c, Supporting information). Seventeen species are known from mainland Scandinavia, and 13 from Atlantic Canada. Of these only *Gyraulus parvus*

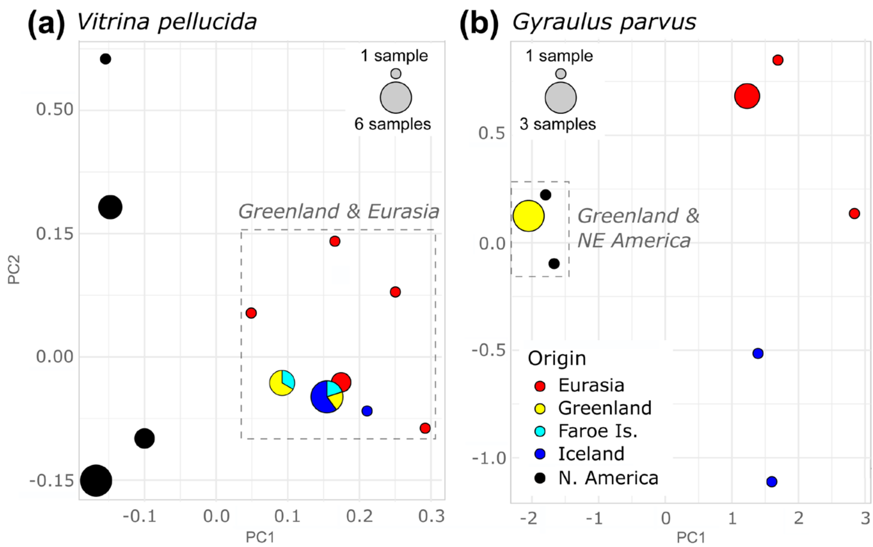

Figure 3. PCoA diagram based on COI p-distance of *Vitrina pellucida* (a) and CytB p-distance for *Gyraulus parvus* (b) using their selected populations across Holarctic.

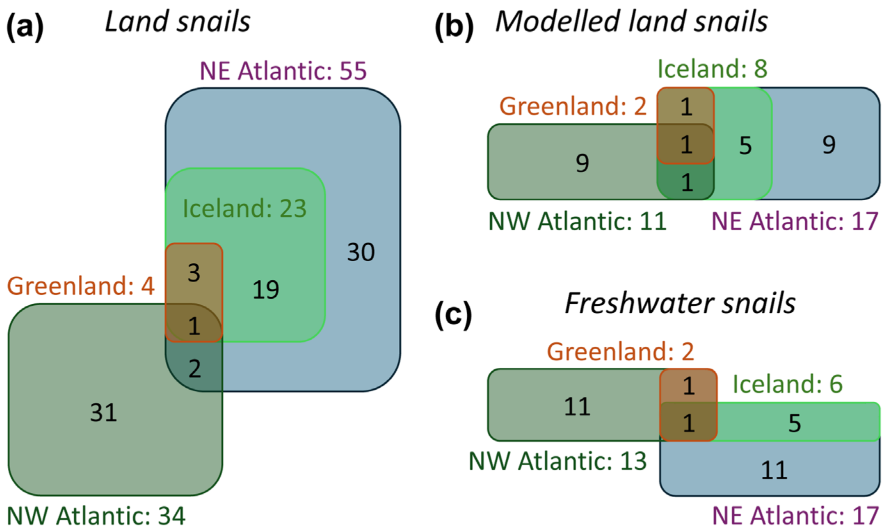

Figure 4. Number of snail species reported from west Greenland, Iceland, and climatically suitable areas of northeastern North America (NW Atlantic) and western Scandinavia (NE Atlantic). Number of land (a) and freshwater (c) snails are based on literature data combined with our records. Counts do not include introduced species and slugs. Numbers in the land snail genera *Euconulus*, *Perpolita*, *Pupilla* and *Vertigo* (b) include species reported from the depicted areas, but only those having appropriate climate in west Greenland based on climatic models adopted from Nekola et al. (2022) and Saito et al. (2024). The analysis is at species level, however all terrestrial species found in Greenland (a, b) are of NE Atlantic affinity, contrary to freshwater species (c) being of NW Atlantic affinity.

co-occurs in both mainland areas, being segregated into distinct North American and Eurasian gene pools (Fig. 3b; and Lorencová et al. 2021). Six of the western Scandinavian species occur in Iceland, with resident *G. parvus* representing European populations. The 1000 km ocean barrier to Iceland has been permeable to >1/3 of the Scandinavian fauna. However, none of these species/populations have yet colonized west Greenland. Rather, both west Greenland freshwater gastropods are sourced from Atlantic Canada. The Davis Strait/Labrador Sea barrier has thus been permeable to 15% of the adjacent Canadian mainland fauna.

Climatic modelling of global Holarctic boreal *Vertigo*, *Perpolita*, *Pupilla* and *Euconulus* species showed that 37 (~ 75% of 49 modelled species) possess appropriate climate niches and theoretically could colonize west Greenland. However, a number of these are limited to the north Pacific and are not members of the adjacent mainland species pools. All 17 western Scandinavian species each were found to possess climate envelopes that included west Greenland (Fig. 4b). Of these eight occur in Iceland, and only two in west Greenland. The North Atlantic Ocean barrier to Iceland was thus ~ 50% permeable to the climatically appropriate Scandinavian fauna with the ocean/ice barrier to west Greenland ~ 50% permeable to the climatically appropriate Iceland fauna. Fourteen of the modelled species are present in eastern Atlantic Canada. Of these eleven possess appropriate climate niches and theoretically could colonize west Greenland. None have, making the Davis Strait/Labrador Sea an apparently complete barrier to eastward movement within these species.

The impact of potential dispersal limitation on the west Greenland fauna is also highlighted by consideration of other co-occurring species. Twenty-one land snail species occur as native populations within Iceland. Eight co-occur with the four species which have colonized west Greenland (Table 2). When only samples from climatically similar areas of northern Iceland are considered, these eight almost always co-occur with multiple west Greenland species. For instance, all northern Iceland *Perpolita hammonis* populations co-occur with at least two west Greenland species and 1/3 with all four. Given these high sympatry rates, it seems highly likely that west Greenland provides appropriate physical environments for at least these eight species.

Table 2. Number of co-occurring west Greenland land snails (bold font) from 36 northern Iceland samples in areas climatically similar to west Greenland (Fig. 1). When the focal species is found on west Greenland, the maximum number of co-occurring west Greenland species = 3.

		Number of sites with co-occurring west Greenland species			
Species	Zero	One	Two	Three	Four
Vitrina pellucida	5	17	9	2	-
Euconulus fulvus	0	16	9	2	-
Perpolita hammonis	0	0	6	2	4
Cochlicopa lubrica	0	1	7	4	1
Vertigo hoppii	0	1	8	2	-
Columella aspera	1	0	8	2	0
Pupilla alpicola	0	2	1	2	1
Punctum pygmaeum	0	0	2	1	1
Arianta arbustorum	0	0	1	2	1
Oxyloma elegans	1	0	2	2	-
Oxychilus alliarius	0	1	2	0	0
Vertigo alpestris	0	0	0	1	0

Bird migration in relation to biogeographic affinity

Out of 61 bird species commonly reported from Greenland, 15 breed in terrestrial and 46 in aquatic habitats (Table 3, Supporting information). Forty species (10 land and 30 aquatic) were identified as malacophagous. Literature reports suggest that 14 terrestrial species migrate to Greenland from Europe while the remaining 12 migrate from North America. While representing few total observations, banded birds from both North America and Europe have been recaptured in west Greenland. Prior literature reports suggest that 35 species of aquatic birds migrate to west Greenland from Europe, and 43 from North America. While the exact binomial test revealed no significant differences ($p > 0.6$) in the proportion of bird migrations from either source to Greenland (Fig. 5), the limited number of observations for recapture of banded birds makes this test of low power (Table 3).

Discussion

This first modern empirical evaluation of the west Greenland non-marine mollusc fauna shows not only the absence of local endemic species and genetic lineages, but also the presence of a highly undersaturated fauna that is missing the great majority of characteristic western Europe and eastern Canadian boreal species. It seems likely that the highly depauperate nature of this fauna is related to dispersal limitation caused by ocean and ice barriers in conjunction with the limited time that terrestrial habitats have become exposed from under retreating glacial ice. We were thus able to verify, using modern empirical methods, that Westerlund (1887 in Vinarski et al. 2017) was correct in assuming that Greenland land snails are mainly of European origin while freshwater aquatics demonstrate a clear affinity with North America. However, the reason for this difference remains obscure, as a detailed analysis of bird migration failed to document any statistically significant differences in the migratory patterns of west Greenland terrestrial and aquatic birds.

Recent immigrants rather than endemics

While the existence of local glacial refugia has been suggested as a mechanism to allow for long-term faunistic survival on

Table 3. Classification of 61 Greenland nesting birds, based on breeding habitat (terrestrial versus aquatic), and known malacophagy (Y versus N). Movement is determined for: EU<->Gr [between Europe and Greenland]; NA<->Gr [between North America and Greenland] with the number before the slash representing potential movements based on co-occurrence of populations in focal mainland area and Greenland. The number after the slash represents documented movements via recapture of banded individuals.

Habitat	Malacophagy	Richness	Migration	
			EU<->Gr	NA<->Gr
Terrestrial	Y	10	10/1	7/1
	N	5	4/0	5/2
Aquatic	Y	30	30/8	29/5
	N	16	15/6	14/2

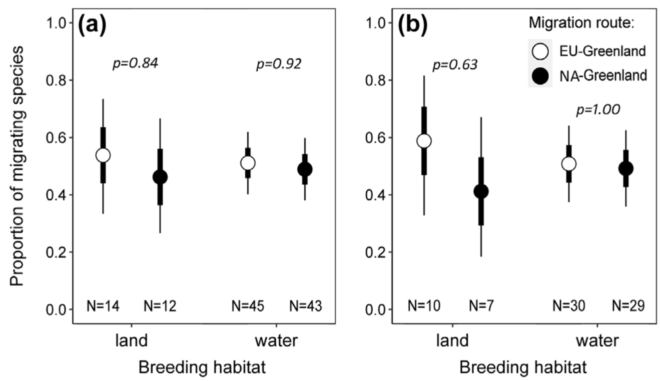

Figure 5. Proportion of bird species reported from Greenland that are confirmed to migrate or potentially migrate along one eastern (Europe–Greenland, white points) or western (North America–Greenland, black points) routes: a), all 61 species; b), only 40 species known to feed on terrestrial or freshwater molluscs. Points represent species proportions out of the total species in a breeding habitat category (breeding on land or water); error bars indicate the standard error (thick) and 95% confidence interval (thin). Significance is based on an exact binomial test, sample sizes below the points show the number of bird species.

North Atlantic islands (Dahl 1987), the position of Last Glacial Maximum terminal moraines 40 km off the west Greenland coast (van Tatenhove et al. 1996) suggests that if such ice-free areas existed, they would have been too climatically extreme to allow for long-term population persistence. Additionally, fossils from the previous interglacial are largely different from the present-day fauna, suggesting stochastic colonization during each interglacial (Böcher 1997). Our findings are in excellent agreement with these reports, with none of the encountered taxa even possessing unique intraspecific lineages. Rather, all populations are essentially identical to their mainland/Iceland source populations. This strongly suggests that modern Greenland biota is a product of mid-to-late Holocene-age colonisation events that occurred after sufficient landmass had become unglaciated.

Dispersal limitation, barrier width, and the role of bird migration pathways

The highly depauperate nature of the west Greenland non-marine mollusc fauna, in combination with lack of genetic variability from apparent source pools and with numerous additional Iceland species sharing similar climatic and environmental niches, strongly suggests that west Greenland occurrence patterns are best explained through recent, limited dispersal rather than extinction. As a result, they may well illuminate important ecological/geographic drivers that influence dispersal-driven systems (Nekola 1999).

While recent data show that the long-distance dispersal across the North Atlantic may be more common than previously thought (Gussarova et al. 2015), for most taxonomic groups there is considerable turnover between eastern Canada and western European species and/or gene pools. West Greenland Diptera and Lepidoptera tend to be of North American origin (Downes 1988, Skidmore 1997). It seems likely that these flying insects can – with the aid of prevailing westerly winds – disperse across the Davis Strait and Labrador Sea (Skidmore 1997). However, this water barrier has been thought to represent the boundary between Palaearctic and Nearctic invertebrate faunas (Lindroth 1957). This result is counter-intuitive given that this barrier is much narrower than the Greenland ice sheet and/or the open North Atlantic Ocean. It appears that the Davis Strait tends to operate as a barrier for heavier non-flying insects, such as some carabid beetles and *Otiorhynchus arcticus* – a heavy, flightless, soil-living weevil which is common in Greenland (Lindroth 1957).

Coope (1986) suggested that such flightless species could disperse to Greenland via ocean circulation, aided by floods of fresh water from rapidly melting glaciers ca 13 ka and 11 ka BP. In these periods, the Gulf Stream would have been redirected south, with low-salinity surface water and entrained rafts of organic matter allowing for long-distance rafting. This would help explain why the apparent source for the non-flying invertebrate fauna is in temperate, coastal France and Iberia. While we cannot discuss the validity of this hypothesis across all invertebrates, we can say with confidence that it does not explain the patterns seen in terrestrial gastropods: not only are the west Greenland species characteristic of boreal/arctic Scandinavia, but additionally their populations show no divergence from modern mainland populations, something that would have been expected if they had been isolated for 10 ka. The Coope's hypothesis also utterly fails at explaining the absence of European freshwater species from this same region.

It seems most likely that migratory birds are the ultimate mechanism allowing for permeability of these ocean/ice barriers. Hermaphroditic taxa, like those found in west Greenland, have been shown capable of making multiple ocean crossings of 7500+ km via this vector (Gittenberger et al. 2006). Birds are likely an important passive dispersal vector for both terrestrial and aquatic snails across shorter distances (Rees 1965, Dorge et al. 1999, Wada et al. 2012), with Dundee et al. (1967) documenting that 11.4% of woodcocks *Scolopax minor* examined in a banding program carried amber snails *Succinea unicolor* (shell length 1.5–9.0 mm). This species is of the same size and ecology as *O. elegans* from the west Greenland fauna. We can convincingly rule out human transmission, as none of the snails show signs of anthropogenic affinity and all terrestrial species recorded are known to be frequently spread by birds. AAlthough humans have colonized Greenland from both directions, with several Inuit cultures migrating from North America via Canada (Gilbert et al. 2008) and Norse settlers from Iceland (Haine 2011), coming into contact around 1100 AD, terrestrial snail species are only of European origin.

While differential source pools of terrestrial versus freshwater snail faunas could be explained if terrestrial and aquatic birds possessed different migration patterns, our meta-analysis documented no clear trends: west Greenland migrating birds possess statistically similar proportions of European and North American species across both terrestrial and aquatic settings. We are not willing to totally rule out this potential mechanism, however, because the lack of overall pattern may obscure differential patterns driven by individualistic responses of a few individual species. For example, two terrestrial European birds (*Turdus pilaris* and *Anthus pratensis*) are known to commonly feed on snails (Simms 1978). And, in acidic environments, *A. pratensis* was found to specifically search out land snails to meet their calcium requirements (Bureš and Weidinger 2000). But it is wholly unclear why migrating terrestrial birds from North America – and aquatic birds from Europe – have not been effective at catalyzing jump dispersal to west Greenland for their associated gastropod faunas.

There are clearly important differential drivers between passive dispersal of terrestrial and freshwater aquatic snails to west Greenland. But their identification will require additional work, perhaps including the dates at which potential source locations became ice free and able to support source pools. Other issues to be considered include idiosyncrasies in biology, ecology, current and past biogeography. No matter, this current work makes clear that the strength of a given dispersal barrier is not a simple function of barrier width, with the narrow Davis Strait/Labrador Sea proving to be a much more effective barrier to terrestrial snail dispersal than the entire rest of the North Atlantic. And, the differential source pools seen among west Greenland taxa groups makes this a potentially important test system in determining how everything does not get everywhere.

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Author contributions

Michal Horsák: Conceptualization (lead); Data curation (equal); Funding acquisition (equal); Investigation (equal); Writing - original draft (lead); Writing - review and editing (equal). **Veronika Horsáková:** Data curation (equal); Formal analysis (equal); Investigation (equal); Writing - review and editing (supporting). **Peter Samaš:** Data curation (equal); Formal analysis (equal); Writing - original draft (supporting); Writing - review and editing (supporting). **Jan Divíšek:** Data curation (equal); Formal analysis (equal); Visualization (equal); Writing - review and editing (supporting). **Brian Coles:** Data curation (equal); Investigation (equal); Writing - review and editing (supporting). **Jeffrey C. Nekola:** Conceptualization (equal); Data curation (equal); Funding acquisition (equal); Writing - review and editing (equal).

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Data availability statement

All raw data are available from the Supporting information..

Supporting information

The Supporting information associated with this article is available with the online version.

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Supporting information for:

Dispersal rather than climate or local environment constrains non-marine snail fauna in West Greenland

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<u>This PDF file includes:</u>

Table S1. List of all samples used in phylogenetic reconstructions and haplotype network analysis.
Table S2. List of land snail species known from western Scandinavia, Iceland and West Greenland based on literature data and our own records.
Table S3. List of land snails recorded in 48 samples across mainland and southern coastal Labrador in areas climatically similar to West Greenland defined in Figure 1.
Table S4. List of freshwater snail species known from eastern Canada, West Greenland, Iceland, and western Scandinavia based on literature data and our own records.
Table S5. Full list of 61 bird species occurring in Greenland, classified by type of molluscs in their diet and their possible migratory routes.

Table S1. List of all samples used in phylogenetic reconstructions and haplotype network analysis.

						GenBank accession number				
Sample Code	**A priori species name**	**Country**	**Settlement/Site**	**Latitude °N**	**Longitude °E**	**COI**	**CytB**	**16S**	**ITS1**	**ITS2**
Succineidae										
SUC36	*Catinella arenaria*	Italy	Ferriere	44.62342	9.53967	PQ526505	-	PQ526478	-	-
SUC38	*Catinella arenaria*	Italy	Campotosto	42.48589	13.36728	PQ526504	-	PQ526477	-	-
H232	*Oxyloma elegans*	Romania	Cârlibaba	47.53556	25.02181	PQ526479	-	PQ526452	-	-
H242	*Oxyloma elegans*	France	Le Bugnon	46.60736	6.00908	PQ526491	-	PQ526464	-	-
H256	*Oxyloma groenlandica*	Iceland	Reykhólar	65.64338	-22.53811	PQ526488	-	PQ526461	PQ536058	-
H257	*Oxyloma groenlandica*	Iceland	Djúpivogur	64.59748	-14.48344	PQ526487	-	PQ526460	PQ536056	-
H403	*Oxyloma elegans*	Czech Republic	Hluboká	49.66653	15.85269	PQ526480	-	PQ526453	PQ536052	-
OE	*Oxyloma elegans*	Sweden	Dalarö	59.13561	18.38042	PQ526483	-	PQ526456	PQ536063	-
SUC02	*Oxyloma elegans*	Norway	Holt	69.06117	19.46175	PQ526492	-	PQ526465	PQ536062	-
SUC04	*Oxyloma elegans*	Norway	Kilbotn	68.71067	16.50467	PQ526493	-	PQ526466	PQ536064	-
SUC05	*Oxyloma elegans*	Norway	Evenskjer	68.57964	16.63317	PQ526490	-	PQ526463	PQ536060	-
SUC12	*Oxyloma elegans*	Czech Republic	Rohozná	49.80373	15.81961	PQ526484	-	PQ526457	PQ536071	-
SUC31	*Oxyloma elegans*	Slovakia	Jablonica	48.59615	17.45194	PQ526482	-	PQ526455	PQ536053	-
SUC33	*Oxyloma elegans*	Slovakia	Sväty Jur	48.23135	17.21081	PQ526494	-	PQ526467	PQ536054	-
SUC35	*Oxyloma elegans*	Italy	Campotosto	42.48589	13.36728	PQ526481	-	PQ526454	PQ536059	-
SUC37	*Oxyloma elegans*	Czech Republic	Kostice	48.73700	16.99902	PQ526485	-	PQ526458	PQ536055	-
SUC39	*Oxyloma groenlandica*	Iceland	Eyrarbakki	63.90036	-21.19419	PQ526486	-	PQ526459	PQ536061	-
H404	*Oxyloma groenlandica*	Greenland	Sisimiut	66.93133	-53.64610	PQ526489	-	PQ526462	PQ536057	-
SUC28	*Oxyloma haydeni*	USA, Alaska	Fairbanks	64.05465	-145.43746	PQ526495	-	PQ526468	PQ536065	-
SUC06	*Oxyloma sarsii*	Sweden	Abisko	68.35203	18.79228	PQ526496	-	PQ526469	PQ536069	-
SUC13	*Oxyloma sarsii*	Estonia	Oru	59.22136	25.00833	PQ526497	-	PQ526470	PQ536070	-
SUC25	*Oxyloma verrilli*	Canada	Churchill	58.6521	-93.82720	-	-	-	PQ536066	-
SUC26	*Oxyloma verrilli*	Canada	Churchill	58.7085	-94.12930	-	-	-	PQ536067	-

SUC30	*Oxyloma verrilli*	Canada	Churchill	58.6521	-93.82720	-	-	-	PQ536068	-
H231	*Succinea putris*	Latvia	Liezers	57.50636	24.70400	PQ526498	-	PQ526471	-	-
H402	*Succinea putris*	Czech Republic	Hluboká	49.66653	15.85269	PQ526499	-	PQ526472	PQ536072	-
SUC14	*Succinea strigata*	USA, Alaska	Delta Junction	64.05465	-145.43746	PQ526502	-	PQ526475	PQ536073	-
SUC16	*Succinea strigata*	USA, Alaska	Fairbanks	64.70789	-148.31981	PQ526503	-	PQ526476	PQ536074	-
SUC34	*Succinella oblonga*	Slovakia	Sväty Jur	48.23135	17.21081	PQ526501	-	PQ526474	-	-
SUC40	*Succinella oblonga*	Slovakia	Šúr NNR	48.23111	17.21111	PQ526500	-	PQ526473	-	-
***Vertigo* spp.**										
H225	*Vertigo arctica*	Iceland	Vatnsdalshólar	65.50044	-20.39814	-	submitted	PQ526513	PQ536076	PQ536083
H224	*Vertigo arctica*	Iceland	Búðir	64.82150	-23.38653	-	submitted	PQ526512	PQ536075	PQ536082
B81	*Vertigo arctica*	Norway	Birtavarre	69.49470	20.82470	-	KY216944	KY216600	KY217352	KY216225
B71	*Vertigo arctica*	Norway	Kongsvoll	62.30050	9.60630	-	KY216943	KY216599	KY217351	KY216224
B70	*Vertigo arctica*	Slovakia	High Tatra Mts.	49.23540	20.21900	-	KY216945	KY216601	KY217353	KY216226
B73	*Vertigo circumlabiata*	Japan	Kotanuka	43.75270	144.84260	-	KY217025	KY216660	KY217433	KY216296
VH92	*Vertigo columbiana*	USA, Oregon	Manhattan Beach	45.64130	-123.94100	-	KY217045	KY216676	KY217451	KY216315
B114	*Vertigo extima*	Norway	Basecakka	69.66120	25.88860	-	KY217087	KY216712	KY217490	KY216353
B31	*Vertigo genesii*	Norway	Kongsvoll	62.26720	9.58550	-	KY217094	JN941043	KY217496	KY216359
H335	*Vertigo hoppii*	Greenland	Nuuk_1	64.20136	-51.62166	-	submitted	PQ526511	PQ536081	PQ536088
H334	*Vertigo hoppii*	Greenland	Qeqertarsuaq_1	69.26657	-53.43849	-	submitted	PQ526510	PQ536080	PQ536087
H333	*Vertigo hoppii*	Greenland	Nuuk_2	64.21082	-51.59443	-	submitted	PQ526509	PQ536079	PQ536086
H331	*Vertigo hoppii*	Greenland	Qeqertarsuaq_2	69.26954	-53.48008	-	submitted	PQ526508	PQ536078	PQ536085
H329	*Vertigo hoppii*	Greenland	Ilulissat	69.20827	-51.10837	-	submitted	PQ526507	PQ536077	PQ536084
H326	*Vertigo hoppii*	Greenland	Kangerlussuaq	67.03125	-50.66803	-	submitted	PQ526506	-	-
B66	*Vertigo modesta*	USA, Alaska	Koyukuk River	67.01970	-150.28860	-	KY217212	KY216818	KY217612	KY216470
B80	*Vertigo ronnebyensis*	Norway	Signaldalen	69.19110	19.98730	-	KY217285	KY216882	KY217682	KY216537
B68	*Vertigo ultima*	USA, Alaska	Earthquake Park 3	61.19970	-149.96670	-	KY217320	KY216912	KY217711	KY216571
Vitrina pellucida										
H336	*Vitrina pellucida*	Greenland	Qeqertarsuaq_1	64.20136	-51.62166	PQ526742	-	-	-	-

H393	*Vitrina pellucida*	Greenland	Qeqertarsuaq_2	69.26718	-53.43069	PQ526737	-	-	-	-
H392	*Vitrina pellucida*	Greenland	Nuuk	69.25623	-53.51833	PQ526739	-	-	-	-
H395	*Vitrina pellucida*	Iceland	Bjarkalundur	65.55688	-22.10108	PQ526738	-	-	-	-
H407	*Vitrina pellucida*	Iceland	Dalvík	65.96439	-18.53183	PQ526743	-	-	-	-
H396	*Vitrina pellucida*	Iceland	Reykjanestá	63.81173	-22.70943	-	-	-	-	-
H401	*Vitrina pellucida*	France	Les Mouilles	45.94808	6.31917	PQ526744	-	-	-	-
NMBE 570989	*Vitrina pellucida*	Russia	N Karelia	69.63500	31.97920	OK393862	-	-	-	-
NMBE 570975	*Vitrina pellucida*	Russia	Lake Baikal	51.90430	105.10200	OK393855	-	-	-	-
NMBE 570976	*Vitrina pellucida*	Germany	Eppenhain	50.16600	8.38890	OK393856	-	-	-	-
NMBE 510181	*Vitrina pellucida*	Switzerland	S-chanf	46.59670	10.07620	MT181518	-	-	-	-
H443	*Vitrina pellucida*	Faroe Islands	Norðskáli	62.21772	-6.99444	PQ526745	-	-	-	-
H444	*Vitrina pellucida*	Faroe Islands	Kirkjubøur	61.94862	-6.77969	PQ526746	-	-	-	-
H406	*Vitrina pellucida*	Iceland	Bjarkalundur	65.55688	-22.10108	PQ526741	-	-	-	-
H405	*Vitrina pellucida*	Iceland	Grindavík	63.81173	-22.70943	PQ526740	-	-	-	-
NMBE 571012	*Vitrina pellucida*	USA, Iowa	Staff Creek Fen	43.44470	-92.50940	OK393839	-	-	-	-
NMBE 571003	*Vitrina pellucida*	USA, Minnesota	Lake Bronson SP	48.71890	-96.57570	OK393851	-	-	-	-
NMBE 571017	*Vitrina pellucida*	USA, Minnesota	Maple Lake Church	47.61380	-96.17250	OK393841	-	-	-	-
NMBE 571001	*Vitrina pellucida*	USA, Minnesota	Higenbotham WMA	48.00690	-96.30350	OK393850	-	-	-	-
NMBE 571005	*Vitrina pellucida*	USA, Minnesota	Dave Pepin Homestead	48.41020	-94.81880	OK393843	-	-	-	-
NMBE 571002	*Vitrina pellucida*	USA, Minnesota	Tatlie Lake	46.98320	-96.31940	OK393847	-	-	-	-
NMBE 571018	*Vitrina pellucida*	Canada, Manitoba	St. Laurent	50.59260	-98.01520	OK393849	-	-	-	-
NMBE 571016	*Vitrina pellucida*	Canada, Manitoba	Beaudry PP	49.85540	-97.47050	OK393842	-	-	-	-
NMBE 571006	*Vitrina pellucida*	USA, North Dakota	Frostfire Mountain	48.91290	-98.07010	OK393840	-	-	-	-
NMBE 571007	*Vitrina pellucida*	Canada, Quebec	Pointe-des-Monts	49.32560	-67.37000	OK393854	-	-	-	-

NMBE 571015	*Vitrina pellucida*	Canada, Quebec	Iron Arm Road 2	54.86780	-66.66080	OK393853	-	-	-	-
NMBE 571014	*Vitrina pellucida*	Canada, Labrador	Leo Fen	54.67260	-66.60920	OK393852	-	-	-	-
Gyraulus parvus										
G475	*Gyraulus parvus*	Iceland	Lake Mývatn	65.60580	-16.99641	-	submitted	-	-	-
G474	*Gyraulus parvus*	Iceland	Lake Ashildarholtsvatn	65.72926	-19.61831	-	submitted	-	-	-
G472	*Gyraulus parvus*	Greenland	Ilulissat	69.20798	-51.10720	-	submitted	-	-	-
G470	*Gyraulus parvus*	Greenland	Kangerlussuaq_1	66.99821	-50.67330	-	submitted	-	-	-
G469	*Gyraulus parvus*	Greenland	Kangerlussuaq_2	67.02892	-50.68420	-	submitted	-	-	-
G465	*Gyraulus parvus*	Czech Republic	Milotice	48.96329	17.14899	-	submitted	-	-	-
G401	*Gyraulus parvus*	Czech Republic	Praha-Vinohrady	50.07530	14.43650	-	MZ130418	-	-	-
G394	*Gyraulus parvus*	USA, New York	Sullivan County	41.47730	-74.91180	-	MZ130445	-	-	-
G331	*Gyraulus parvus*	USA, New Mexico	Albuquerque	35.21673	-106.59921	-	MZ130440	-	-	-
G294	*Gyraulus parvus*	Croatia	Ljubački	44.24383	15.30681	-	MZ130420	-	-	-
G292	*Gyraulus parvus*	Croatia	Prndelje	44.15147	15.88650	-	MZ130410	-	-	-

Table S2. List of land snail species known from western Scandinavia, Iceland and West Greenland based on literature data and our own records. All slug species and introduced species or their populations were excluded from the list and the analysis. Species reported as native also from NE North America are shown. Note that North American population of *Euconulus fulvus* and *Vertigo lilljeborgi* genetically differ from the those in Eastern Atlantic and are considered as distinct subspecies (Nekola et al. 2023).

Land snail species	W Scandinavia	Iceland	W Greenland	E Canada
Acanthinula aculeata	x	-	-	-
Aegopinella pura	x	x	-	-
Arianta arbustorum	x	x	-	-
Balea perversa	x	x	-	-
Carychium minimum	x	-	-	-
Carychium tridentatum	x	x	-	-
Cepaea hortensis	x	-	-	-
Clausilia cruciata	x	-	-	-
Clausilia dubia	x	-	-	-
Clausilis bidentata	x	-	-	-
Cochlicopa lubrica	x	x	-	-
Cochlicopa lubricella	x	x	-	-
Cochlodina laminata	x	-	-	-
Columella aspera	x	x	-	-
Columella columella	x	-	-	x
Columella edentula	x	x	-	-
Discus ruderatus	x	-	-	-
Euconulus alderi	x	x	-	-
Euconulus fulvus fulvus	x	x	x	-
Euconulus fulvus egenus	-	-	-	x
Euomphalia strigella	x	-	-	-
Fruticicola fruticum	x	-	-	-
Helicigona lapicida	x	-	-	-
Macrogastra plicatula	x	-	-	-
Oxychilus alliarius	x	x	-	-
Oxychilus cellarius	x	-	-	-
Oxyloma elegans	x	x	x	-
Oxyloma sarsi	x	-	-	-
Perpolita hammonis	x	x	-	-
Perpolita petronella	x	-	-	-
Perpolita radiatella	x	-	-	-
Punctum pygmaeum	x	x	-	-
Pupilla alpicola	x	x	-	-
Pupilla muscorum	x	-	-	-
Quickella arenaria	x	-	-	-
Succinea putris	x	-	-	-
Trochulus hispidus	x	-	-	-

Vallonia costata	x	-	-	-
Vallonia pulchella	x	-	-	-
Vertigo alpestris	x	x	-	-
Vertigo antivertigo	x	-	-	-
Vertigo extima	x	-	-	-
Vertigo genesii	x	-	-	-
Vertigo geyeri	x	-	-	-
Vertigo hoppii	x	x	x	-
Vertigo lilljeborgi lilljeborgi	x	x	-	-
Vertigo lilljeborgi vinlandica	-	-	-	x
Vertigo parcedentata	x	-	-	-
Vertigo pusilla	x	-	-	-
Vertigo pygmaea	x	-	-	-
Vertigo ronnebyensis	x	-	-	-
Vertigo substriata	x	x	-	-
Vitrea contracta	x	x	-	-
Vitrea crystallina	x	x	-	-
Vitrina pellucida	x	x	x	x
Zonitoides nitidus	x	x	-	-
Zoogenetes harpa	x	-	-	x

Table S3. List of land snails recorded in 48 samples across mainland and southern coastal Labrador in areas climatically similar to West Greenland (Fig. 1). Numbers document counts of the species occurrences and their relative frequency. Three true calciphile species, unlikely to be present in West Greenland due to bedrock chemistry, are marked by an asterisk. Introduced species or their populations were excluded from the list and the analysis.

Snail species	Sites	Snail species	Sites
Euconulus fulvus egenus	45	*Succinea ovata*	5
Vertigo cristata	44	*Gastrocopta tappaniana*	4
Discus whitney	38	*Vertigo arthuri**	4
Perpolita binneyana	31	*Oxyloma verrilli*	3
Perpolita electrina	29	*Vallonia gracillicosta**	3
Columella simplex	27	*Vertigo lilljeborgi vinlandica*	3
Zoogenetes harpa	26	*Catinella avara*	2
Zonitoides arboreus	22	*Punctum* sp. A	2
Vitrina pellucida	21	*Pupilla hudsonianum*	2
Vertigo ventricosa	19	*Succinea* sp.	2
Punctum minutissimum	14	*Vertigo oughtoni*	2
Vertigo modesta	13	*Columella columella*	1
Columella sp. A	10	*Vertigo genesioides*	1
Cochlicopa sp. A	9	*Vertigo ultima*	1
Striatura exile	9	*Vertigo morsei**	1
Striatura ferria	7	*Vertigo perryi*	1
Planogyra asteriscus	5	-	-

Table S4. List of freshwater snail species known from eastern Canada, West Greenland, Iceland, and western Scandinavia based on literature data and our own records. Species are ordered alphabetically. Introduced species or their populations were excluded from the list and the analysis.

	E Canada	W Greenland	Iceland	W Scandinavia
Amnicola limosa	x	-	-	-
Ampullaceana balthica	-	-	x	x
Ancylus fluviatilis	-	-	-	x
Anisus spirorbis	-	-	x	x
Aplexa hypnorum	-	-	-	x
Bathyomphallus contortus	-	-	x	x
Campeloma decisum	x	-	-	-
Ferrissia rivularis	x	-	-	-
Galba truncatula	-	-	x	x
Gyraulus acronicus	-	-	-	x
Gyraulus crista	-	-	-	x
Gyraulus deflectus	x	-	-	-
Gyraulus parvus	x	x	x	x
Gyraulus stroemi	-	-	-	x
Ladislavella catascopium s. lat.	x	x	-	-
Lymnaea jugularis	x	-	-	-
Lymnaea stagnalis	-	-	-	x
Physa heterostropha	x	-	-	-
Planorbarius corneus	-	-	-	x
Planorbella campanulata	x	-	-	-
Planorbella trivolvis	x	-	-	-
Pseudosuccinea columella	x	-	-	-
Radix auricularia	-	-	x	x
Stagnicola fuscus	-	-	-	x
Stagnicola palustris	-	-	-	x
Valvata piscinalis	-	-	-	x
Valvata sibirica	-	-	-	x
Valvata sincera	x	-	-	-
Valvata tricarinata	x	-	-	-

Table S5. Full list of 61 bird species occurring in Greenland, classified by type of molluscs in their diet (Eat Molluscs) and their possible migratory routes: EU<->Gr, Europe to Greenland; NA<->Gr, North America to Greenland. The migration confirmed by retraps of ringed individuals is indicated in the columns "confirm" separately for each route. Species are ordered alphabetically within the molluscs in diet classes, with species breeding in terrestrial habitats marked by an asterisk.

Bird species name	Eat molluscs	EU<->Gr	confirm	NA<->Gr	confirm
*Acanthis flammea**	terrestrial	yes	no	yes	no
*Lagopus lagopus**	terrestrial	yes	no	yes	no
*Lagopus muta**	terrestrial	yes	no	yes	no
*Oenanthe Oenanthe**	terrestrial	yes	no	yes	no
*Plectrophenax nivalis**	terrestrial	yes	yes	yes	yes
Alle alle	aquatic	yes	yes	yes	no
Anas acuta	aquatic	yes	no	yes	no
Anas crecca	aquatic	yes	no	yes	no
Arenaria interpres	aquatic	yes	yes	yes	no
Bucephala islandica	aquatic	yes	no	yes	no
Calidris alba	aquatic	yes	no	yes	no
Calidris alpina	aquatic	yes	no	yes	no
Calidris maritima	aquatic	yes	yes	yes	yes
Cepphus grylle	aquatic	yes	yes	yes	no
Gavia immer	aquatic	yes	no	yes	no
Gavia stellata	aquatic	yes	no	yes	no
*Haliaeetus albicilla**	aquatic	yes	no	no	no
Histrionicus histrionicus	aquatic	yes	no	yes	yes
Larus glaucoides	aquatic	yes	no	yes	no
Larus hyperboreus	aquatic	yes	yes	yes	no
Mergus serrator	aquatic	yes	no	yes	no
Phalaropus fulicarius	aquatic	yes	no	yes	no
Phalaropus lobatus	aquatic	yes	no	yes	no
Rhodostethia rosea	aquatic	yes	no	yes	no
Somateria spectabilis	aquatic	yes	no	yes	yes
Sterna paradisaea	aquatic	yes	no	yes	no
Uria aalge	aquatic	yes	yes	yes	no
Uria lomvia	aquatic	yes	yes	yes	no
Xema sabini	aquatic	yes	no	yes	yes
Anas platyrhynchos	terr. & aqut.	yes	no	yes	yes
*Anthus pratensis**	terr. & aqut.	yes	no	no	no
*Corvus corax**	terr. & aqut.	yes	no	yes	no
Charadrius hiaticula	terr. & aqut.	yes	yes	yes	no
Chroicocephalus ridibundus	terr. & aqut.	yes	no	yes	no
Larus marinus	terr. & aqut.	yes	no	yes	no
*Motacilla alba**	terr. & aqut.	yes	no	yes	no
Numenius phaeopus	terr. & aqut.	yes	no	yes	no
Pluvialis apricaria	terr. & aqut.	yes	no	no	no

Pluvialis squatarola	terr. & aqut.	yes	no	yes	no
*Turdus pilaris**	terr. & aqut.	yes	no	no	no
*Acanthis hornemanni**	not detected	yes	no	yes	no
Alca torda	not detected	yes	yes	yes	no
Anser albifrons	not detected	yes	yes	yes	no
Anser brachyrhynchus	not detected	yes	no	no	no
Anser caerulescens	not detected	yes	no	yes	yes
*Anthus rubescens**	not detected	no	no	yes	no
Ardenna gravis	not detected	yes	no	yes	no
Branta bernicla	not detected	yes	yes	yes	no
Branta canadensis	not detected	yes	no	yes	yes
Branta hutchinsii	not detected	no	no	yes	no
Branta leucopsis	not detected	yes	no	no	no
*Calcarius lapponicus**	not detected	yes	no	yes	no
Calidris bairdii	not detected	yes	no	yes	no
*Falco peregrinus**	not detected	yes	no	yes	yes
*Falco rusticolus**	not detected	yes	no	yes	yes
Fulmarus glacialis	not detected	yes	yes	yes	no
Phalacrocorax carbo	not detected	yes	no	yes	no
Stercorarius longicaudus	not detected	yes	no	yes	no
Stercorarius parasiticus	not detected	yes	yes	yes	no
Stercorarius pomarinus	not detected	yes	no	yes	no
Stercorarius skua	not detected	yes	yes	yes	no