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Herbivore species coexistence in changing rangeland ecosystems: First high resolution national open-source and open-access ensemble models for Iceland

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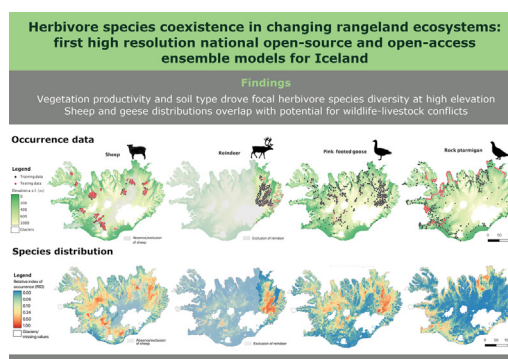
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HIGHLIGHTS

- Rapid changes in northern rangelands have implications for management and species coexistence.
- We compiled nationwide occurrence data and predictors for herbivore species in Iceland.
- We developed the first ensemble model workflow using ML and open-source GIS for these species.
- Vegetation productivity and soil type drove focal species diversity at high elevation.
- Sheep and geese distributions overlap with potential for wildlife-livestock conflicts.

GRAPHICAL ABSTRACT



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ABSTRACT

Rangeland ecosystems are changing worldwide with the abandonment of extensive pastoralism practices and greater interest for species coexistence. However, the lack of compiled data on current changes in the abundance and distribution of herbivores challenges rangeland management decisions. Here we gathered and made available for the first time the most extensive set of occurrence data for rangeland herbivores in Iceland in an Open Access framework for transparent and repeatable science-based decisions. We mapped fine scale species distribution overlap to identify areas at risk for wildlife-livestock conflict and overgrazing. Nationwide and long term (1861–2021) occurrence data from 8 independent datasets were used alongside 11 predictor raster layers (“Big Data”) to data mine and map the distribution of the domestic sheep (*Ovis aries*), feral reindeer (*Rangifer tarandus tarandus*), pink-footed geese (*Anser brachyrhynchus*), and rock ptarmigan (*Lagopus muta islandorum*) over the country during the summer. Using algorithms of Maxent in R,

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Reindeer
Rangeland management
Rock ptarmigan

RandomForest, TreeNet (stochastic gradient boosting) and MARS (Splines) in Minitab-SPM 8.3, we computed 1 km pixel predictions from machine learning-based ensemble models. Our high-resolution models were tested with alternative datasets, and Area Under the Curve (AUC) values that indicated good (reindeer: 0.8817 and rock ptarmigan: 0.8844) to high model accuracy (sheep: 0.9708 and pink-footed goose: 0.9143). Whenever possible, source data and models are made available online and described with ISO-compliant metadata. Our results illustrate that sheep and pink-footed geese have the greatest overlap in distribution with potential implication for wildlife-livestock conflicts and continued ecosystem degradation even under diminishing livestock abundance at higher elevation. These nationwide models and data are a global asset and a first step in making available the best data for science-based sustainable decision-making about national herbivores affecting species coexistence and environmental management.

1. Introduction

Maintaining sustainable levels of biodiversity and ecosystem functionality will require science-based data and a political will to adapt management practices to local and global processes (Boonstra et al., 2018; Zhang et al., 2021), especially under a changing climate (Vuorinen et al., 2020). Management actions on rangelands, when linked to real-world conditions on the land, have generally targeted livestock with policies aimed at maintaining pasture productivity and minimizing negative species interactions by measures such as predator suppression (du Toit et al., 2017). A recent focus on reconciling conservationist and agricultural interests has brought forward the realities for species coexistence on a finite landmass (Czech et al., 2000; Daly and Farley, 2011). In the wake of this movement, several studies have documented nuanced sets of species interactions varying through space and time from facilitation to competition (Niamir-Fuller et al., 2012; Stears and Shrader, 2020).

Agricultural land abandonment and the general diminution in extensive livestock grazing practices and pastoralism worldwide, especially in marginal lands such as arctic and alpine ecosystems (Mantero et al., 2020), is leading to changes in shrub and tree cover (FAO and UNEP, 2020), fire regimes (Grau et al., 2020) and nutrient cycling (Andriuzzi and Wall, 2018; Cromsigt et al., 2018; Vuichard et al., 2008). In these changing ecosystems, native species - both herbivores and their predators - are recolonizing areas with reduced human footprint (Navarro and Pereira, 2015). These processes, sometimes coined “natural rewilding”, have notably been documented for herbivores such as large ungulates in Europe (Austrheim et al., 2011) and North America (Foster et al., 2002), native camelid populations in the Andes (Grau et al., 2020) as well as apex predator species (Prugh et al., 2009; Rana et al., 2018). Beyond the political interest to promote species coexistence, there is thus a practical need to understand the ongoing shift in species composition and its impact on ecosystem function and biodiversity (König et al., 2020; Lemes et al., 2020; Speed et al., 2019a).

Having sound and robust data on species distribution is a prerequisite for developing appropriate management strategies. Species distribution models (SDM) can provide quantitative answers to those questions (Elith et al., 2006; Guisan and Zimmermann, 2000). SDMs tend to assume niche conservatism, which is that individual species' environmental requirements are preserved through space and time (i.e., evolution; Peterson, 2011). Although more traditionally applied to the study of wild species, SDM concepts are increasingly used as a rapid assessment tool to study a variety of organisms such as domesticated plants (Zhao et al., 2021), or processes, like disease transmission (Gulyaeva et al., 2020) or livestock-wildlife interactions (Bleyhl et al., 2019; Li et al., 2017). Linked with Machine Learning (ML) and Artificial Intelligence (AI) techniques, e.g. inference through predictions (Breiman, 2001), SDMs can be powerful tools for conservation and natural resource management (Humphries and Huettmann, 2018) and can aid to target management actions (Guillera-Aroita et al., 2015; Guisan et al., 2013).

Ensemble modelling approaches combine the strengths of a series of individual models based on the Machine Learning and AI concept that “many weak learners make for a strong learner” (Friedman et al., 2000). Different techniques may be used to combine the results of individual models into an ensemble, although averaging (i.e., average predictions across models) has been shown to be generally suitable (Marmion et al., 2009). A recent

review of modelling algorithms for presence only data highlighted the powerfulness of ensemble modelling techniques when using a subset of well-tuned models (Valavi et al., 2021). Thus, ensemble modelling of herbivore species offers a valuable analysis approach to map and understand species coexistence on rangelands.

Due to the environmental legacy of centuries of extensive livestock grazing (Arnalds, 1987), Iceland offers a unique model to infer and understand wildlife-livestock interactions and how to manage for multiple herbivores on rangelands. Although relatively poor in species, Icelandic tundra ecosystems have a comparable level of herbivore diversity to other Arctic ecosystems (Barrio et al., 2016) and thus present a rather good case study system for understanding broader processes across the biome. Like in many rangelands worldwide, Iceland has seen a recent diminution in the density of free-ranging livestock (Arnalds and Barkarson, 2003) and shift in herbivore assemblages amidst a changing climate (Björnsson et al., 2018). In Iceland, just over 50 % of the land is classified as grazing land and used as such from June to September. Sheep (*Ovis aries* L., North European short-tailed sheep; Baldursdóttir, 2019; Tapio et al., 2005) can be found across the rangelands while only relatively small areas are currently used as grazing commons for horses (*Equus ferus caballus*, Icelandic breed). Sheep are released in late June or early July in grazing commons, largely located in uninhabited areas located above the potential treeline (at approx. 200–300 m a.s.l.), also referred to as the highlands. Sheep are not released in certain areas due to a variety of reasons, such as low productivity or difficulty of access, and are actively excluded from other areas with poor land condition or special conservation status through a combination of natural barriers, fences, and other management practices.

Studies have documented the historical impact of sheep on the Icelandic highlands and its role in widespread ecosystem degradation (Barrio et al., 2018; Eddudóttir et al., 2020; Ross et al., 2016) with many parallels in rangelands worldwide (Albon et al., 2007; Rose et al., 1995; Sainnemekh et al., 2022). While the abundance of sheep has steadily decreased since an historical maximum in the late 1970s, it is argued that overgrazing is ongoing in some parts of the country and that current grazing management could be improved (Arnalds and Barkarson, 2003; Marteinsdóttir et al., 2020). It is, however, unknown where sheep really occur as a detailed geographic inventory does not exist and rangeland conditions have just recently started to be systematically monitored (Soil Conservation Service of Iceland, 2021b). It is also unknown how other herbivore species may be contributing to total grazing pressure at a given location, especially since sheep farmers have been expressing growing concerns about the impact of wild and feral herbivores on land degradation (J. H. Stefánsson, Soil Conservation Service of Iceland, personal communication; Þorvaldsson, 2016). There is thus a growing livestock-wildlife interaction conflict for which national data and range maps are widely absent.

In the highlands of Iceland, livestock co-occurs with three other main herbivore species (i.e., in terms of occurrence and population abundance): the reindeer (*Rangifer tarandus tarandus* L., feral population, Taxonomic Serial Number (TSN) 625197), the pink-footed goose (*Anser brachyrhynchus* Baillon; population breeding in Iceland and Greenland and overwintering in the United Kingdom, TSN 175036; Mitchell et al., 1999) and the rock ptarmigan (*Lagopus muta islandorum* Faber, TSN 677716). Reindeer were introduced from Norway in the late 18th century onwards (Þórisson, 1984); they are restricted to the Eastern part of the country through a combination of management and natural barriers (Þórisson et al., 2021).

Reindeer have no natural predators in Iceland and unlike other populations are not affected by warble flies (*Hypoderma tarandi* and *Cephenemyia trompe*) and mosquitoes (*Aedes nigripes*) (Þórisson, 1993). Their abundance is thus largely constrained by hunting pressure and to a lesser extent food availability (Þórisson, 2018), with current levels representing a historical high (Þórisson et al., 2021).

Since the 1950s when it first started to be actively monitored, the population of pink-footed geese increased from about 30,000 to 500,000 individuals and started occupying breeding sites beyond the Þórsárver area in central Iceland where it was initially restricted (Brides et al., 2021; Kerbes et al., 1971). Pink-footed geese use lowland pastures in Iceland, now often agricultural land, to feed during the pre-breeding (i.e., April–May) and fall staging season (i.e. September–October; Fox and Leafloor, 2018). Breeding individuals largely move to the highlands in May, although breeding sites have been increasingly found in lowland areas in recent years (Sigfússon, 2012; Snæþórsson et al., 2020). Failed breeders and non-breeders also move to the highlands at the end of the pre-breeding season although only an unknown fraction of them will remain in the highlands during the moulting season in June while the rest will seek moulting sites in northeast Greenland (Fox and Leafloor, 2018).

Finally, the rock ptarmigan is of circumpolar occurrence and a local migrant species; although breeding sites are found throughout the country (Icelandic Institute of Natural History, 2021b) most individuals use lowland areas during the breeding season (mid-April–August), move to the highlands during fall (September–October) and spend winter at mid-elevation (November–mid April; Garðarsson, 1971). Icelandic rock ptarmigan populations are hunted and currently in decline (IUCN, 2021). The population has not shown characteristic peaks in abundance in recent years (Fuglei et al., 2020).

The main terrestrial predators in Iceland are the arctic fox (*Vulpes lagopus*), raptors (notably the gyrfalcon, *Falco rusticolus*) and the raven (*Corvus corax*). These predators have a negligible impact on sheep (Pálsson et al., 2016) and reindeer (Þórisson, 1993) but significantly affect the rock ptarmigan and pink-footed goose populations (Nielsen, 1999; Skarphéðinsson et al., 1990).

The absence of compiled data on current changes in the distribution and abundance of wild, feral and domesticated herbivore species raises challenges as to how to manage multiple herbivores without knowledge of fine-scale distribution and competitive interactions. In support of a science-based management on changing rangeland ecosystems worldwide, here we present a standard and quantified path to better assess spatial distribution and potential environmental niche overlap of these species. We compiled eight nationwide species occurrence datasets for the four most widespread herbivore species in Iceland during the summer (June, July and August) and developed ML and AI ensemble models of species distribution. The resulting information will fill a gap in our understanding of species interactions in a changing landscape. They represent an asset for rangeland management globally and will be important locally to target management actions.

2. Material and methods

This study focuses on the period (June to August) and species most relevant for rangeland management in Iceland due to their abundance, distribution, legacy and public and economic relevance as game species and livestock. These four species can be found across a range of elevation but are known to spend a considerable amount of time grazing on tundra vegetation in the highlands (Arnalds and Barkarson, 2003; Egilsson, 1983; Fox and Leafloor, 2018; Garðarsson, 1971). Although definitions vary, the highlands are 'remote' wilderness areas in Iceland characterized as the uninhabited areas located beyond the potential treeline (approx. 200–300 m a.s.l.) which are dominated by subarctic-alpine tundra vegetation (Thórhallsdóttir, 1997). Overall, elevation tends to be lower on the coast and increase going inland (Fig. 1). Similarly, human infrastructures and fertilized pastures are concentrated along the coast where vegetation productivity (i.e. NDVI) tends to be higher and temperatures milder. More detailed

visual representations of the environmental characteristics of the study areas can be found in Figures S1 to S11 in Supplementary data S1.

To develop SDM for sheep, reindeer, pink-footed geese and rock ptarmigan we used data from citizen science reports, Geographic Positioning System (GPS) collars and bird band recovery. Depending on data availability and sampling design, the different datasets were used as either training or testing data. We describe below the data processing procedure for occurrence data and predictor variables. Further methodological details associated with raw data collection are described in the Supplementary data. A summary table presenting the sources and processing steps as well as biases of each occurrence dataset is also available in Supplementary data S2. Unless otherwise mentioned, data manipulation was done in spreadsheets, text editors and using the R statistical software (version 4.0.2; R Core Team, 2020). Due to the robust modelling approach involving 'tree' algorithms, we found no need to address or correct directly for autocorrelation (Betts et al., 2009; Diniz-Filho et al., 2003), but random selections were executed for better model data using the *slice_sample* function in the *dplyr* package (version 1.0.7; Wickham et al., 2021).

2.1. Data used for model development

2.1.1. Sheep occurrence data

a) Model development. During 2018–2020, the Soil Conservation Service of Iceland (2021a) in collaboration with sheep farmers, installed GPS collars on 239 ewes belonging to 15 farms to better understand rangeland use and inform management practices (Supplementary data S3). The exact release and roundup dates varied per year and region, with the earliest release in late May and the latest roundups in early October. We first eliminated all GPS collar records before release and after roundup, to keep only records of sheep in the rangelands. Then for consistency with other species, we selected only the records from June, July and August. For a representative population-level data set, we only kept ewes with over 40 or more occurrence points and randomly selected 40 points from each ewe remaining for a total of 8360 records (Fig. 1a). **b) Model evaluation.** A statistical subset of the GPS collar location data was used to validate the models. We used the *createDataPartition* function in the R package *caret* (version 6.0–90; Kuhn, 2021) to perform a stratified random sampling of the dataset with a ratio of 75 to 25 for the training and testing data respectively (Fig. 1a). Due to confidentiality issues and the possibility of linking sheep to their farm, it was not possible to make the sheep GPS data available in open access.

2.1.2. Reindeer occurrence data

a) Model development. As part of an initial research conducted to evaluate the impact of the Kárahnjúkar hydropower project on animal populations (Þórisson and Ágústsdóttir, 2014), eight GPS-collared reindeer females were monitored in 2009–2011 (Supplementary data S3). Due to the reindeer herd behavior, the GPS locations are believed to be a representative sample of the habitat used by the Snæfells herd; this sub-herd represents about half of the total population and covers just over half of the current species distribution (Þórisson, 2018). We subset the raw dataset to obtain records from June, July and August. The minimum number of records available for a cow during the study period was 340, we thus randomly selected 340 records from all cows to balance the dataset, for a total of 2720 locations (Fig. 1b). **b) Model validation.** Since 2017, citizens have been invited to report reindeer sightings by contacting staff at the East Iceland Nature Research Centre directly or by recording observations on the organisation webpage (East Iceland Nature Research Centre, 2021). We used observations recorded with location information during June, July and August for a total of 161 observations between 2017 and 2021 (Fig. 1b). As a legacy of this research, the full GPS collar locations dataset was uploaded to the MoveBank website (<https://doi.org/10.5441/001.1.vp4cf4qg>) and the citizen science observations dataset was uploaded to the GBIF website (<https://doi.org/10.15468/zmcqdz>). The processed occurrence datasets used in the models are available on Mendeley data (<https://doi.org/10.17632/b79jvhm9pt.1>).

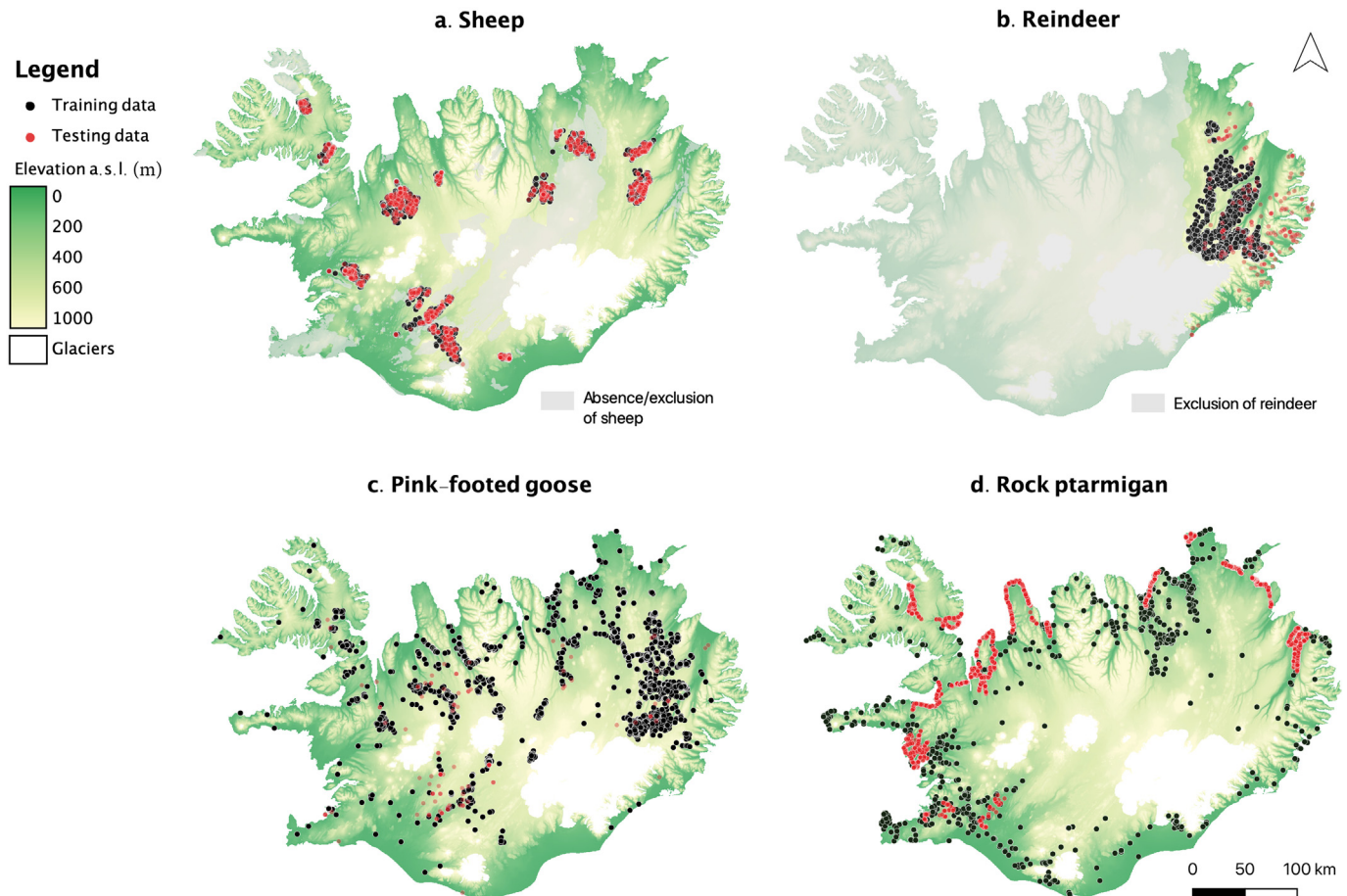


Fig. 1. Occurrence data used for training and testing the models for a) the sheep, b) the reindeer, c) the pink-footed geese and the rock ptarmigan overlay on the digital elevation model of Iceland (m). Gray masks correspond to areas where a) sheep are absent/excluded and b) reindeer are excluded.

2.1.3. Pink-footed goose occurrence data

a) Model development. We combined two datasets to best describe the whole population of pink-footed geese in Iceland during the summer. First, we retrieved data from Global Biodiversity Information Facility GBIF.org (<https://www.doi.org/10.15468/dl.xjmx3>) which includes citizen observations, mainly from eBird, and museum records. We scanned them for model-relevant errors, removing absence records and all coordinates with uncertainty over 250 m using the R package *scrubr* (Chamberlain, 2021). The full dataset was subset to the months of June, July and August for a total of 1070 records collected between 1910 and 2021. This is the longest record we are aware of for this species in Iceland. Secondly, we used GPS collar data collected by The Wildfowl and Wetlands Trust (2021) in collaboration with Orsted (an energy company based in Denmark; Orsted, 2021) for an initial study on pink-footed geese movements and interactions with wind turbines (Supplementary data S3). The data available for this study consisted in a single location for each GPS collar which was randomly selected for each 24-hour period when the geese were in Iceland. To avoid over-representing certain individuals, we randomly selected the records for only one season for each bird. After data treatment, and because some geese with collars were shot before arriving in Iceland, location data from 70 tagged pink-footed geese were available for analysis. We subset the dataset for records in June, July and August, for a total of 3440 records (Fig. 1c). **b) Model evaluation.** Band sighting and recovery data were obtained from the Icelandic Ringing Scheme at the Icelandic Institute of Natural History (2021a). We compiled data from geese banding in Iceland and abroad and cleaned the dataset to remove entries without coordinates or information as to the circumstance of the observation or recovery. We also filtered out instances when only the rings were recovered

(i.e., without the evidential carcass) or attached to an old carcass (i.e., we only kept locations where a goose was seen alive). Finally, we subset the dataset to June, July and August recoveries for a total of 228 locations between 1951 and 2021 (Fig. 1c). The GPS collar and band sighting data are available from the respective institutions managing them.

2.1.4. Rock ptarmigan occurrence data

a) Model development. The primary data used to build models for rock ptarmigan in Iceland were locations recorded between 1860 and 2021 and freely available from GBIF.org (<https://www.doi.org/10.15468/dl.rk83zs>). We scanned the datasets for model relevant errors as described above for the pink-footed goose. For this species only, we used data from the months of May, June, July, and August as ptarmigan are known to stay in the same area during that period (Garðarsson, 1971), for a total of 3047 sightings (Fig. 1d). **b) Model evaluation.** Since 1981, the Icelandic Institute of Natural History has surveyed rock ptarmigan using a distance sampling methodology (Buckland et al., 2001) along road transects located in the lowlands to derive population indices (Icelandic Institute of Natural History, 2021b). Transects are monitored in late April or early May, which corresponds to the period when birds are expected to have moved to the breeding grounds, where they will stay until the end of August (Gardarsson, 1988). During sampling, observers recorded the location on the transect when a bird was observed as well as the distance from the transect to the bird and whether it was located on the left or the right side of the transect (Ferrarini, 2022). In 2011, data from 2005 to 2010 were processed and assigned a geographic position for each bird sighting, i.e., using the distance to the individual and direction of the observation, geographic records were moved from the transect to the estimated location of the animal

(Fig. 1d). We used the processed locations recorded in May ($n = 4434$) for model validation. Occurrence data derived from the road transect survey were made available as part of this study on the GBIF website (<https://doi.org/10.15468/k6ytqn>). All processed occurrence data used in the models for rock ptarmigan are available in Mendeley data (<https://doi.org/10.17632/b79jvhm9pt.1>).

2.1.5. High resolution predictor variables

Based on expert knowledge of the environmental requirement of each species and data availability, we selected a consistent set of 11 high resolution environmental predictors. These predictors were used for all models and consisted of three categorical variables: land cover classes (13 classes), soil types (16 classes), wilderness (presence/absence, proxy related to human presence); and eight continuous variables: elevation, Euclidean distance to fenced pastures, Euclidean distance to freshwater (inland), peak Normalized Difference Vegetation Index (NDVI), slope, as well as average precipitation, temperature and wind speed for June, July and August. Environmental and climate variables, available in vector format and raster files, were extracted from public repositories or obtained directly from the authors. Detailed information on each predictor layer source, original format and the calculations applied can be found in Supplementary data S1. Due to our analysis approach and the aim of this study, correlations between predictor variables were not a concern (Humphries and Huettmann, 2018), but predictor raster files were still tested for multicollinearity using the *cor* function in the *caret* package (version 6.0–90; Kuhn, 2021); none showed a correlation above 0.75. All files were converted to raster format, resampled at a 250 m spatial resolution, and projected in Lambert 2016 Icelandic Projection. All processed predictor layers are available in raster format at 250 m resolution in Mendeley data (<https://doi.org/10.17632/b79jvhm9pt.1>).

2.2. Data analyses

Following approaches by Thuiller et al. (2009), Hardy et al. (2011) and Meißner et al. (2014), we developed ensemble models for Iceland for each herbivore species based on the results of five modelling algorithms, namely: Maximum Entropy (Maxent; Phillips, 2005), Classification and Regression Trees (CART; e.g. Vayssières et al., 2000), Multivariate adaptive regression splines (MARS; e.g. Leathwick et al., 2006), Random Forest (RF; e.g. Zhang et al., 2022) and Tree Net (TN; e.g. Friedman, 2002). Maxent models were developed using the R software package *Maxnet* (version 0.1.4; Phillips et al., 2017) and 80,000 random background points. The other four models are binary machine learning techniques and were handled in Salford Predictive Modeler 8.3 (SPM) using 1,027,333 background points. The relative indices of occurrence (RIOs) were produced for a regular lattice of points (1 km resolution) and the ensemble models were computed as the mean of the output of the five models for each species. The discrimination capacity of each ensemble model was calculated on the final raster file using the area under the curve (AUC) based on the receiver-operating characteristic (ROC) with the *evaluate* function in the *dismo* package (version 1.3–5; Hijmans et al., 2021).

We evaluated and quantified similarities among RIO values of all species at each 1 km lattice point using the *varclus* function in the R package *Hmisc* (version 4.5–0; Harrell Jr et al., 2021) which provides a tree form visualization of species clusters (Baltensperger and Huettmann, 2015). We first performed this analysis using the RIO predicted for each species by the ensemble models, hereafter called potential distribution. We then ran the analysis again using the predicted RIO for the pink-footed goose and rock ptarmigan but for the sheep and reindeer, predicted values were set to 0 where these species are known to be absent or actively excluded, hereafter called realized distribution.

For easier assessment of herbivore species diversity, we derived from the models a binary (presence/absence) relative index of occurrence (RIO) using threshold values for each species. For the reindeer, the pink-footed geese and the rock ptarmigan, for which occurrence data present a good coverage of the study area, we used a threshold value between the

95 % and lowest training presence (e.g., Pearson et al., 2007; Raxworthy et al., 2007) selected after visual optimization, for a binary threshold of respectively 0.24, 0.10, and 0.05. For the sheep, where occurrence points were more geographically limited, we assigned a threshold of 0.10 based on the known widespread occurrence of the species. For the sheep and the reindeer, the binary index was set to 0 inside the areas where each species is excluded through management actions. From these binary ensemble models, we calculated the sum of the presence for the four species as a proxy of herbivore diversity across the entire country during the summer and mapped the resulting calculation in open-source GIS (QGIS Development Team, 2021). To capture the association between herbivore diversity and the environment in quantitative multivariate terms, we then data mined the presence file using TreeNet (Humphries and Huettmann, 2018) to quantify environmental variables associated with diverse species association.

3. Results

We created a 1 km ensemble model for each of the four important vertebrate herbivore species co-occurring in the rangeland of Iceland during summer (Fig. 2). Areas under the curve (AUC) for the sheep, reindeer, pink-footed goose and rock ptarmigan ensemble models are respectively 0.9708, 0.8817, 0.9143 and 0.8844. The results of the ensemble models are available in raster format at 1 km resolution on Mendeley data (<https://doi.org/10.17632/b79jvhm9pt.1>).

The species clustering analyses identified the sheep and pink-footed goose as the main species sharing the environmental space during the summer according to both the potential (i.e., full species range: Fig. 2 without masks and Fig. 3a) and realized distributions (i.e., considering sheep and reindeer exclusion areas, Fig. 2 with masks and Fig. 3b). The exclusion of sheep (i.e., masked areas) does little to reduce this overlap; the species overlap on c. 20 % of the country under the potential distribution and c. 18 % under the realized distribution. Under the potential distribution scenario, the rock ptarmigan showed the least species clustering with the other herbivore species while this shifted towards the reindeer under the realized distribution scenario.

The herbivore diversity map (Fig. 4a) showed the influence of the reindeer in the East, the only region where the four herbivore species are present. The region characterized by three of the four species is thus located in the East, and also the Northeast and to a smaller extent the Southwest interior. The data mining analysis identified the soil type - mainly soil type 4 (cryosol-gleyic andosol) and 5 (gleyic andosol-brown andosol) - as well as NDVI as the main predictor variables associated with higher diversity of herbivores (Fig. 4b). In other words, these herbivore species tend to aggregate in productive areas with underlying permafrost, thus higher elevation, or fertile soils.

4. Discussion

In this study, we present, used, and make publicly available “Big Data” on herbivore species in Iceland and present a workflow for rangelands to assess areas of overlap and their underlying conditions by providing state-of-the-art models and analyses. These data fill a gap in available data for Iceland (e.g., BIOTIME: Dornelas et al., 2018; CAFF: Aronsson et al., 2021) and will provide the foundations to better understand species interactions and target management actions nationwide.

The species distribution models (SDMs) developed in this study show that during June, July and August, the sheep and pink-footed geese are the main herbivore species with overlapping distribution. These species are also the most abundant nationwide as well as those that feed most heavily on fertilized pasture in Iceland, as well as abroad for the geese (Fox and Leafloor, 2018). Moreover, current management areas do little to decrease the extent of this overlap. Since this study focuses on the summer, it cannot be excluded that reindeer and rock ptarmigan also use the area where sheep and pink-footed geese overlap at other times of the year, but they certainly do so to a lesser extent during the growing season.

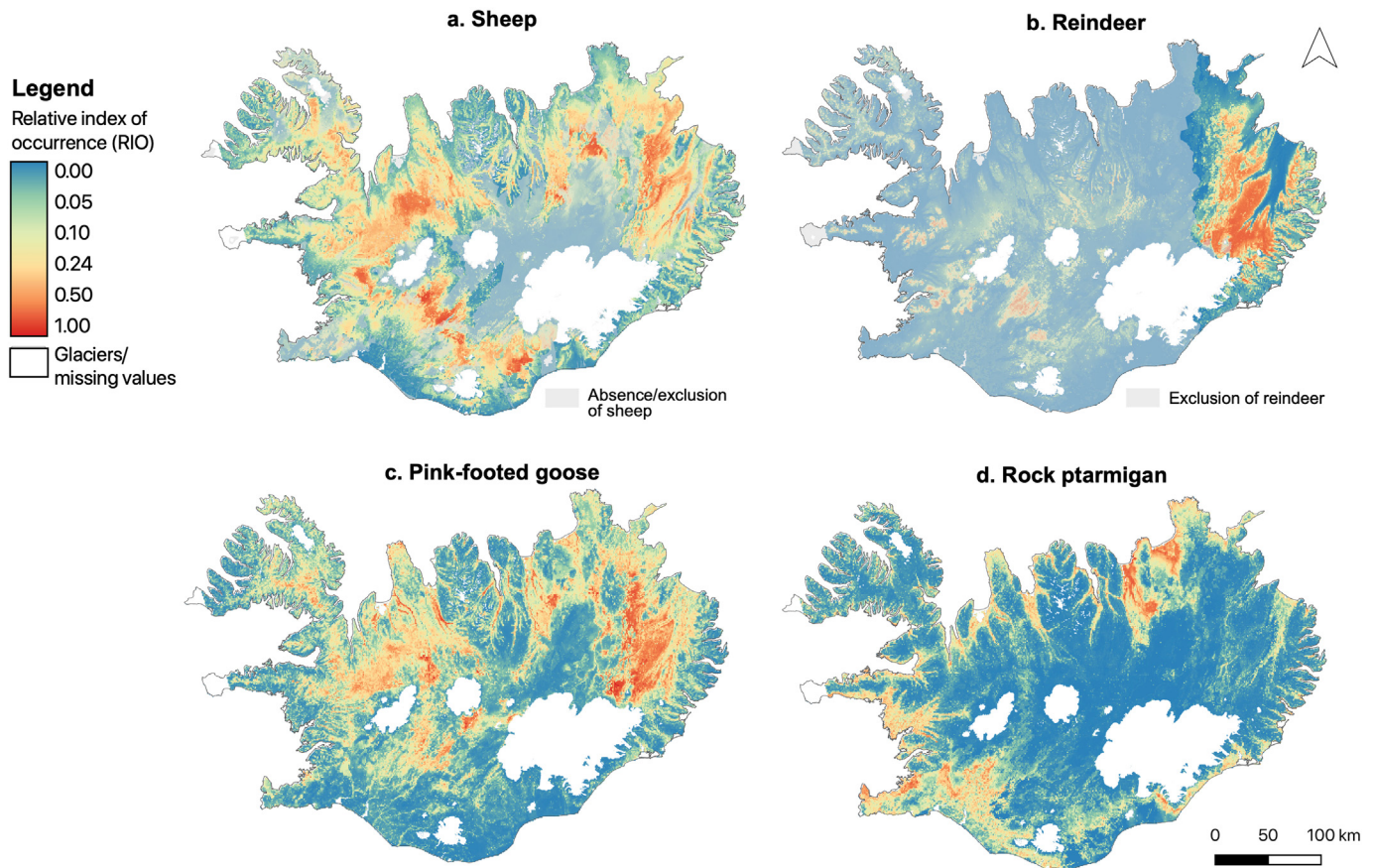


Fig. 2. Predicted distribution for the a) sheep, b) reindeer, c) pink-footed goose and d) rock ptarmigan in Iceland as calculated by ensemble models for the months of June, July and August. Gray masks correspond to areas where a) sheep are absent/excluded and b) reindeer are excluded.

Spatial overlap shows relation but does not necessarily provide information on diet overlap as herbivores may be sharing space but still feeding on different species (Fernandez et al., 2021). However, sheep are generally known to target grasses as well as other graminoids and willow species on the tundra in Iceland (Þorhallsdóttir and Þorsteinsson, 1993; Þorsteinsson, 1980). Studies on geese diet elsewhere have shown that they also primarily feed on grasses and sedges during the summer (Van Eerden et al., 2005) and are thus likely to compete for resources with sheep. The additive effect of pink-footed geese and sheep - both heavily driven by wider farming policies on the range and outside (e.g., European

Union) - likely has an additive impact on vegetation and ecosystem degradation, notably soil erosion in the Icelandic highlands (Arnalds and Barkarson, 2003). Overgrazing by sheep is believed to have shifted plant community composition towards less palatable plant species in Iceland (Barrio et al., 2018; Marteinsdóttir et al., 2017) and many rangeland areas show slow increase in productivity or change in plant species composition even after years of sheep exclusion (Jónsdóttir et al., 2005; Mörsdorf et al., 2021). However, our results suggest that overgrazing may be driven by the cumulative impact of sheep and pink-footed geese with implications for sustainable management on rangelands.

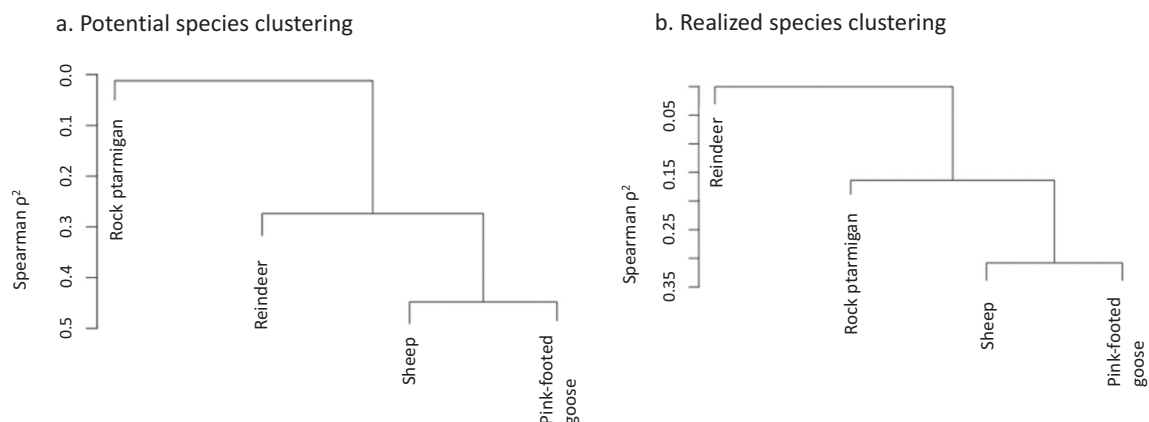


Fig. 3. Species clustering according to the *varclus* analyses conducted on the a) potential distribution (i.e., without considering absence/exclusion areas) and b) realized distribution (i.e., RIO set to 0 inside absence/exclusion areas).

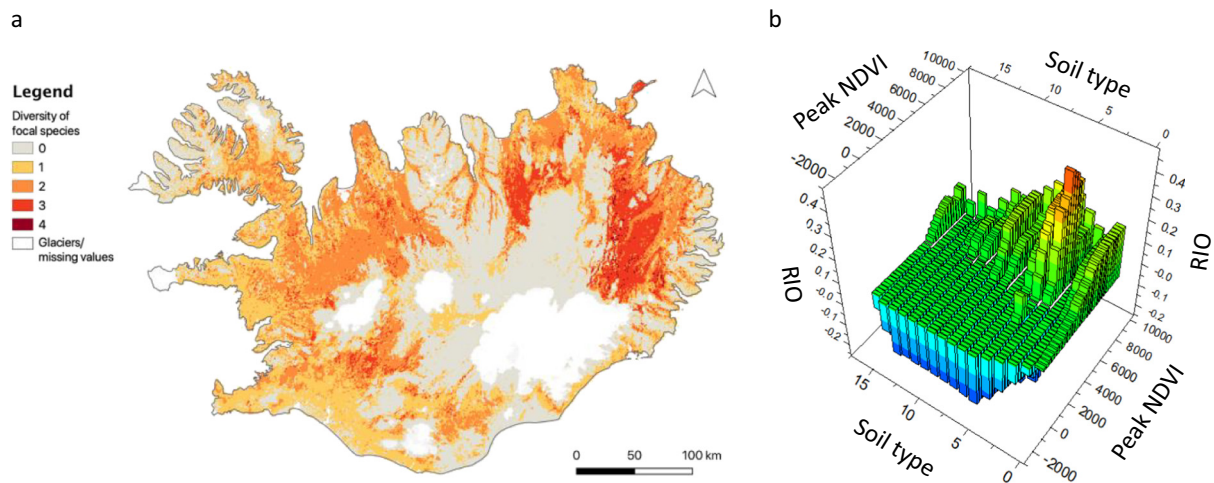


Fig. 4. a) Herbivore diversity map for the main species occupying the Icelandic highlands and b) contribution of the two main environmental predictor variables in explaining diversity of the focal species (RIO).

Although the rock ptarmigan showed less overlap with the sheep and pink-footed geese during summer, there is a potential diet overlap. Ptarmigan actively seeks bulbils of *Bistorta vivipara* in the highlands from the time that they become available in July and are a main food source in the fall (Garðarsson, 1971; Garðarsson, 1988). Moreover, the rhizomes of *B. vivipara* are heavily consumed by pink-footed geese in the spring (Fox and Bergersen, 2005). On the other hand, the increase in geese abundance elsewhere has been linked to a decrease in other ground nesting birds due to alternative prey selection (Lamarre et al., 2017). Although this has not been demonstrated for Iceland, Pálsson et al. (2016) showed that the arctic fox diet in the highlands has shifted from rock ptarmigan to pink-footed geese as the populations experienced opposite trends in abundance. In Iceland, like on Svalbard for instance, the absence of small rodents makes the ptarmigan one of a few living (i.e., as opposed to carcasses) inland food sources for the arctic fox in winter (Eide et al., 2012; Fuglei et al., 2003). If the arctic fox population grows due to abundant food availability during the summer, it may have a negative impact on the rock ptarmigan in winter. Nevertheless, both the distribution overlap in the fall as well as the diet overlap would require further study to answer those questions for the declining Icelandic rock ptarmigan population.

4.1. Limitations and uncertainties

The occurrence data presented in this study covers a wide temporal (1861–2020) and geographic range as well as different life cohorts (i.e., breeding, none-breeding, etc.). Nevertheless, it represents a subset of existing species data for Iceland (e.g. Skarphéðinsson et al., 2016) and our model workflows offer themselves to be refined as more data become available. Whenever possible, we combined occurrence datasets from various sources to minimize the impact of sampling biases (Supplementary data S2). These notably include a strong association to human infrastructures, largely located in the more densely populated lowland areas, for all citizen science and road transect data. Contrastingly, all GPS collar data were collected from adult females using the more remote areas at higher elevations.

We conducted our analyses using 11 high resolution predictor variables of ecological relevance which could be directly obtained or easily derived from available GIS layers (Supplementary data S1). These variables were chosen based on expert knowledge to represent the main environmental requirements of each species. They captured well the distribution and species overlap of our four vertebrate herbivores at the scale of study, matching other studies on the drivers of herbivore diversity in the Arctic (Barrio et al., 2016; Speed et al., 2019b). Although these were assessed to be the best layers available at the time of this work, most lack a science-based error assessment and ground-truthing which could have contributed to

some of the weaker models. Here again, increase in the stock of good quality authoritative environmental layers could contribute to the future refinement of models and better sustainable policy eventually.

Finally, we did not include any biotic interactions in our models, as these likely occur at a finer scale. Moreover, the nature of these interactions in Iceland is largely speculative and lacking experimental proof (Dormann et al., 2018). Nevertheless, these may be important to consider in future studies as anecdotal evidence suggest that geese can be territorial and scare away sheep.

We found that sheep are widely distributed in Iceland during the summer which is outlined by the predicted distribution map. However, in the absence of detailed inventory data it cannot be excluded that sheep are also found in regions of very low RIO on the current map since the occurrence data used to train the model only represented a subset of the species environmental niche. If sheep are found in certain areas with low RIO, it would likely further support the argument that they are kept in areas that are suboptimal for the species. The AUC value for the sheep ensemble models was very high (0.9708), which may partly be attributed to the fact that the training and evaluation data were subsets of the same GPS collar dataset. More occurrence data from across the country, such as citizen science data and monitoring, as well as detailed analysis of the sheep GPS-collar data used in this study may yield further insights into this question.

As for the reindeer, the distribution identifies the East as the main region suitable for this species. This is in line with historical records indicating that reindeer were initially introduced in four distinct locations, but by the mid-19th century all populations became extinct except for a small herd in the East (Þórisson, 2018). The conditions that allowed the maintenance of reindeer in the East are still being investigated although research points to the influence of a more continental climate and diverse microtopography allowing for new growth, rich in nutrients, for a longer period during the summer (Þórarinsdóttir and Ágústssdóttir, 2015). Moreover, areas with higher RIO to the west of the current distribution (i.e., under the mask of the exclusion areas; Fig. 2b), also correspond to regions where reindeer which escaped the management areas were found (Þórisson, 2016). Although these observations are anecdotal, they suggest that the current model for reindeer is a good representation of the species' environmental niche. Nevertheless, reindeer AUC for the ensemble model are good but not high (0.8817), which is likely associated to systematic and contrasting biases in the training (i.e. GPS collars) and testing (i.e. citizen observations) datasets.

The distribution of pink-footed geese obtained in this study is the most comprehensive one to date for Iceland due to the inclusion of both breeding and non-breeding individuals and should yield useful information for

population management (e.g., Solovyeva et al., 2021). The inclusion of different datasets clearly had a net positive impact on model accuracy as expressed by the AUC value (0.9143). Future questions on this species may aim at improving occurrence datasets as well as getting a better understanding of the relative population density across Iceland. The latter would give an estimate of grazing pressure which is likely to be higher in the breeding areas than in the lowlands.

Finally, based on expert knowledge and a previous study on the species in Iceland (Skarphéðinsson et al., 2016), the rock ptarmigan distribution map accurately highlights areas of known species occurrence to the exception of highland areas in the northeast. However, currently available occurrence data did not cover that region, and thus future research could build on this work to fill the gap. This would contribute to increase model accuracy which is good but not high (AUC value: 0.8844) for the rock ptarmigan ensemble model.

4.2. Implications for management

Like elsewhere in subarctic and Arctic regions (McKenzie and Shaw, 2017) the impact of rapidly growing populations of geese feeding on agricultural pastures on the more productive wintering grounds is raising challenges and modifying species interactions (Mason et al., 2018). With the current trend in pink-footed geese abundance, and other goose populations occupying the lowlands over the summer, we can expect growing wildlife-human conflicts as well as zoonotic pandemic risks in Iceland as elsewhere in Europe (Stroud et al., 2017). Moreover, this study suggests that current management practices would benefit from considering herbivore species overlap and their potential additive effect on land conditions to achieve sustainability targets.

Models such as achieved here provide a quantitative summary explicit in space and time and can be insightful to tackle those mentioned questions for better policy decisions. Similar approaches have notably been used to study wild and domesticated sheep niche partitioning in the Southern Caucasus (Bleyhl et al., 2019) as well as giant pandas and livestock interactions in China (Li et al., 2017) and provided data to target conservation areas for specific species. In contrast to those other studies however, our target was not species specific but aimed at identifying areas where additive grazing pressure may contribute to land degradation and in turn affect ecosystem functioning more broadly. To this end, we specifically identified the environmental variables associated with species overlap for a general framework to implement management actions. These actions could notably aim at reducing both sheep and geese populations in sensitive areas to limit wildlife and livestock conflicts while maintaining productive ecosystems. This approach highlights the potential of species distribution models to be used beyond “species” to address pressing questions for sustainable land management.

5. Conclusion

In this study, bringing together citizen science data with the best available scientific research datasets analyzed with machine learning ensembles helps to better map and understand the distribution and species overlap of the main herbivore species in Iceland. The documented raw occurrence data made available through this study as well as the modelled distributions will contribute to build the pool of biodiversity data to better manage changing rangeland ecosystems. These models can be a first step in an ongoing process of model refinement using increasingly available occurrence data towards science-based sustainability policies. The identification of potential distribution overlaps as well as the main environmental factors driving the presence of the targeted herbivore species provides guidance as to how and where future research and management can be implemented to better achieve species coexistence while preventing ecosystem degradation. The data, workflow, and analyses presented in this research are a first step to further our understanding of changing herbivore species assemblages on rangelands like done here for Iceland and present a methodology that could be expanded to answer similar questions worldwide.

Research data

The following data are available on Mendeley data (<https://doi.org/10.17632/b79jvhm9pt.1>):

1. Environmental predictor raster layers and associated metadata: i.e. three categorical variables: land cover classes (13 classes), soil types (16 classes), wilderness (presence/absence, proxy related to human presence); and eight continuous variables: elevation, Euclidean distance to fenced pastures, Euclidean distance to water (inland), Normalized Difference Vegetation Index (NDVI), slope, as well as average precipitation, temperature and wind speed for June, July and August at 250 m resolution.
2. Species occurrence data used to compute the models and associated metadata: i.e. two set of training occurrence data (reindeer GPS and rock ptarmigan GBIF), two sets of testing data (reindeer citizen observations, and rock ptarmigan road transect distance sampling).
3. Ensemble models and associated metadata for sheep, reindeer, pink-footed geese and rock ptarmigan (raster file at 1-km resolution).

CRediT authorship contribution statement

Noémie Boulanger-Lapointe: Conceptualization, Methodology, Investigation, Formal analysis, Writing - Original Draft; **Falk Huettmann:** Methodology, Formal analysis, Writing - Original Draft; **Isabel C. Barrio** and **Ingibjörg Svala Jonsdóttir:** Conceptualization, Writing - Review & Editing, Funding acquisition; **Mathilde Defourneaux:** Visualization, Formal analysis, Writing - Review & Editing; **Marteinn Möller:** Formal analysis, Writing - Review & Editing; **Kristín Ágústsdóttir, Bryndís Marteinsdóttir, Carl Mitchell, Ólafur Karl Nielsen, Arnór Þórir Sigfússon** and **Skarphéðinn Þórisson:** Investigation, Data Curation, Writing - Review & Editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2022.157140>.

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