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Evidence for dispersal limitation of burrowing earthworms in northern forests

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ABSTRACT

While litter-dwelling earthworms are widespread in northern Scandinavian forests, burrowing earthworms, i.e., species commonly considered as ecosystem engineers, are largely missing in these ecosystems. We hypothesized that their absence results not only from environmental filtering by unfavorable soil and climatic conditions but also from dispersal limitation. We examined earthworm presence-absence across Swedish forests by environmental DNA (eDNA) sequencing of 312 soil inventory samples. We then used statistical models to identify factors best explaining their occurrence among a set of variables representing soil properties, climatic factors, vegetation and distances to anthropogenic activities (e.g. roads and agricultural fields). Soil pH and texture were strong explanatory variables for the presence of burrowing earthworms, while distance to agricultural fields explained a significant part of the remaining variation. The importance of proximity to agricultural fields was especially pronounced in northern Sweden (>60° latitude). In contrast, occurrence of litter-dwelling earthworms was only weakly linked to environmental variables. Additionally, based on random forest modelling we predicted earthworm presence for almost 7000 soil inventory sites, and created high-resolution probability maps of earthworm occurrence in Swedish forests, including a scenario without potential dispersal limitation. These maps show that occurrence of burrowing earthworms would be more likely in large parts of the northern inland forests of Sweden without dispersal limitations, suggesting that these forests may be more susceptible to earthworm establishment upon introduction than previously anticipated. Our results highlight the importance of anthropogenic activities in dispersion and distribution of burrowing earthworms in northern forests. While environmental filtering largely governs burrowing earthworm occurrence, their current distribution is also substantially influenced by dispersal limitation - an underestimated factor to date.

1. Introduction

Dispersal of species to new environments by anthropogenic activities can have severe consequences for ecosystems and their services (Crowl et al., 2008). The arrival of earthworms into previously uncolonized ecosystems relies strongly on external factors, such as human activity, because soil-dwelling earthworms disperse slowly by themselves; on average 10 m year^{-1} (Terhivuo and Saura, 2006; Eijsackers, 2011). Northern ecosystems that were covered by ice-sheets until approximately 10,000 years ago represent a vast, potentially suitable habitat for earthworms to colonize. The consequences of earthworm establishment in such ecosystems are likely to be enormous, as shown by the colonization of North American forests by peregrine European earthworm species. These species were introduced by agricultural settlers from the mid-19th century onwards (Mathieu et al., 2024) and were further distributed by e.g., sport fishing activities and vehicle transport (Cameron et al., 2007, 2009). In this part of the world, bioturbation by earthworms (Dempsey et al., 2011) greatly affects the size and distribution of soil carbon (C) and nitrogen (N) pools (Jennings and Watmough, 2016; Ferlian et al., 2020; Jang et al., 2021; Lejoly et al., 2021) and drives major shifts in soil biota and plant communities (Eisenhauer et al., 2007, 2009; Craven et al., 2017; Frelich et al., 2019).

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Given the strong ecological cascades driven by earthworms (Frelich et al., 2019), it is important to anticipate which forests are most susceptible to colonization following potential introduction.

Scandinavia was left mostly earthworm-free after the Pleistocene, similarly to the northern part of North America (Terhivuo, 1988). Only a few 'litter-dwelling' species may have survived glaciations in ice-free refugia (Støp-Bowitz, 1969) or were early colonizers after the glacial retreat arriving with cocoons through water transport (Terhivuo, 1988; Terhivuo and Saura, 2006; Wackett et al., 2018). In contrast, recolonization of Scandinavia by other, mostly soil-dwelling 'burrowing earthworms' from southern areas was a slow process most likely connected to human agency (Terhivuo, 1988; Wackett et al., 2018). In boreal forests these earthworms were only documented sporadically (Terhivuo, 1988; Terhivuo and Saura, 2006), without causing great concerns about their presence. However, recent studies presented remarkable influence of burrowing earthworms on northern ecosystems after human-mediated colonization at sites in subarctic Scandinavia (Wackett et al., 2018). After establishment they outnumbered native litter-dwelling earthworms (Wackett et al., 2018), and pushed ecosystems towards a more fertile, grass dominated (Wackett et al., 2018; Blume-Werry et al., 2020) and bioturbated state (Klaminder et al., 2023), consequently altering C and N distribution among plants and soils (Blume-Werry et al., 2020; Jonsson et al., 2025) and inducing trophic cascades (Jonsson et al., 2023), effects comparable to those observed in earthworm-invaded North American forests (Eisenhauer et al., 2007, 2009; Craven et al., 2017; Frelich et al., 2019). Yet, we do not know whether burrowing earthworms only occur in Scandinavian northern forests as environmentally isolated local populations, or as a result of widespread migration facilitated by a warming climate and/or anthropogenic dispersal.

Scandinavian boreal forests have historically been regarded as hostile habitats for burrowing earthworms (Huhta et al., 1998) with clear environmental filtering. Coniferous forests, that grow commonly in areas with cold climate, recalcitrant litter, and coarse textured soils with an acidic organic topsoil, were strongly dominated by small, litter-dwelling earthworms (Nordström and Rundgren, 1973; Terhivuo, 1988). These species disperse relatively easily (Terhivuo, 1988; Eijsackers, 2011) and are (upon exposure) more cold-tolerant (Holmstrup and Zachariassen, 1996) and better adapted to acidic conditions than other earthworms (Desie et al., 2020). However, there are reasons to doubt whether burrowing earthworms are incapable of establishing in northern forests as there are several observations of burrowing earthworms from coniferous forests too (Nordström and Rundgren, 1973; Terhivuo, 1988; Lejoly et al., 2021). Also, not all burrowing species appear to be highly sensitive to frost and low pH (Holmstrup and Overgaard, 2007; Desie et al., 2020), and even within species there may be lineages that are more adapted to adverse environmental conditions (Holmstrup and Overgaard, 2007). Burrowing species may also modify their own environment after colonization. For example, they may increase soil pH (Desie et al., 2020) and promote herbaceous plants in the understory vegetation (Craven et al., 2017; Jonsson et al., 2023), which could feed back positively on their own fitness, increase population densities, and further improve the soil for other, more sensitive species (Eijsackers, 2011; Desie et al., 2020).

According to historic zoogeographic maps, litter-dwelling earthworms are predominant in most northern Scandinavian forests, whereas burrowing species are confined to more southern and coastal regions (Julin, 1950; Terhivuo, 1988). On one hand, this distribution agrees with the correlation between earthworm species richness and climatic factors in global models (Phillips et al., 2019). On the other hand, the less frequent occurrence of burrowing earthworms in northern Sweden also coincides with lower levels of human activity and agricultural cultivation, suggesting that the opportunities for introduction of these earthworms into more remote northern forests may be limited. However, it is not possible to draw conclusions on factors constraining burrowing earthworm occurrence in Scandinavian forests based on local earthworm surveys (Nordström and Rundgren, 1973; Räty and Huhta, 2004; Olsson et al., 2012; Wackett et al., 2018) or historic earthworm inventories (Julin, 1950; Terhivuo, 1988), since they often specifically target earthworm-inhabited sites. For objective identification of such factors, and to study the importance of dispersal limitation, earthworm presence-absence observations are needed from a large, unbiased selection of sites.

In this study, we used environmental DNA (eDNA) analysis of soil samples to detect earthworm species presence (Bienert et al., 2012; Pansu et al., 2015; Lilja et al., 2023; Cuartero et al., 2025) across a broad selection of forested sites surveyed by the Swedish Forest Soil Inventory (Fridman et al., 2014). We hypothesized that (I) burrowing earthworms would have more pronounced environmental filtering and dispersal limitation than litter-dwelling earthworms, and that current burrowing earthworm distribution across Swedish forests would be best predicted by soil properties and distance to human activities, rather than climate or vegetation. Furthermore, we expected that (II) dispersal limitation of burrowing earthworms would be stronger in northern than in southern Sweden, i.e. that their occurrence would be more strongly linked to the vicinity of human activity in the north. Based on model optimization we identified factors linked to occurrence of burrowing and litter-dwelling earthworms in Swedish forests among a set of soil and vegetation properties, climatic variables, and distances to anthropogenic activities. Additionally, we explored species-specific occurrences in relation to environmental factors and created high-resolution probability maps for burrowing and litter-dwelling earthworms based on random forest modelling, for almost 7000 soil inventory sites. These maps depict current distribution of earthworms across Swedish forests, as well as potential distribution for a scenario in which dispersal limitations were relieved.

2. Materials and methods

2.1. Soil sampling

We used topsoil samples from the Swedish Forest Soil Inventory, which conducts soil sampling on the permanent plots of the Swedish National Forest Inventory (Fridman et al., 2014). The plots are distributed systematically in a grid across Sweden (Fig. S1), and sites are resampled for soil every 10 years (inventory cycle). For soils with a clearly distinguishable organic layer ("O" horizon; mor soils), topsoil samples were collected spanning the whole organic layer to the top of the mineral soil layer (but maximum until 30 cm depth from the organic layer surface). For topsoils consisting of a mineral-mixed "A" horizon (mull soils), samples spanned the upper 10 cm. Samples were pooled to reach a minimum volume of 1 l, combining soils from 1 to 9 locations within each site. After soil collection, the soil samples were air-dried, homogenized, sieved through 2 mm sieves, and archived. For the current study, we analyzed 312 samples from the year 2022 for earthworm presence, and an additional 6727 sites of the most recent (2013-2022) soil inventory cycle were used for spatial predictions (Fig. S1).

2.2. Earthworm species identification based on DNA markers

DNA was extracted from 312 soil samples from the 2022 inventory year, representing an evenly distributed draw of Swedish forest sites, with peat soils excluded (Fig. S1). We extracted DNA from the air-dried and sieved soil samples (0.6 ml, corresponding to 80 - 850 mg of soil, depending on mineral content), using the NucleoSpin soil kit (Macherey-Nagel, Düren, Germany). DNA concentrations were measured with a Nano-drop microvolume spectrophotometer (Thermo Fisher Scientific, Waltham, USA), and all DNA extracts were diluted to 0.5 ng μl^{-1}.

For earthworm community analysis, we targeted a 254-266 bp region of the 16S mitochondrial DNA with primers specific to *Clitellates* (earthworms, enchytraeids and other clitellum forming annelids). As a forward primer, we used a slightly modified 16S AnnF primer (Sjölin

et al., 2005) for a better coverage of earthworms and terrestrial enchytraeids (5′– GCGGTATCCTAACCGTGCWAAGGTA –3′). As a reverse primer, we used ewE (5′– CTGTTATCCCTAAGGTAGCTT –3′), designed by Bienert et al. (2012). Amplicons were prepared using a two-step PCR with the Nextera-kit (Illumina, San Diego, USA). The first PCR reactions of 30 μl contained both primers fitted with Nextera adapters at 0.3 μM concentration, a Phusion hot start DNA polymerase enzyme with ready-made master-mix (Thermo Fisher Scientific), and the template DNA at a concentration of 0.22 ng μl^{-1}. The thermal conditions of the PCR were 98 °C for 5 min, followed by 30 cycles of 98 °C for 30 s, 60 °C for 1 min and 72 °C for 30 s, with a final elongation step of 72 °C for 5 min.

PCR products were cleaned with Sera-Mag (Sigma-Aldrich, St. Louis, USA) magnetic-beads (1:1 ratio of Sera-Mag to PCR product). The second PCR contained the cleaned PCR products, the same polymerase enzyme and sample-tagged Nextera-primers at 0.2 μM concentration. Samples with a reaction volume of 30 μl were run in duplicates. The PCR conditions were 98 °C for 3 min, followed by 8 cycles of 98 °C for 30 s, 55 °C for 30 s and 72 °C for 45 s, with a final cycle of 72 °C for 5 min. After Sera-Mag cleaning, the final PCR products were quantified by Qubit (Sigma-Aldrich), pooled in equimolar concentrations, and cleaned again with an E.Z.N.A Cycle Pure Kit (Omega Bio-Tek, Norcross, USA). Samples were sequenced by SciLifeLab (NGI, Stockholm, Sweden), on a MiSeq (Illumina) platform with Version2 chemistry. After global singleton removal, sequences were clustered into species level clusters by 1.5% distance single-linkage clustering using the bioinformatics pipeline SCATA (http://scata.mykopat.slu.se/). We verified species-level clustering and assigned species names to clusters based on a Swedish *Clitellata* mitochondrial 16S reference dataset (Erséus et al., 2023).

2.3. Earthworm presence, grouping, and explanatory variables

Presence/absence data was used for statistical analyses, but to account for index-hopping during sequencing, a threshold of minimum 9 reads per species per sample was applied for species to be recorded as present. This threshold was set based on sequenced samples that did not yield any PCR products according to Qubit measurements but still had some reads assigned to their sample-tags.

Subsequently, earthworms were grouped into burrowing and litter-dwelling species (Table S1), following classification of Fennoscandian earthworms by Terhivuo (1988). Since in boreal forests with a thick organic soil layer, earthworms may cause significant mixing even without deep burrowing into the mineral soil, we included *Lumbricus rubellus*, which is often considered an epigeic earthworm (Bottinelli et al., 2020) but referred to as an 'intermediate' species by Terhivuo (1988), in the burrowing earthworm group. Burrowing activity by *L. rubellus* involves exploration of mineral soils (Terhivuo, 1988; Felten and Emmerling, 2009; Olsson et al., 2012), and it consequently has larger effect on bioturbation of forest soils than other litter-dwelling earthworms (Olsson et al., 2012; Hale et al., 2008). Classified like this, the burrowing earthworm group comprises all earthworm species, whose activity is not limited entirely to the uppermost litter layer. To confirm robustness of results and that our main conclusions are unaffected by classification of *L. rubellus* as a burrowing species, we repeated analyses of the burrowing earthworm group in the *Supplementary materials* (section S5), restricted to earthworms commonly classified as endogeic (Table S1).

To analyze earthworm occurrences in the 312 sites and predict probabilities of earthworm presence in additional 6727 sites of the soil inventory, we selected explanatory variables that were previously found to be associated with earthworm occurrence (Table S2). These included: (I) soil properties and vegetation indices (soil texture, soil pH, soil carbon to nitrogen (C:N) ratio, forest type and understory vegetation type) measured by the forest or soil inventory, (II) climate variables (average yearly precipitation (hereafter precipitation) and mean annual temperature (hereafter temperature)) from E-OBS high-resolution land-observation climate data (Haylock et al., 2008), (III) sampling site distance to anthropogenic activity (spatial distance to nearest roads and to the closest agricultural fields based on Swedish land cover data (Nilsson et al., 2020)). Dependence of earthworm presence on these spatial distances may be evaluated in two ways. A short distance to agricultural fields or roads may be considered a general approximation of higher likeliness of any type of human activity, which may (stochastically) involve spreading earthworms or their cocoons (i.e., jump dispersal), for example soil transport on vehicle wheels (Cameron et al., 2007, 2009). Yet, in agricultural fields earthworms may live and thrive, so they could be considered direct, continuous sources of earthworm dispersal into neighboring habitats (Lagerlöf et al., 2002).

For measurements and calculations of site-specific environmental variables as well as their simple statistical relations with earthworm groups, see *Supplementary materials* (sections S1-2), and for variable properties see Tables S3–4.

2.4. Statistical modelling

All modelling was done in R (version 4.3.0) in the R Studio environment (R Core team, 2023). Presence of earthworms was modeled using logistic regression (generalized linear models for binomial data) with backward selection of explanatory variables based on the Akaike information criterion (AIC) (Ripley et al., 2013). Because we test hypotheses on the importance of individual environmental variables in all sampled forests, no interactions were defined, and separate models were made for litter-dwelling and burrowing earthworm groups. All continuous variables were scaled and centered to aid model interpretation.

To test whether burrowing earthworms are more dispersal-limited in northern than in southern Sweden, we fitted the optimized model again but included an interaction-term between any potentially retained distance to anthropogenic activity and an additional binomial north-south categorical variable. The north-south division of sites was based on latitude 60° N, which is roughly considered the border between the true boreal and the nemo-boreal zones in Sweden.

For all logistic regressions, distances to anthropogenic activities (distance to roads and agricultural fields) were log-transformed. We used log-transformation, since a causal relationship between anthropogenic dispersal sources and earthworm presence is less likely at longer distances, given the low active dispersal rates of earthworms and decreasing likeliness of passive dispersal further away from anthropogenic sources.

Additionally, to assess similarities and differences between earthworm species within and across our litter-dwelling and burrowing groups, we used canonical correspondence analysis to link earthworm community composition to the explanatory variables. For more abundant species (present in more than 15 sites, equivalent to more than 5% of the total number of sites) we also ran individual logistic regressions for all explanatory variables to quantify species-specific responses (Table S5).

For predictions of earthworm occurrences across Swedish forests, we used random forest analysis in the R-package "randomForest" (Breiman et al., 2018) to consider all explanatory variables without model overfitting. We trained down-sample classification random forest models, which should be more robust for predictions based on presence-absence data, particularly when there is class-overlap between presence and background sites, i.e., not all inhabitable sites are occupied by the studied organism (Valavi et al., 2021). Given the likeliness of false negative observations in eDNA based species detections (Ficetola et al., 2014), we expected such class-overlap. In practice, in the down-sample random forest models, the parameter "sampsize" (number of samples to draw at each decision tree) was set to the number of positive earthworm-observations for both presence and absence samples, while other parameters were left as default.

Three types of random forest models were created. We predicted

occurrences of both burrowing (1) and litter-dwelling (2) earthworms with all predictor variables, and modeled occurrence probability of burrowing earthworms with anthropogenic distances omitted from the set of predictors (3), aiming to represent a hypothetical scenario where dispersal limitation is not playing a role in earthworm distribution. Since random forest modelling involves splitting the whole dataset into a training (70%) and a validating (30%) dataset, we repeatedly run each of the three types of models on ten different randomly selected training and validating datasets. In this way we aimed to account for differences arising from the splitting of the total datasets. We assessed average model performances based on out-of-bag errors and area-under-curve (AUC) values (Sing et al., 2015) and then calculated average relative predictor importances from the mean decrease in Gini index. Probability of earthworm presence was predicted for 6727 sites (excluding peat soils) of the most recent (2013-2022) soil inventory cycle (Fig. S1). For mapping purposes, we interpolated earthworm-occurrence probabilities for Sweden using an inverse-distance-weighted technique in ArcGIS (ESRI, Redlands, USA).

3. Results

We identified 13 earthworm species (Table S1) present in 121 out of the 312 sites. The most commonly detected species was *Dendrobaena octaedra* (88 sites, 28.2% of all sites), followed by *Lumbricus rubellus* (17 sites, 5.4%) and *Aporrectodea caliginosa* (16 sites, 5.1%). When considering species groups, 94 sites (30.1%) had litter-dwelling earthworms, and 45 sites (14.4%) had burrowing earthworms.

Canonical correspondence analysis of species composition (Fig. 1) indicated distinct niches of the most abundant litter-dwelling earthworms (*D. octaedra*, *Bimastos rubidus*), compared to the most abundant burrowing earthworms (*L. rubellus*, *A. caliginosa*, *Octolasion lacteum*, *Octolasion tyrtaeum*). Litter-dwellers occupied sites with relatively low pH and high C:N ratio, except for the stenotopic earthworm *Eiseniella tetraedra*, which clustered apart from the other litter-dwelling species and appeared to prefer higher pH. Burrowing species were more common in forest soils with relatively high pH, closer proximity to agricultural fields or roads, higher temperature and more dominant herbaceous vegetation. Nevertheless, they clustered in two main groups (Fig. 1), *Allolobophora chlorotica*, *O. lacteum* and *O. tyrtaeum* more related to high soil pH and fine soil texture, and *L. rubellus*, *A. caliginosa* and *Aporrectodea rosea* more related to proximity of agricultural fields or roads, warmer climate, less demanding towards high pH and fine soil texture.

In simple logistic regressions, all variables except precipitation related significantly ($p < 0.05$) to burrowing earthworm presence (Fig. 2, blue bars), whereas none of the explanatory variables related significantly ($p > 0.05$) to litter-dwelling earthworms (Fig. 2, red bars). The optimized logistic regression for burrowing earthworms retained soil pH ($p < 0.001$, Fig. 2a), distance to agricultural fields ($p < 0.05$, Fig. 2h), soil texture ($p = 0.07$, Fig. 2c) and precipitation ($p = 0.13$, Fig. 2g) as explanatory variables ($R^2 = 0.17$, AIC = 223, Table S6). The probability of burrowing earthworm presence increased at higher soil pH and decreased with increasing distance to agricultural fields and with increasing precipitation. Further, earthworm presence was most likely with fine textured soil, followed by medium and coarse soils, and least likely on bedrock without mineral soil. Inclusion of an interaction term between the north-south predictor and distance to agricultural field did not increase the explanatory power substantially relative to the model without the interaction term ($R^2 = 0.19$, AIC = 222, Table S7), but indicated that burrowing earthworm occurrence related more to proximity to agricultural fields in the north (interaction term $p < 0.05$, Fig. 3).

For litter-dwelling species, the best multiple logistic regression retained distance to agricultural fields ($p < 0.05$, Fig. 2h), C:N ratio ($p < 0.05$, Fig. 2b) and precipitation ($p = 0.12$, Fig. 2g) as explanatory variables (Table S8), but the overall explanatory power was low ($R^2 = 0.014$, AIC = 381). Probability of litter-dwelling earthworm presence increased with increasing distance to agricultural fields and decreased with increasing C:N ratio and precipitation.

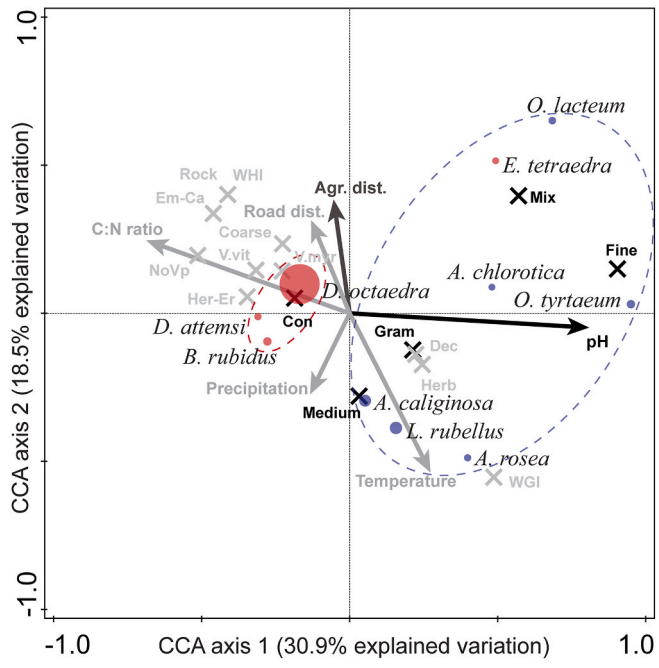

Fig. 1. Canonical correspondence analysis (CCA) of earthworm species (burrowing species – blue circles, litter-dwelling species – red circles, the size of circles represents observation frequency). Explanatory variables marked with black or dark grey ($p < 0.05$ and $p < 0.1$, respectively) contributed the most to the explained variation after forward selection. Abbreviations for categorical variables: (I) Forest type: WGl – wooded grassland, Dec – deciduous forest, Mix – mixed forest, Con – coniferous forest, WHl – wooded heathland; (II) Understory vegetation: Gram – graminoid dominated, Herb – herbaceous dominated, Her-Er – herbaceous-ericaceous mix, V.myr – *V. myrtillus* dominated, V.vit – *V. vitis-idaea* dominated, Em-Ca – *Empetrum* – *Calluna* dominated, NoVp – no vascular plants. Fine, medium, coarse and rock refers to soil texture. Note, that species with less than three observations are not represented in this plot. Further, explanatory variables in the CCA only explain variation between species at sites where the plotted earthworms are present (120; 38.5% of total sites), whereas logistic regressions (Tables S5–8) are based on all sites. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

The random forest model for burrowing earthworms with all explanatory variables had an average out-of-bag error rate of 24% and AUC values of 0.74 and 0.77 for the training and validating datasets, respectively. In accordance with our multiple regression model, soil pH and distance to agricultural field had highest predictor importance (Table 1). When distances to roads and agricultural fields were left out from the model, the average AUC values were unaffected (0.74 for training and 0.78 for validating datasets). In this model, soil pH and C:N ratio were the most important predictors (Table 1). Predictions of burrowing earthworm presence probabilities were spatially heterogenous, but in general higher for southern than for northern Sweden (Fig. 4a). When predictions were made with the model trained on data without road and agricultural field distances, probabilities decreased for southern and coastal sites but increased in the more sparsely populated northern inland (Fig. 4b).

The random forest model for litter-dwelling earthworms had high out-of-bag error (41%), and low AUC values (0.57 for the training and 0.58 for the validating dataset), with C:N ratio, pH and distance to agricultural fields being the most important predictors (Table 1). The average probability for presence of litter-dwelling earthworms across Swedish forests was higher than for burrowing ones, without a clear latitudinal pattern (Fig. 4c).

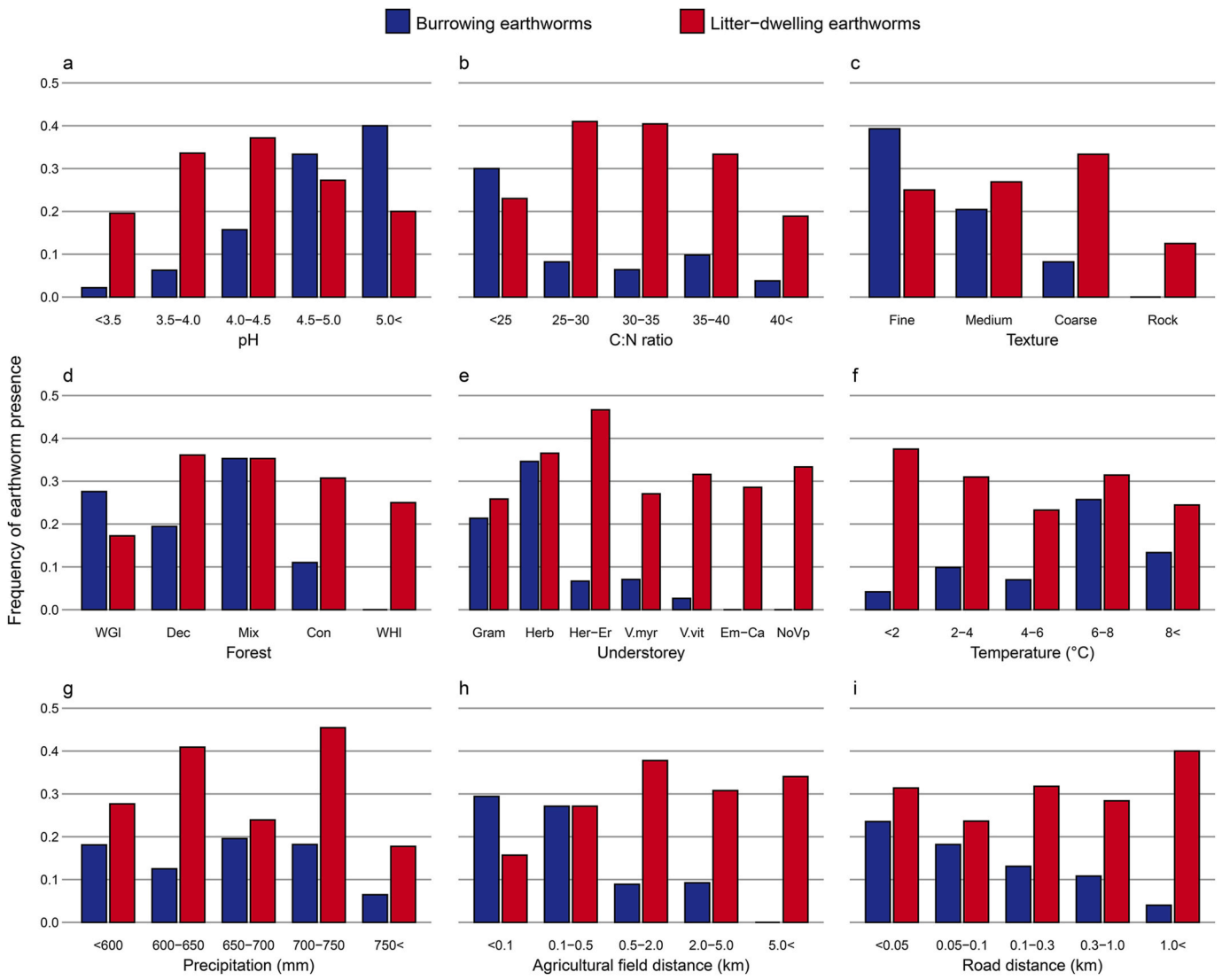

Fig. 2. Earthworm presence frequencies across intervals and categories of all selected explanatory variables for burrowing (blue bars) and litter-dwelling (red bars) earthworms. The optimized logistic regressions for burrowing earthworms retained soil pH (a), soil texture (c), agricultural field distance (h) and precipitation (g), and models for litter-dwelling earthworms retained agricultural field distance (h), soil C:N ratio (b) and precipitation (g). Abbreviations for categorical variables: Forest type (d): WGl – wooded grassland, Dec – deciduous forest, Mix – mixed forest, Con – coniferous forest, WHl – wooded heathland; Understory vegetation (e): Gram – graminoid dominated, Herb – herbaceous dominated, Her-Er – herbaceous-ericaceous mix, V.myr – *V. myrtillus* dominated, V.vit – *V. vitis-idaea* dominated, Em-Ca – *Empetrum* – *Calluna* dominated, NoVp – no vascular plants. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

4. Discussion

We found that burrowing earthworm occurrence in Swedish forests could be predicted by soil properties combined with proximity to human activities, whereas occurrence of litter-dwelling earthworms was only weakly linked to environmental variables. Furthermore, our analyses show that burrowing earthworms are particularly dispersal-limited in the northern part of Scandinavia, implying that their occurrence may increase upon introduction into northern forests. Species-specific relationships with environmental factors suggest that the occurrence of the more frequently observed litter-dwelling species *D. octaedra* and the burrowing *A. caliginosa* and intermediate/burrowing *L. rubellus* drive observed differences between the two earthworm groups.

Soil texture and pH were strong explanatory variables for burrowing earthworm occurrence in Swedish forests, with increasing probability of presence in soils with higher pH and finer texture. Both texture and pH have been considered main drivers in regulation of earthworm populations (Reich et al., 2005; Cameron and Bayne, 2009; Salako et al., 2023; Cuartero et al., 2025) and suggested as limiting factors for earthworm occurrence on a global scale (Ruiz et al., 2021). Nevertheless, we detected burrowing earthworms across a large range of soil pH (Fig. 2a), implying that in Swedish forests there is less clear soil pH threshold under which burrowing earthworms cannot persist. Earthworm activities may increase pH, leading to bidirectional causalities and potentially amplifying feedbacks between earthworm colonization and soil conditions (Eijsackers, 2011; Desie et al., 2020). These findings therefore suggest that more forests than previously expected may be open for burrowing earthworm colonization in northern environments.

In addition to soil pH and texture, distance to agricultural fields was retained as an important explanatory variable in the optimized logistic regression. When included in a random forest model, distance to agricultural fields was the second-best predictor (Table 1). These findings support our hypothesis (I) that burrowing earthworms are, to some extent, dispersal limited in Swedish forests, implying they are absent from suitable habitats because they have not been introduced. In Scandinavia, cultivated fields have often been explicitly identified as

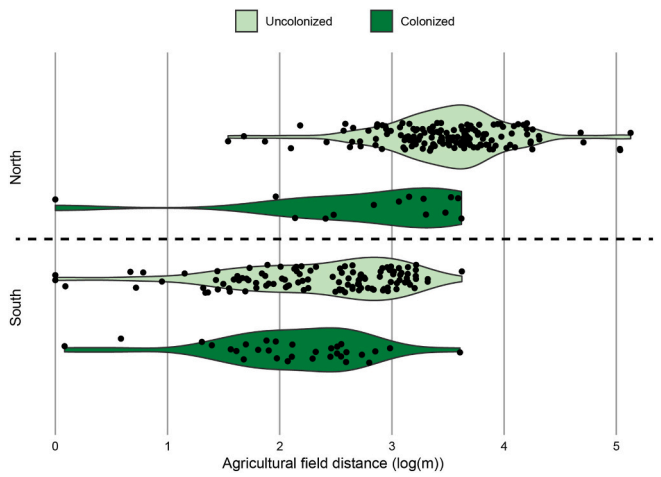

Fig. 3. Relation between distance to agricultural field and burrowing earthworm occurrence probability for northern (>60° N) and southern (<60° N) Sweden. In northern Sweden colonized forests generally lie closer to agricultural fields than uncolonized forests. Note log-scale on x-axis; n = 152 for north-uncolonized, n = 14 for north-colonized, n = 115 for south-uncolonized and n = 31 for south-colonized.

sources of burrowing earthworm dispersal (Lagerlöf et al., 2002; Terhivuo and Saura, 2006; Wackett et al., 2018), similarly to some agricultural sites in North America (Buchkowski et al., 2024).

Unlike global and larger-scale models of earthworm distribution (Phillips et al., 2019; Ruiz et al., 2021; Li et al., 2023; Salako et al., 2023), climatic factors were not among the best explanatory variables for earthworm presence across Sweden. Although precipitation was identified as the most important predictor for earthworm distribution at a global scale (Phillips et al., 2019) it was not a significant predictor in our study (Fig. S2g). While climate shapes species distribution across broad ecosystem gradients, within a specific habitat (like northern forests in our study), edaphic factors and human activities may play a more important role in determining burrowing earthworm occurrence.

Although the occurrence of burrowing earthworms related to most explanatory variables (Fig. 2), earthworms more strictly confined to surface litter (our litter-dwelling earthworm group) had no, or only weak relations with these factors (Fig. 2). Further, the weak optimized logistic regression and uncertain random forest model performance suggests that the distribution of litter-dwellers is not strongly linked to the tested environmental factors in Swedish forests. Their relatively higher occurrence at sites further away from agricultural fields and missing relation with road distance suggests that anthropogenic activity was not a major factor for litter-dwelling earthworm distribution in Scandinavia, unlike observations in North America (Cameron et al., 2007; Eisenhauer et al., 2007). Nevertheless, results of litter-dwelling earthworms are mainly driven by the most abundant species *D. octaedra*, which accounted for 94% of the occurrences. Both Terhivuo (1988) and Wackett et al. (2018) proposed that *D. octaedra* is likely not relying on human-mediated dispersal in Scandinavia but rather on water transport of cocoons, which could explain our observations.

As hypothesized, the presence of burrowing earthworms was more strongly related to anthropogenic activity in the north of Sweden (Fig. 3). Though, because of the limited number of sites near agricultural fields in the north, we may have overestimated the importance of a few earthworm observations. Nevertheless, the largest discrepancies in probability of burrowing earthworm occurrence were indeed found in the sparsely populated northern inland Scandinavia, where large areas had higher occurrence likeliness if anthropogenic distances were excluded from the random forest models (Fig. 4b). With more widespread agriculture and a longer cultivation history in the south and along the coast, earthworms may have had more time and opportunities to spread and fill most of the suitable habitats. In the north, agricultural cultivation is more recent and still sparsely distributed, leaving potential habitats without burrowing earthworms. To illustrate this, assuming that (1) the only source of burrowing earthworm colonization is agricultural fields, (2) earthworm populations disperse actively with an average rate of 10 m year^{-1} (Eijsackers, 2011), and (3) their dispersal is not hindered by any other barriers, it would take between 1 and 400 years to colonize all southern Swedish habitats (<60° latitude), while up to 13,000 years to reach the furthest forests in the north.

Predicted spatial patterns of burrowing and litter-dwelling earthworms (Fig. 4a–c) align rather well with earthworm distribution maps from the mid-20th century (Julin, 1950). Nevertheless, there are large areas without historical earthworm observations, but where we predict a relatively high probability for occurrence of burrowing earthworms (Fig. 4a), with further increased probabilities when dispersal limitation is relieved (Fig. 4b), particularly in the northwestern parts of Sweden. This may either depend on underrepresentation of historical observations from these areas, or on ongoing earthworm colonization. A large proportion of these areas are subalpine birch forests, where there is indeed evidence of sporadic, more recent burrowing earthworm establishment (Wackett et al., 2018).

We acknowledge that grouping earthworms into broad categories such as litter-dwellers and burrowers is reductive, as species within each group span a range in environmental preferences. However, limited observations for some species constrain our capability to quantify species-specific patterns. Nevertheless, the canonical correspondence analysis (Fig. 1) revealed distinct niches: litter-dwelling earthworms were associated with lower soil pH, courser soils, higher C:N ratios and greater distances from roads and agriculture. Litter-dwelling species such as *D. octaedra* and *B. rubidus* occur indeed across a wide range of forested habitats, including dry coniferous forests (Nordström and Rundgren, 1973; Terhivuo, 1988). However, *E. tetraedra* that favors moist, often waterlogged environments near streams and rivers (Terhivuo, 1988), was an exception in our study, aligning more closely with conditions associated with burrowing species. Burrowing

Table 1
Average relative predictor importance of random forest models, calculated from the mean decrease in Gini index. Since predictor importances are relative, their direct comparison between models with different performances may be misleading.

Explanatory variable		Burrowing earthworms, all predictors	Burrowing earthworms, distances to human activities excluded	Litter-dwelling earthworms, all predictors
Soil properties	pH	18.7%	23.1%	15.1%
	C:N ratio	15.2%	20.5%	16.9%
	Texture	5.5%	7.9%	3.2%
Vegetation	Forest type	2.9%	4.9%	3.5%
	Understory	9.4%	12.4%	8.9%
Climate	Temperature	10.6%	16.3%	12.1%
	Precipitation	10.7%	14.9%	13.6%
Distances to human activities	Agricultural field distance	17.0%	-	14.2%
	Road distance	10.0%	-	12.5%

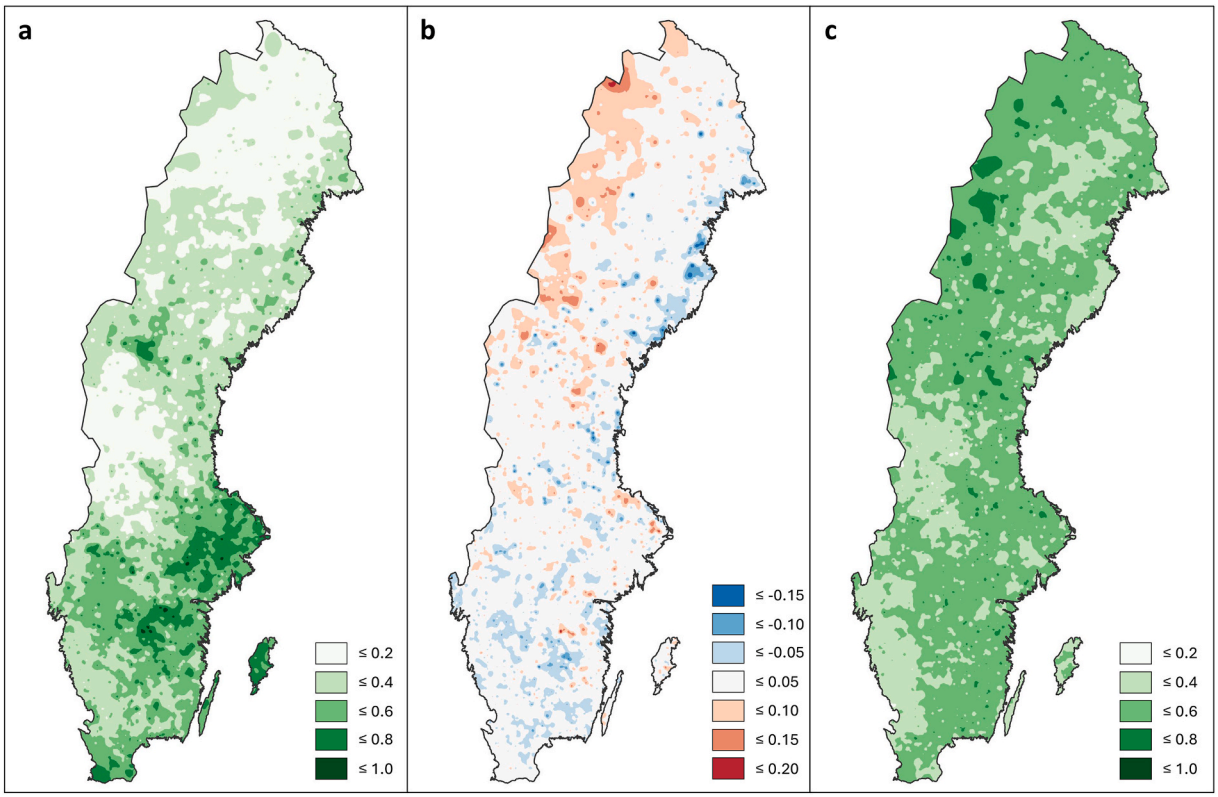

Fig. 4. Earthworm occurrence probabilities for (a) burrowing earthworms with all explanatory variables, (b) the difference in burrowing earthworm probability when anthropogenic distance is excluded as predictor (prediction without anthropogenic distances – predictions with anthropogenic distances) and (c) litter-dwelling earthworms with all explanatory variables. In map b), the areas in which probabilities are higher (red) without anthropogenic distance as predictor would be more likely to have burrowing earthworms if dispersal would not limit their distribution. Conversely, areas in which probabilities are lower (blue), represent forests in which human activities are especially important for current burrowing earthworm occurrence. Note that these probability differences are relative; areas with increasing probabilities may still have a lower overall probability for burrowing earthworm occurrence than areas in which probabilities decline (Fig. S5b). All probabilities were predicted with repeated random forest models for sampling locations of the most recent soil inventory cycle (n = 6727, see approximate locations in Fig. S1), and the gradient maps were created using an inverse-distance weighed interpolation technique. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

earthworms (including the intermediate *L. rubellus*) were more widespread in ordination space, but generally related to higher soil pH with finer soil texture and plant species indicating higher fertility. The most abundant intermediate/burrowing species (*L. rubellus* and *A. caliginosa*) showed similar associations favoring slightly higher pH and temperatures than most litter-dwellers and were more frequently observed in forests closer to roads and agricultural fields. Less abundant burrowing earthworms (e.g. *A. chlorotica, O. tyrtaeum* and *O. lacteum)* were associated with high soil pH and fine textured soils, suggesting a stronger importance of environmental filtering. Given their positive association with human activities shown by also significant species-specific simple logistic regressions (Table S5), we suggest *A. caliginosa* and *L. rubellus* are the most dispersal limited earthworms in Swedish forests. This finding is consistent with the recent spread of *Lumbricus* and *Aporrectodea* species in northern Scandinavian forests (Wackett et al., 2018).

The use of metabarcoding to assess presence of earthworms in many sites over large geographical scales has already yielded increased understanding of earthworm distribution in relation to environmental factors (Pansu et al., 2015; Cuartero et al., 2025). However, this approach involves some challenges, such as designing representative schemes for soil sampling, optimization of molecular techniques, and availability of reference databases (Ficetola et al., 2014; Pansu et al., 2015; Cuartero et al., 2025). For our study, the main methodological limitations were likely the relatively low spatial coverage per site and small available soil volumes from which DNA was extracted, which probably led to some false negative observations and an underestimation of earthworm occurrence at the site-scale (Bienert et al., 2012; Ficetola et al., 2014). While mapping a dataset with false-negative observations may cause misinterpretation of species distribution, our statistical modelling was less affected by stochastic false-negative observations, which are unrelated to the tested explanatory variables. Therefore, instead of mapping single species observations across Sweden, we used the data to improve our understanding of earthworm distribution to enable modelling of occurrence probabilities based on environmental factors. Thus, our findings may be relevant for understanding earthworm distributions beyond the study region and for assessing distribution changes under future environmental scenarios.

Given the large effects that burrowing earthworms can have on forest soils, it is important to predict which forests are likely to be colonized in the future. Forests are not only important for wood production, but also for C sequestration, and biodiversity conservation. Some of the northern forests in which burrowing earthworms may establish provide particularly high nature values, often with unique plants and soil biota. Arrival of burrowing earthworms may change these ecosystems, for example by facilitating invasion of graminoid plant species (Jonsson et al., 2023), which may outcompete the native flora and change conditions for other soil biota. For intensively managed forests with lower conservation value, colonization of such earthworms may be beneficial, for example by facilitating seedling growth (Haimi et al., 1992; Welke and Parkinson, 2003). Earthworm effects on C-sequestration may be bidirectional; increased earthworm activity may stimulate decomposition and CO_2 release to the atmosphere (Frelich et al., 2019) but may also increase C sequestration in the long term by promoting stabilization of soil C pools by the formation of stable soil aggregates (Ferlian et al.,

2020). Because of these unpredictable effects that can have large consequences, precautions may be needed to limit earthworm dispersal into uncolonized ecosystems. We found support that some northern forests are more susceptible to earthworm establishment than previously anticipated. While environmental filtering for a large part governs burrowing earthworm occurrence in these forests, their current distribution is also substantially influenced by dispersal limitation - an overlooked factor underestimated to date.

CRediT authorship contribution statement

Péter Garamszegi: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Karina E. Clemmensen:** Conceptualization, Methodology, Supervision, Writing – review & editing. **Christofer Engberg Hydén:** Resources, Writing – review & editing. **Thomas Keller:** Conceptualization, Methodology, Supervision, Writing – review & editing. **Mårten J. Klinth:** Resources, Writing – review & editing. **Björn D. Lindahl:** Conceptualization, Methodology, Supervision, Writing – review & editing. **Eveline J. Krab:** Conceptualization, Funding acquisition, Methodology, Project administration, Supervision, Writing – review & editing.

Data availability statement

The raw sequence data analyzed during this study are available on NCBI SRA under the accession number PRJNA1507363. The R codes and data for analyzes are available at Zenodo: https://doi.org/10.5281/zenodo.21769013.

Declaration of competing interests

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.soilbio.2026.110291.

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