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RESEARCH ARTICLE

Predictive mapping to identify refuges for plant communities threatened by earthworm invasion

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Abstract

1. Biological invasions by cryptic ecosystem engineers can alter the ecological and socio-economic values of ecosystems in ways that may take decades to detect. The invasion of North American glacial refuges by non-native earthworms offers a prominent but understudied example of a cryptic invasion. Non-native earthworms are known to alter carbon sequestration, disrupt mycorrhizal networks and homogenize plant communities, but natural resource managers still lack robust protocols to identify and safeguard high conservation value communities (HCVCs) from such invasions. In the absence of such protocols, or reliable methods to eradicate non-native earthworm populations once established, there is an urgent need for methods to identify HCVCs at risk of or potentially shielded from earthworm invasion by the existence of abiotic barriers to their dispersal or persistence in such sites.
2. We developed species distribution models (SDMs) using in situ field surveys and remotely sensed data to (1) identify factors limiting the occurrence of non-native *Lumbricus* earthworms in imperilled coastal Douglas-fir (*Pseudotsuga menziesii*) forest and Garry oak (*Quercus garryana*) and maritime meadow ecosystems endemic to glacial refugia of the Pacific Northwest of North America and to (2) evaluate their influence on plant species diversity and identify abiotic factors capable of preventing their dispersal or persistence at a site.
3. As predicted, shallow, drier soils and steeper terrain limited earthworm occurrence and abundance in our highly heterogeneous study area, and earthworm presence appeared to reduce plant species richness. Our results indicated that HCVCs endemic to shallow-soil ($< 12 \pm 3$ cm) sites that experience regular summer drought appear to act as refuges from invasion by non-native earthworms. Our results also elevate concerns for the conservation of deep-soil habitats not isolated from earthworm invasions by shallow soil, saltwater or other barriers to earthworm dispersal.
4. The SDMs developed here offer guidance to the identification of potential refuges for the conservation of imperilled native species and communities from the detrimental effects non-native earthworms in glacial refugia of western North America and should thereby facilitate proactive planning by conservation practitioners.

KEYWORDS
Garry oak, invasive species, *Lumbricus terrestris*, non-native earthworms, *Quercus garryana*, species distribution model

1 | INTRODUCTION

Biological invasions by non-native 'ecosystem engineers' can radically alter the ecological and socio-economic values of ecosystems in ways that can take decades to detect (Crooks, 2002; Mack et al., 2000), as revealed recently in syntheses of the ecosystem-level effects of invasion by non-native earthworms globally (Craven et al., 2017; Frelich et al. 2019). Because such invasions, including by earthworms, are facilitated by anthropogenic habitat conversion, migration and trade (Hulme, 2009; Levine & D'Antonio, 2003), management frameworks to minimize impacts on native species and ecosystems have prioritized actions that limit the abundance or distribution of invaders (Courchamp et al., 2003; Simberloff et al., 2013), manage over-abundant or non-native species that facilitate invasion success (Best & Arcese, 2009; MacDougall et al., 2004) and remove non-native invaders from sites where re-invasion is unlikely, such as on islands (e.g., Holmes et al., 2019). However, because few practical methods exist to eradicate invasive earthworms at scales relevant to conservation area design, protecting valued communities from the deleterious effects of earthworm invasions must necessarily focus on identifying sites likely to resist invasion due to their effective isolation by edaphic, geographic, biological or other factors limiting earthworm dispersal or persistence (cf. Myers et al., 2000; Bennett & Arcese, 2013; Keppel et al., 2015).

In insular and forested ecosystems adapted to human use, conservation measures taken in response to widespread invasion by earthworms have focused on preventing new invasions and identifying potential 'refuges' (Callaham et al., 2006). Empirical studies indicate that Garry oak (*Quercus garryana*) and maritime meadow communities display the highest ratios of native to non-native species cover and occurrence in sites isolated from the deleterious effects of humans, including those arising directly via habitat conversion and fragmentation and indirectly via the facilitation of invasive and over-abundant species (Arcese & Rodewald, 2019; Bennett, 2014; Bennett & Arcese, 2013; MacDougal et al., 2004; Schuster & Arcese, 2013). Here, we use empirical data on factors limiting the distribution and occurrence of non-native earthworms to develop and test the application of species distribution models (SDMs) to (1) predict the occurrence of earthworms in the genus *Lumbricus* in Garry oak and maritime meadow habitats, (2) test the hypothesis that edaphic and/or topographic factors limit *Lumbricus* dispersal or persistence and (3) thereby create potential 'habitat refuges' for native species in invaded landscapes.

European earthworms invaded many north-temperate ecosystems after ~1700, assisted by human migration, land use conversion and climate warming (Addison, 2009; Hendrix and Bohlen, 2002; Tiunov et al., 2006). Such invasions have facilitated reductions in soil carbon, disrupted mycorrhizal associations and altered plant communities (Bohlen et al. 2004; Frelich et al. 2019). Over decades, often in concert with over-abundant herbivores (Estes et al. 2011), earthworm invasions have also reduced native plant species richness and contributed to the homogenization of plant and animal communities (Arcese & Rodewald, 2019; Dobson & Blossey, 2015; Frelich et al. 2006; Holdsworth et al. 2007; Migge-Kleian et al. 2006). As a consequence, the invasion of European earthworms into historically earthworm-free soils represents a pervasive threat to biodiversity and conservation.

At global scales, earthworm distribution and species richness are well-predicted by variation in precipitation and temperature (Phillips et al., 2019). At local scales, however, it is less clear how soil moisture, heat loading or seasonal drought affect earthworm density or distribution, or whether such factors interact with topographic factors to influence earthworm occurrence. SDMs offer one approach to filling this knowledge gap by estimating the occurrence of species and identifying sites more or less prone to invasion given habitat type and condition (Cabeza et al., 2010; Jiménez-Valverde et al., 2011). For instance, road and stream networks facilitate earthworm dispersal (Cameron & Bayne, 2009; Paudel et al., 2016), especially in species that burrow deeply and thus rarely persist in shallow microsites with $\leq$30 cm soil depth due to desiccation during drought (Fisichelli et al., 2013). Meta-analytical reviews also indicate that soil moisture and plant species diversity are useful predictors of the risk of invasion by earthworms (Cameron et al., 2016; Craven et al., 2017). Suárez et al. (2006) hypothesize that climate and topography could indirectly restrict the movement of earthworms by influencing spatial and temporal variation in soil moisture. Our goal was to test whether SDMs can be used to predict the occurrence of non-native earthworms based on topographic and/or edaphic features hypothesized to affect earthworm dispersal or persistence and identify potential refuges from earthworm invasion.

Specifically, we asked if topographic and/or edaphic features limit the occurrence of non-native earthworms on Sidney Island, British Columbia, Canada, where native earthworms are absent (Marshall & Fender, 2007) and many shallow-soil plant communities of high value to conservation still remain extant (Bennett, 2014; Gonzales, 2008; MacDougall, 2005). Habitats on Sidney Island reflect a legacy of traditional land management by Indigenous Peoples, and habitat conversion by more recent colonists, resulting in a patchwork of oak savannah, maritime meadow, old-field, young and mature forest and rural habitat types. Given this context, we addressed two main questions: (1) do natural refuges from earthworm invasion exist in shallow soil habitats in regions where an invasion has already occurred, and (2) does plant community composition differ in sites with earthworms present versus absent when controlling for habitat type? In general, we expected to detect earthworms more often nearer to roads or trails, in deeper, wetter soils and in areas with lower slope and north-eastern exposure. We also expected to identify potential refuges from earthworm invasion in areas further from roads or trails, with shallower, drier soils and/or steeper slopes with a southern exposure and sparse canopy. Last, we predicted that sites in which earthworms were detected would have less diverse plant communities than expected by habitat type alone.

2 | MATERIALS AND METHODS

2.1 | Study area

The Southern Gulf Islands, British Columbia, Canada, host >100 species at risk species from the critically endangered Garry Oak (*Quercus garryana*) and maritime meadow communities (Bennett, 2014; Bennett et al., 2013; GOERT 2011). The sub-Mediterranean climate in this region has mean annual temperatures of ~9.8 to ~10.6°C and mean annual precipitation from ~670 to ~1100 mm (MacDougall, 2005; Wang et al., 2016). The geologic history of the Gulf Islands means that present-day islands were inundated or glaciated by the Late Wisconsin Cordilleran Ice Sheet ~14,500 years ago (Eyles et al., 2018), suggesting that any native earthworms present prior to that time were extirpated except in glacial refugia far from our study site (Addison, 2009; Reynolds, 1977). Currently, about 75% of earthworm species detected in British Columbia arrived actively or passively from Eurasia, in parallel with the region's colonization by non-indigenous settlers after ~1860 (Marshall & Fender, 2007). Our surveys on Sidney Island, BC, cover a range of more and less intact habitats, including endangered maritime meadow plant communities, typically occurring on shallow soil (≤30 cm) sites near sea level with little overhead canopy (Bennett, 2014; Fuchs, 2001; Gonzales, 2008).

2.2 | Field sampling

We sampled three hundred 0.1 m^2 quadrats in one hundred 10-m-radius circular plots located randomly in regions of the island identified by examining existing variation in spatial predictors of interest, with the goal of maximizing sampling variance across each predictor variable of interest. At each plot, three 0.1 m^2 quadrats were spaced ~ 18 m apart, further than the annual dispersal distance of *Lumbricus* earthworms, in a triangular orientation (Cameron & Bayne, 2014; Hale et al., 2005). At each quadrat, we recorded the total number of earthworms detected, evidence of earthworm activity (e.g. castings and burrows), soil depth (using a graduated metal rod) and location using a handheld GPS (accuracy: ± 8 m ,Garmin eTrex® 20x). We used 50 g of mustard powder mixed into 1 gallon of water, poured slowly over each quadrat to extract earthworms following Gunn (1992), Lawrence and Bowers (2002) and Arcese and Rodewald (2019) and identified all adults to species and juveniles to genus before returning them to an area adjacent to the sample quadrat.

We also recorded the presence or absence of all understory plant species that were rooted inside a quadrat prior to extracting earthworms to estimate species richness, as well as canopy cover and dominant tree species over each quadrat. We recorded the occurrence, status (e.g. native vs. non-native), lifecycle (perennial vs. annual), growth form (herbaceous, graminoid, woody) and relative abundance of every plant species detected in quadrats across Sidney Island (Table A1 in the Supporting Information).

2.3 | Environmental variables

Seven environmental variables were selected for modelling based on a priori hypotheses regarding earthworm dispersal (Table 1). We measured soil depth in each quadrat ($n = 300$), and at 252 other locations identified statistically (see below), by forcing a graduated rod by hand into the soil until restriction, and then recording the mean of three measurements at each quadrat to the nearest centimeter. We next estimated soil depth continuously over the island by fitting soil depth data to a semi-variogram and interpolating between sample sites using simple kriging (2 m^2 resolution; R package: gstat; Figure A1 in the Supporting Information) (Gräler et al., 2016). The 252 measurements noted above were allocated to 'data deficient' areas identified by the semi-variogram.

We used a high-resolution, digital elevation model (DEM; 2 m^2 resolution) based on LiDAR data (summer 2006; Terra Remote Sensing Inc., Sidney, BC, Canada) collected in the southern Gulf Islands and assembled by Jones et al. (2010). We next derived geospatial layers to estimate slope (radians) and topographic wetness (Mattivi et al., 2019) using the terrain analysis tool in the System for Automated Geoscientific Analysis (SAGA 7.2.0) (Conrad et al., 2015). We calculated a heat load index following equations in McCune and Keon (2002) using slope and aspect estimates in ArcMap 10.6 (ESRI, 2020). Distance to nearest road or trail was calculated using the 'Euclidean distance' tool on a digitized road map in ArcMap 10.6. The land use classification was acquired from the Islands Trust BC MapIT database 'Terrestrial Ecosystem Mapper' tool. All data were projected into NAD83 UTM zone 10N.

2.4 | Data analyses

We used an ensemble approach to species distribution modeling for non-native earthworms in our study area; specifically by combining predictions from random forest (RF), maxent (MAXENT), boosted regression tree (BRT) and a hierarchical Bayesian generalized linear mixed effects model (BAYES; see Equation A1 in the Supporting Information for model specifications) to construct different SDMs using the dismo (Hijmans et al., 2017) and rstanarm packages (Goodrich et al., 2020) in R version 3.5.1. These models were selected to reduce the likelihood of overfitting our data and to balance model performance and accuracy (Marmion et al., 2009). SDMs were based on the analysis of all 300 quadrats where earthworms or their casts or burrows were 'present' versus 'absent'. We did not use pseudo-absences in our SDMs as doing so reduced model fit. However, we did employ K-fold cross validation to partition data (75% training, 25% testing) and estimate area under the curve (AUC) using receiver-operating criteria to assess model fit and accuracy. Models were built using all available data to capture as much uncertainty as possible, and ensemble models were

TABLE 1 Environmental variables tested in SDMs. Variables are ordered by most to least importance as defined by model ensembles

Variables	Observed range	Collection and data processing
Soil depth (cm)	2–50	Soil depth probe; derived using gstat.krige function from gstat in R 3.5.1
Land use	1–6	Digitization of air photos with ground truthing
Topographic wetness index	1.5–14.3	Derived from DEM using basic terrain analysis in SAGA 7.2.0
Heat load index	0.22–0.97	Derived from DEM using arcpy.aspect and arcpy.slope in ArcGIS 10.6
Slope (rad)	0–0.82	Derived from DEM using arcpy.slope function in ArcGIS 10.6
Distance to road (m)	0–409	Digitization of air photos; derived using arcpy.near function in ArcGIS 10.6
Distance to trail (m)	0–541	Digitization of air photos; derived using arcpy.near function in ArcGIS 10.6

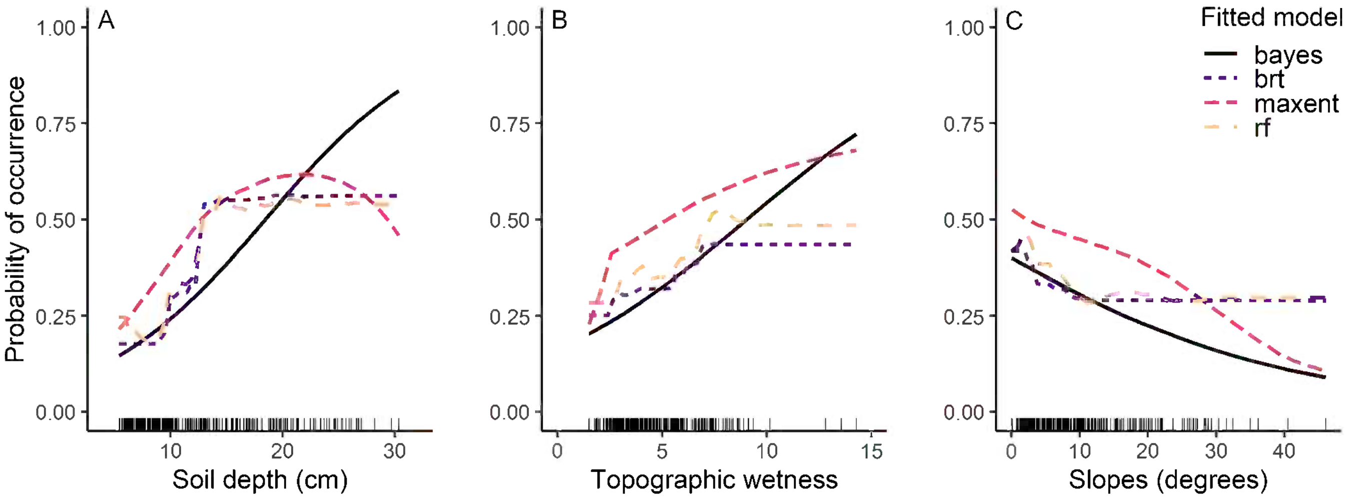

FIGURE 1 On average, the least suitable earthworm habitat occurred in areas with shallower, relatively dry soils on steep terrain. Partial dependence plots showing how earthworm occupancy varied as a function of the most important variables, soil depth (a), topographic wetness (b) and slope (c) for each of component model (Figure A2)

taken as the AUC-weighted mean of each component model (wherein all models had an average AUC ≥ 0.70).

We used likelihood ratio tests and G-statistics to test if the occurrence of earthworms was correctly predicted by the ensemble model. We also delineated potential 'refuges' from earthworm invasion by assuming that all mapped habitat predicted to be < 30% likely to harbour earthworms represented habitat resistant to invasion by earthworms or were unlikely to support persistent populations of earthworms. In addition, we classified all mapped habitat predicted to be >70% likely to support earthworms as being suitable habitat for earthworm populations to persist. We validated this assumption by calculating the proportion of quadrats in and outside of 'refuges' that were or were not invaded by earthworms, as well as the proportion of quadrats in suitable earthworm habitat that lacked evidence of their occurrence.

We used a generalized linear mixed effects model fitted to a Poisson distribution to determine if plant species richness differed between survey sites with earthworms present versus absent in forest and meadow habitats and test whether soil depth varied predictably among those sites. We used earthworm occurrence (present vs. absent), soil depth, topographic wetness, heat load and distance to roads and trails as fixed effects, and plot ID and land use as random effects. Finally, we tested for interactions between earthworm occurrence and every fixed effect based on a priori hypotheses and present the best model identified by corrected Akaike information criterion (AICc).

3 | RESULTS

3.1 | Earthworm occurrence

Lumbricus terrestris or *L. rubellus* were detected in 13.3% and 4.6% of 300 quadrats, respectively, but in 29.3% quadrats with juveniles included. Casts and burrows were detected in the absence of earthworms in 7.0% of all quadrats. On average, we observed 2.2 ± 0.17 earthworms per quadrat in occupied sites (maximum = 9).

Earthworms were detected most often in areas with deep, moist soils, low or no slope, nearer to roads and trails and in forests (Figure 1). In contrast, sites with steep slopes, shallow, dry soils and little or no forest canopy rarely supported earthworms. All four models comprising the ensemble model included soil depth as the most influential predictor (Figure A2 in the Supporting Information). At depths below 9 cm, earthworms were less than 25% likely to occur compared to being over 50% likely when depths were above 15 cm (Figure 1a). We found

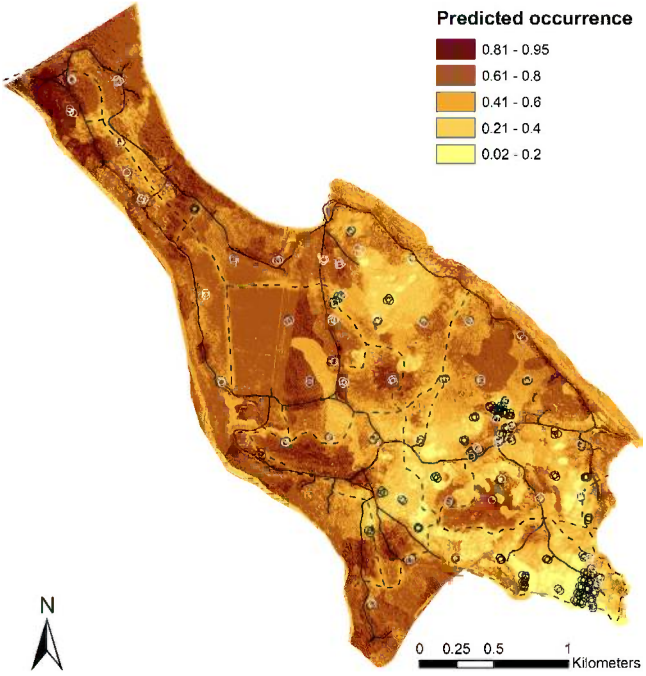

FIGURE 2 Predicted probability of non-native, *Lumbricus* earthworms being detected on Sidney Island, BC. Lighter shading indicates a lower probability of occurrence. Circles represent 0.1 m^2 quadrats used during our surveys. Open black circles indicate quadrats where we did not detect earthworms or evidence of earthworms while open white circles show positive detections. Solid black lines are road networks and dashed lines are trails

weaker relationships of soil moisture and slope on earthworm occurrence (Figure 1b, c). In general, steep terrain promotes soil erosion and surface water run-off. Contrary to predictions (Table 1), roads and trails had relatively weak effects on earthworm occurrence. These findings suggest that earthworm occurrence was reduced in more rugged and drier habitats, consistent with our hypothesis that natural refuges from earthworm invasion may occur.

A weighted ensemble model provided the best discrimination among sites with and without earthworms present (AUC = 0.93) which, when mapped, suggested a mosaic of more and less suitable habitats for earthworms, including a substantial number of refuges wherein they were unlikely to occur (Figure 2). Potential refuges were particularly common on the south-eastern portion of Sidney Island (Figure 3). Only 2.4% of 123 quadrats located in potential refuges had evidence of earthworms, as compared to 96% of 50 quadrats in regions predicted to be suitable earthworm habitat ($G = 164.81$, $df = 1$, $p < 0.001$).

Earthworm presence was associated with reduced plant species richness across habitat types ($\chi^2 = 5.63$, $df = 1$, $p = 0.017$). The number of plant species detected at a site declined substantially in response to earthworm occurrence ($\beta = -1.58$ [0.67], $z = -2.37$, $p = 0.08$) and soil depth ($\beta = -0.04$ [0.01], $z = -4.56$, $p > 0.001$). These results imply that richness declined from 2.72 species per 0.1 m^2 in the absence of earthworms, to 0.21 species per 0.1 m^2 in areas where earthworms occurred. Soil depth and earthworm occurrence also interacted to affect species richness ($\chi^2 = 4.59$, $df = 1$, $p = 0.032$). However, we detected no influence of heat load or its interaction with earthworm occurrence. No other edaphic variables were retained in the final model (Table A2 in the Supporting Information).

4 | DISCUSSION

Our results suggest that non-native earthworms represent a threat to the integrity of deep soil Garry Oak meadows and point to the potential conservation value of shallow soil sites that appear to be unsuitable as habitat by *L. terrestris*. Moreover, because the invasion history of non-native earthworms is closely linked to human development in the region we studied (e.g. Arcese & Rodewald, 2019), our results also suggest that prioritizing the conservation of islands not yet invaded by earthworms could help conserve intact examples of critically endangered Garry oak and maritime meadow habitat. Specifically, we showed that on Sidney Island the occurrence of non-native earthworms was limited by edaphic factors linked to soil depth, soil moisture and terrain in ways that revealed the presence of many potential refuges against the effects of earthworm invasion for native species inhabiting those areas. Given that earthworm presence also predicted a reduction in plant species richness in the habitats in which they occurred versus were absent, our cumulative results indicate that invasions by non-native earthworms have the potential to undermine efforts to conserve native plant communities in sites with deeper, moist soils more so than in sites with shallower, drier soils.

4.1 | Refuges from invasion

We used SDMs to identify suitable habitat for non-native earthworms and potential refuges from invasion that may offer protection to Garry Oak and maritime meadow plant communities throughout their range in the Pacific Northwest of North America. Habitats free of non-native earthworms were characterized by shallower soils and steeper terrain on average, and thus represented savanna and meadow habitats that tend to shed water (Figure 1). Such sites may act as refuges against invasion by earthworms because summer drought can reduce earthworm survival and limit their distribution (Eggleton et al., 2009). In contrast, because soil moisture depends strongly on seasonal variation in rainfall, which tend to be high from October to March annually, it is also possible that earthworms disperse into shallow-soil habitat patches regularly but do not establish persistent populations (Vasudev et al., 2015). For example, Potvin and Lilleskov (2017) found that deep soil provides *L. terrestris* individuals some protection from high summer temperatures and desiccation and facilitates the establishment of persistent populations. Overall, therefore, our results are consistent with the prediction that soil depth and moisture will influence the vulnerability of Garry Oak and maritime meadow habitats to invasion by non-native earthworms (Table 1).

Previous research has also shown that earthworm occurrence tends to decline as distance to the nearest roads and/or trails increases,

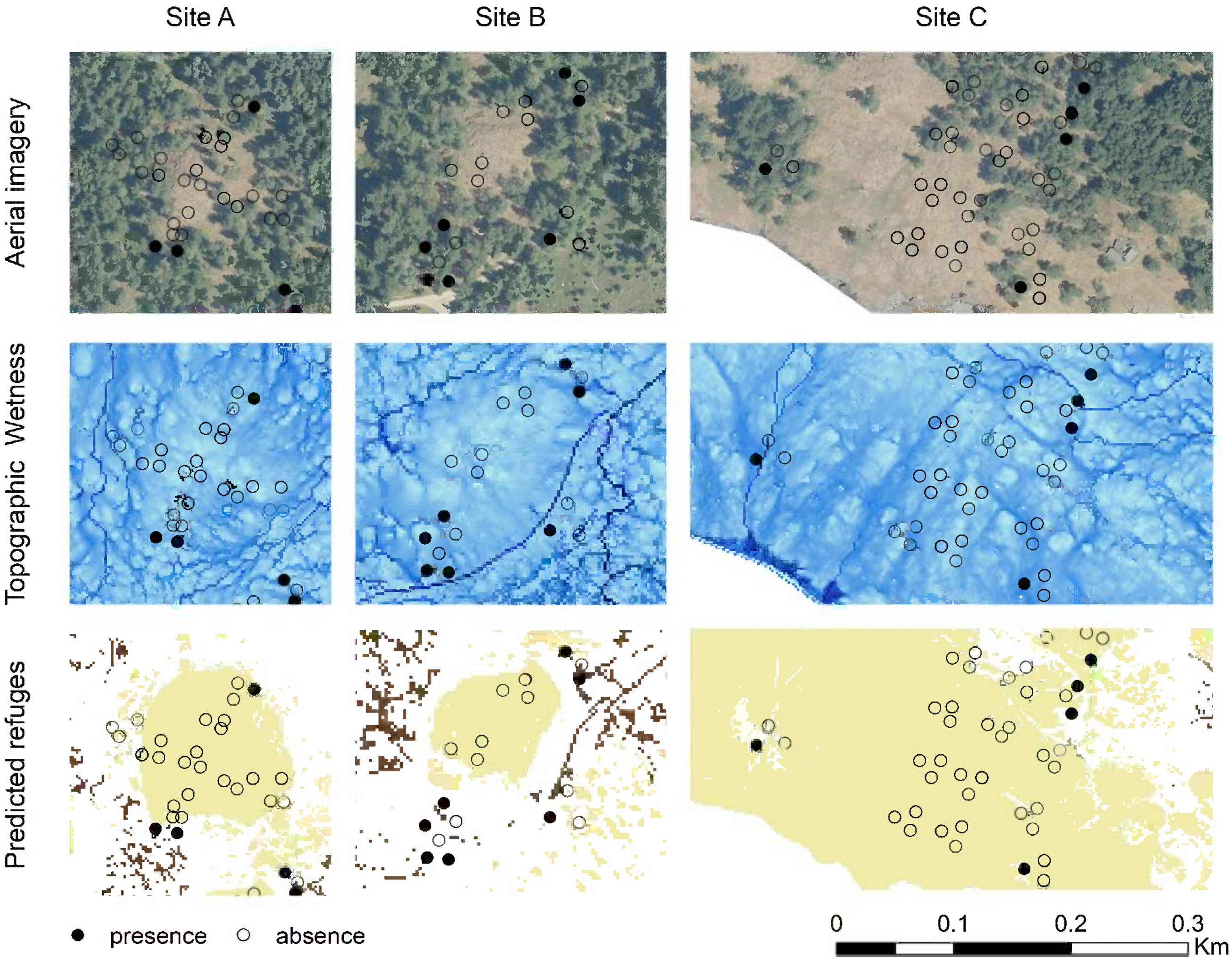

FIGURE 3 Edaphic refuges and potential dispersal corridors for earthworms at three sites. Topographic wetness is a relative measure wherein the darker colors indicate wetter drainages in the catchment and lighter colors are drier. Row 3 shows where the ensemble SDM predicts refuges from earthworms occur in a light brown color (< 30% predicted occurrence) and where earthworms are most likely to be found in dark, brown (>70% predicted occurrence)

but neither of these features were a strong predictor of earthworm occurrence on Sidney Island (Figure A3 in the Supporting Information; Cameron & Bayne, 2009; Paudel et al., 2016). Schneider et al. (2016) cautioned that the performance of SDMs for earthworms may vary when comparing earthworms across functional groups. Cameron and Bayne (2014) also noted that spatial links between earthworms and roads should weaken as invasions 'mature' and the distribution of invasive earthworms is limited more so by the environmental factors affecting survival and reproduction than dispersal.

Factors such as soil pH, percent organic matter, cation exchange capacity (CEC), and calcium concentration can also influence the dispersal of earthworms across landscapes and within soil profiles. Ferlian et al. (2020) used a meta-analysis to suggest that invasive earthworms can alter the chemical properties of soils in ways that enhance earthworm persistence. Positive feedbacks between earthworm abundance, humic formation, and pH are also reported from European forests with soil pH ≤ 5 (Desie et al., 2020). Soil profiles of our study area had the lowest pH in the uppermost soil horizon but declined in percent organic carbon and CEC as soil depth increased (Van Vliet et al., 1991). This indicates that soil features that we did not record may have also influenced earthworm occurrence or persistence and could be included in future studies.

In addition to environmental factors acting on earthworm demography and dispersal, the relatively recent history of colonization, agriculture and habitat conversion on Sidney Island by non-Indigenous human colonists and empirical findings indicating that human settlement was a precondition to detecting earthworms on 25 other nearby islands surveyed by Arcese and Rodewald (2019) both indicate that earthworms have probably been present on Sidney Island for 100 years or longer. Therefore, we suggest that our results are consistent with the idea that earthworms now occur on Sidney Island in most suitable habitat patches available to them, but remain largely absent from many small patches of refugial habitat where dispersal limitation and/or desiccation preclude their colonization or persistence (Figures 2 and 3).

4.2 | Earthworms and plant species richness

We found that sites with earthworms present had lower plant species richness, independent of habitat type (Table A2). This result is consistent with meta-analytical reviews suggesting that earthworms reduce plant species diversity in a variety of other habitats globally (Cameron et al., 2016; Craven et al., 2017). Less intensive surveys of nearby islands revealed a positive relationship between earthworm occurrence and non-native shrub, and herbaceous plant cover but did not consider how soils might affect such relationships (Arcese & Rodewald, 2019). Our models support the hypothesis that invasions by non-native earthworms reduce plant species richness in areas where earthworms were not present historically (Fleri et al., 2021) but also suggest that shallow-soil plant communities may find refuge from the effects of earthworm invasions unable to survive annual drought. Eisenhauer et al. (2010) showed that earthworms changed the composition of soil seedbanks and identified seed and seedling size as defining characteristics which affected a species' vulnerability to depredation by earthworms. Dobson and Blossey (2015) also reported that earthworms altered forest plant communities by reducing seedling survival in 12 plant species. Our observation of a decline in species richness where earthworms were present versus absent on Sidney Island was expected given the results above and extend those results by demonstrating that similar effects are detectable in Garry oak and coastal Douglas-fir (*Pseudotsuga douglasii*) forests of the Georgia Basin.

4.3 | Implications for conservation planning

Systematic conservation planning has been widely adopted by decision scientists to identify the most cost-effective conservation strategies given a defined set of desired outcomes (McIntosh et al., 2017). Spatially explicit SDMs can facilitate such efforts by providing predictions of species responses to current or future conditions (Guisan & Thuiller, 2005), estimate connectivity among habitats and thereby help to optimize conservation plans (e.g. Domisch et al., 2019). We suggest that SDMs like the one described here could also be developed to predict the distribution and dynamics of non-native earthworm invasions in insular and forested habitats regionally (e.g. Hale et al., 2006). In the Georgia Basin, maritime meadow habitats on small, relatively isolated islands tended to harbour a higher than expected number of rare and endangered species given observations on larger islands less isolated from disturbance by humans and hyper-abundant deer and geese (Bennett & Arcese, 2013; Best & Arcese, 2009; Martin et al., 2011). Our results suggest that shallow soil meadows appear to be more robust to invasion by non-native earthworms than deep soil sites and may therefore represent refuges from the deleterious impacts of non-native earthworms on species richness and community composition in Garry oak and maritime meadow habitats of high conservation value in Canada (Parks Canada Agency, 2006a, 2006b). Taken together, these results suggest further that deep-soil sites that are also subject to disturbance processes linked to humans or their commensal species are more likely to experience invasions by non-native earthworms that coincide with reduced native species richness in coastal Douglas-fir forest and Garry oak savannas of the Pacific Northwest of North America.

Non-native earthworms can also alter soil composition, nutrients and below-ground communities (Ferlian et al., 2018, 2020). As a consequence, their persistence in deep-soil Garry oak habitats have the potential to facilitate novel ecological processes, communities or dynamics in response to anthropogenic inputs (e.g. Fleri et al., 2021). However, more work will be needed to understand how the restoration of Indigenous land management activities such as burning, encroachment by Douglas-fir or over-browsing by hyper-abundant herbivores may interact with invasive earthworms to affect community outcomes (Arcese et al., 2014; Best & Arcese, 2009; Pellatt & Gedalof, 2014). Saltmarsh et al. (2016) found that non-native earthworms were often present near boat launches in an Alaska wildlife refuge and suggested prohibiting the use of *Lumbricus* spp. as bait to limit their spread. Similar policy recommendations may be well suited for islands in the Georgia Basin that have freshwater lakes and streams but no such systems occur on the island we studied. Moreover, historic agriculture and present-day gardening have been noted as common precedents for earthworm presence in our study region (Arcese & Rodewald, 2019). As a result, educational programmes that discourage the introduction of earthworms into gardens may be particularly effective on small islands with low human densities (Callaham et al., 2006). Conservation plans are more likely to fail when known threats are underestimated. Therefore, conservation planners should anticipate that such invasions will continue in areas inhabited by humans. We suggest that planners implement spatial mapping tools like those developed here to predict where invasions are most likely to occur, determine what natural barriers to invasion may exist and identify potential refuges in which native communities are most likely to persist in an intact state.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

JRF and PA conceived the ideas and designed methodology; collected the data; analysed the data and wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.3xsj3txg6 (Fleri & Arcese, 2021).

PEER REVIEW

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