EARTHWORM INVASION: CONSEQUENCES AND CONSERVATION IMPLICATIONS FOR THE ENDANGERED GARRY OAK (*Quercus garryana*) AND MARITIME MEADOW ECOSYSTEMS

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Abstract

Biological invasions by non-native 'ecosystem engineers' can radically alter the ecological and socio-economic values of ecosystems in ways that may require decades to detect. The invasion of North American glacial refuges by non-native earthworms is a prominent but understudied example of a cryptic invasion by an ecosystem engineer. Non-native earthworms are known to reduce soil carbon, disrupt mycorrhizal networks, and homogenize plant communities in their role as seed predators, root foragers, and in nutrient cycling and redistribution. However, natural resource managers have struggled to discern the scale at which non-native earthworms influence plant species diversity across invaded biomes. With no effective methods to eradicate or control established earthworm populations, there is great need for preemptive strategies to identify highvalue conservation areas at risk of invasion. Herein, I address two main questions with implications for forest management: 1) Can the influence of non-native earthworms on plant community assembly be reliably predicted using plant traits? 2) Can abiotic factors be used to identify and predict natural refuges from earthworms in heterogenous habitats? I found that the presence of earthworms contributed to the simplification of plant communities in experimental mesocosms and observational surveys of *in-situ* forest and meadow habitat. In general, earthworms were associated with plant communities dominated by species with large seeds and fibrous roots, whereas species with small seeds and taproots only persisted in multi-species mesocosms without earthworms. These findings suggest that earthworms shape community composition in the early stages of invasion by acting as ecological filters on morphological plant traits. Last, I constructed an ensemble species distribution model for non-native earthworms using data from 300 survey plots to identify the suite of environmental conditions needed to limit the dispersal and persistence of invading earthworms. This model showed that shallow and dry

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soils on steep terrain strongly limit the occurrence and abundance of non-native earthworms. My results show that earthworms reduce plant species richness in coastal forest and meadow habitats of southwest British Columbia and highlight the conservation value of shallow-soil habitats that limit earthworm distribution and persistence.

Lay Summary

Global declines in biodiversity are due in part to the conversion of natural landscapes to human use and associated spread of non-native, invasive species. Species capable of manipulating their environment have disproportionately large impacts in the habitat they occupy, such as North American beavers or European earthworms. However, unlike beaver, earthworms are cryptic and their impacts are difficult to detect. Research has shown that the presence of earthworms boosts CO₂ emissions, reduce soil nutrients, and encourage other non-native species to establish which contributes to the loss of native plant and animal diversity. My work 1) evaluates how non-native earthworms affect plant species diversity in an endangered ecosystem that previously did not have earthworms; and 2) aims to predict whether natural barriers linked with soil depth or topography might impede earthworm invasion and be used to identify areas that are naturally resistant to invasion.

Preface

Chapter 2 describes a mesocosm experiment conducted at UBC from November 2018 to June 2019, and a version of it has been submitted for publication. Fleri, J.R., T.G. Martin, A.D. Rodewald, P. Arcese. Non-native earthworms alter plant community assembly. I worked with co-authors to design and carry out the experiment, analyze data, and write the manuscript. Drs T.G. Martin and A.D. Rodewald provided valuable advice on data analysis, provided early advice on experimental design, and assisted with manuscript edits. Dr. P. Arcese provided extensive commentary and advice at every stage listed above.

The 3rd chapter uses field data collected on Sidney Island, BC during Summer 2019 and uses publicly available spatial data from the Island Trust BC as well as LiDAR data from Dr. T. Jones at UBC. I collected all field data with field assistance of M. Bull and P. Puri. A version of chapter 3 will be submitted for publication. Fleri, J.R., P. Arcese. Predictive mapping to identify refuges for plant communities threatened by earthworm invasion. I was responsible for survey design, data handling, analysis, and wrote the manuscript. Dr. P. Arcese provided guidance on experimental design, analysis, and manuscript feedback.

This research did not require ethics approval.

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Dedication

To my mother, who taught me follow my passion. Who instilled in me a deep rooted appreciation of nature.

And to my father, who taught me that to be successful one must be persistent, lucky, and willing to learn from failure.

Chapter 1: General Introduction

1.1 Overview

Biological invasions represent a contentious problem in ecology and conservation biology because of the difficulty of 1) predicting the outcome of novel interactions between native species and non-native invaders positioned within and across trophic levels, and 2) identifying key factors that limit the dispersal and distribution of invasive species. I address these limitations for the on-going invasion of non-native earthworms (Lumbricus spp.) in the Southern Gulf Islands of British Columbia, which support the most intact examples of the critically endangered Garry Oak (Quercus garryana) and maritime meadow ecosystems in Canada (Gonzales 2008, Bennett 2014). Understanding the ecological effects and spatial dependencies that allow non-native earthworms to invade an ecosystem is particularly relevant for evaluating the effectiveness of protected area design. A growing literature suggests that non-native earthworms facilitate rapid change in ecosystems by reducing soil carbon storage, disrupting mycorrhizal associations, and destabilizing plant communities (Bohlen et al. 2004, Frelich et al. 2019). However, there are no known methods for eradicating earthworm populations once they become established. Because non-native earthworms alter ecosystem structure and function, it is important to know how vulnerable plant communities are and whether limits on their distribution or spread result in some areas acting as effective refuges from earthworms. Specifically, I set out to address two questions with management implications for Garry Oak and maritime meadow ecosystem: 1) Can the influence of non-native earthworms on plant community assembly be reliably predicted using plant traits? 2) Can abiotic factors be used to identify and predict natural refuges from earthworms in heterogenous habitats?

1.2 Earthworms, soils, and plant communities

Earthworms are 'ecosystem engineers' (Jones et al. 1994) that can drive below- and above-ground community dynamics by affecting soil nutrients, structure, and development and thereby influence plant demography and competitive interactions. However, the strength and direction of such effects remains uncertain due to the relatively recent focus on invasion processes in below-ground systems (Craven et al. 2017), and because data on the taxonomic identifiers, life histories, occurrence, distribution of earthworms, and their influence on plant communities is still fragmentary (Phillips et al. 2019).

It is clear that some species of earthworm consume soil organic matter (SOM), leaf litter, and plant seeds and thus have the potential to alter humus-forming processes, while also consolidating organic material in casts near burrows (Amador et al. 2006, Eisenhauer et al. 2007, Straube et al. 2009). Deep burrowing earthworms (anecic) mix soil horizons (Gundale 2002) and promote soil erosion by reducing soil stability, abrading plant roots, and undermining top soil via extensive belowground excavation (Orgiazzi and Panagos 2018). Such processes clearly have the potential for multiple interactive effects on soil quality, composition, and the plant communities growing on them. However, it remains unclear how earthworms will respond to the harsh edaphic and topographic features that are common in Garry Oak and maritime meadow habitats.

Non-native earthworms cause disturbances that cascade across trophic levels, but their impacts are most visible in ecosystems that do not have native earthworms (Frelich et al 2019). Earthworm activity can directly affect seed survival, dispersal and/or facilitation in plant communities. Forey et al (2011) found that earthworms preferentially consume small plant seeds and seedlings but bury large seeds in burrows to promote decomposition. Furthermore, Clause et al. (2015) showed that seeds from non-native species can pass through the gut of earthworms

relatively unharmed and be deposited in nutrient-rich casts that have higher germination rates than the surrounding soil in nutrient-poor grasslands. However, the influence of seed size, shape, and species on the rate of seed ingestion, viability, and the potential spill-over effects on how plant communities assemble remain poorly understood (Eisenhauer et al. 2010). Changes to these factors could help to explain why biodiversity tends to decrease in presence of earthworms (Craven et al 2017).



Figure 1.1. Earthworms can reduce soil organic matter and native plant species diversity while increasing cover of non-native plants, especially grasses (Craven et al. 2017, Frelich et al. 2019), by consuming seeds, damaging roots, and redistributing nutrients.

1.3 Study Area

My study system is the Southern Gulf Islands of the Pacific Northwest of North America, and is home to >100 highly threatened, at-risk species from the critically endangered Garry Oak (Quercus garryana) and maritime meadow communities (GOERT 2011, Bennett et al. 2013, Bennett 2014). The region has a sub-Mediterranean climate with mild, wet winters and dry summers with frequent drought (MacDougall 2005). Mean annual temperatures fluctuates between ~9.8 to ~10.6 C and mean annual precipitation ranges from ~670 to ~1100 mm (Wang et al. 2016). The Gulf Islands exhibit a unique geologic history due to most of the islands being inundated or glaciated by the Late Wisconsin Cordilleran Ice Sheet roughly 14,500 years ago (Eyles et al. 2018). As a consequence, native earthworms are thought to have been largely extirpated from the islands, with a few extant species restricted to glacial refugia far from my study site (Reynolds 1977, Addison 2009). At present, roughly 75% of earthworm species detected in British Columbia are thought to have originated in Eurasia, arriving actively or passively in the region following colonization by non-indigenous settlers after ~1860 due to the importation of agricultural products, and more recently via recreational fishing and gardening (Marshall and Fender, 2007).

1.4 Earthworm effects on community assembly

In the Gulf Islands, native and exotic species can act in both ecologically distinct and overlapping ways depending the parameter, scale, and metrics observed (Bennett et al. 2012). MacDougall and Turkington 2005 posited that invasive species are frequently 'passengers' of environmental change; inherently acting as symptoms of change rather than being their true cause. Earthworms may indeed be acting as 'agents of change', creating an environment more suitable, if not ideal, for evolutionarily co-evolved plant invaders (Bohlen et al. 2004). Non-

native nitrogen fixers may also exacerbate the magnitude of environmental perturbations on local plant communities by promoting colonization of nitrogen-demanding exotic species that may ultimately lead to alternative successional pathways (Dornbusch et al., 2018; Stinca et al., 2015). Refining links between below-ground disturbance and non-native recruitment at higher trophic levels is key to implementing a successful management strategy in the Gulf Islands.

Management of Garry oak and maritime meadows is designed to mitigate the effects of over abundant herbivores, fire suppression, and invasive plant species but does not account for belowground disturbances (Parks Canada Agency 2006a, 2006b). I set out to determine whether earthworms act as agents of change that facilitate non-native plant species (Bohlen et al. 2004). I examine how earthworms influence germination and establishment rates in native and non-native plants and the extent to which those effects are related to species and functional traits.

1.5 Dispersal barriers and potential refugia

Given the uncertainties about how non-native earthworms affect plant communities across the globe, it is prudent to ask whether natural barriers to earthworm dispersal or persistence are likely to limit the spatial spread of invaders into sensitive ecosystems. Because biological invasions tend to coincide with habitat conversion, human migration, and trade (Levine and D'Antonio 2003, Hulme 2009), preemptive management strategies have been adapted to target actions that lower the likelihood of invaders colonizing new habitat (Courchamp et al. 2003, Simberloff et al. 2013) or ameliorate stressors that facilitate invasion success (MacDougall et al. 2004, Best and Arcese 2009). Such strategies are particularly relevant for constraining the spread of non-native earthworms because there are presently no methods for controlling or eradicating established populations. My research uses a robust spatial dataset for the Gulf Island archipelagos with comprehensive field surveys to understand if topographic and

edaphic features can act as barriers to the dispersal of non-native earthworms and whether the location of such barriers can be predicted in a heterogenous landscape.

Chapter 2: Non-native earthworms alter the assembly of a meadow plant community

2.1 Introduction

Non-native invasive species can profoundly affect the composition of native plant and animal communities (Vilà et al. 2011, Pyšek et al. 2012, Rodewald and Arcese 2016) and are often facilitated by over-abundant herbivores that alter nutrient dynamics (Best 2008, Borer et al. 2014) and/or reduce the cover and growth of native plant populations via herbivory (Gonzales and Arcese 2008, Estes et al. 2011). Recent global syntheses suggest that non-native earthworms (*Lumbricidae*) in particular, can reduce native plant species diversity, increase non-native plant cover, and favor graminoid over woody species (Craven *et al.* 2017; Frelich *et al.* 2019; Phillips *et al.* 2019), via their roles as seed predators, root foragers, and in nutrient cycling and redistribution (Forey et al. 2011, Cameron et al. 2014, Jarić et al. 2019). However, a scarcity of experimental studies of such processes has left the question of whether earthworms are 'drivers' or 'passengers' of change in communities unresolved (MacDougall and Turkington 2005).

Recently, Arcese & Rodewald (2019) compared insular plant communities with and without non-native earthworms of the genus *Lumbricus* to suggest that their introduction to endangered maritime meadow habitats of the Pacific Northwest of North America reduced the diversity and abundance of native herbaceous and woody plant species, independent of the occurrence of deer (Cervidae) or geese (*Branta canadensis*), each of which causes rapid trophic downgrading in the absence of native predators or human hunting (Best and Arcese 2009, Isaac-Renton et al. 2010, Martin et al. 2011, Arcese et al. 2014). Here, I test whether earthworms act

as direct agents of change in maritime meadows by enhancing conditions favorable to the exotic plants species that co-evolved with earthworms (Bohlen et al. 2004).

To date, studies of earthworms and plant communities have focused mainly on the life history traits and phylogenetic origins (hereafter 'origins') of invading species (e.g., Craven *et al.* 2017; Frelich et al. 2019; Phillips et al. 2019). In contrast, very little is known about the traits of plants most affected by earthworms, the belowground processes they influence, or their synergistic interaction with above-ground herbivores (e.g. Dobson & Blossey 2015), particularly in systems where earthworms were historically absent (Arcese and Rodewald 2019). Initial studies indicate that anecic earthworms affect plant roots directly and negatively via abrasion, but also indirectly and positively via burrow construction (Cameron et al. 2014). Earthworms also depredate seeds and seedlings, but may do so less often as seed and seedling size increase (Cassin and Kotanen 2016). However, whether such effects help explain the meta-analytical results reported to date remains unknown.

I addressed these knowledge gaps by assembling and monitoring 300 experimental mesocosms to estimate the direct and indirect effects of invasion by the anecic (burrowing) earthworm *Lumbricus terrestris* on six native and six non-native plant species which occur commonly in endangered maritime meadows of the Pacific Northwest of North America. Specifically, I asked if non-native earthworms acted as direct 'agents of change' in maritime meadows by reducing seed and seedling survival through depredation and burial (Bohlen et al. 2004). Based on previous findings (Craven *et al.* 2017), I predicted that earthworm presence would (1) reduce seedling survival, (2) promote the establishment of non-native over native species, (3) limit establishment in plants with small seeds and fibrous, and (4) lead to simplified plant communities.

2.2 Methods

2.2.1 Seed source and study system.

Garry oak and maritime meadow ecosystems have been drastically reduced in extent and integrity with less than 5% remaining in good condition. These intact sites occur in the Southern Gulf and San Juan archipelagos of British Columbia and Washington State, respectively (Arcese et al. 2014, Bennett 2014). The region experiences a transitional Mediterranean climate typified by mild, wet winters and dry summers, with a mean annual temperature of ~9.8 to ~10.6 C; mean annual precipitation ranging from ~670 to ~1100 mm (Wang et al. 2016). Maritime meadows are characterized by shallow soil (0-30 cm), elevation near sea level, and sparse canopy cover (Fuchs 2001).

Many annual plants in this system germinate in fall, whereas perennials tend to germinate in mid- to late winter, with the main growing and flowering period occurring from March to July, followed by seasonal drought from July to August (Gonzales & Arcese 2008; Bennett 2014; unpublished observations). All seeds were collected locally in southwest BC in May and June 2018. Focal species were selected to represent many of the most abundant and functionally diverse native and exotic plant species in Garry Oak and maritime meadow ecosystems (Bennett et al. 2013) (Table 2.1).

2.2.2 Mesocosms

I established 300 mesocosms lined with 1 mm fiberglass window screen (Cassin & Kotanen 2016) in 8L plastic pots (sterile 1:1 mix of sand:organic matter) to create and monitor species monocultures and communities at Totem Field Agricultural Center, University of British Columbia. I added three adult *L. terrestris* to half of the mesocosms, reflecting densities within field (Gibson et al. 2013, Choi et al. 2017, Laushman et al. 2018). I established all mesocosms in

the first week of November 2018, and commenced surveys of single species pots weekly to biweekly through June 2019. In most surveys, I estimated the number of individuals present in mesocosms repeatedly, after practicing on samples in which precise counts of all individuals were made. In terminal surveys, I censused all mesocosms precisely. Experimental communities were censused twice; in early May, after all single species had germinated, and again in late June.

Table 2.1. Classification of species by traits. Predicted resilience is based on hypothesized interactions between earthworms, seeds, and roots, where ↑, ↓, and - denote positive, negative, and neutral predictions. For example, Species with small seeds and fibrous roots are predicted to have low resilience and large seeds and taproots are predicted to have high resilience to earthworm invasion. MI denotes Mandarte Island, NU is nursery grown, SI is Sidney Island.

Species	Seed	origin	lifecycle	Seed weight	seed class	root	Predicted
	source			(mg)		system	resilience
Camassia leichtlinii	MI	native	perennial	9.24	large	fibrous	-
Achillea millefolium	NU	native	perennial	0.11	small	fibrous	\downarrow
Brodiaea coronaria	SI	native	perennial	1.26	large	fibrous	-
Collinsia parviflora	NU	native	annual	0.98	large	taproot	1
Grindellia stricta	MI	native	perennial	2.17	large	taproot	1
Cerastium arvense	NU	native	perennial	0.19	small	fibrous	\downarrow
Rumex acetosella	SI	exotic	perennial	0.53	small	taproot	-
Hypochaeris radicata	SI	exotic	perennial	0.71	small	fibrous	\downarrow
Dactylis glomerata	MI	exotic	perennial	0.75	small	fibrous	\downarrow
Senecio vulgaris	MI	exotic	annual	0.44	small	taproot	-
Plantago lanceolata	SI	exotic	perennial	1.02	large	taproot	1
Holcus lanatus	MI	exotic	perennial	0.42	small	fibrous	\downarrow

I used 240 single species mesocosms (12 spp x 20 rep x 2 treatments) to estimate how earthworms affected germination and seedling survival in the absence of competition with other species. Specifically, I spread 100 seeds (by weight) over each replicate mesocosm, blocked by species (2 x 5), and arranged them in columns (2 x 30) spaced at ~ 0.5m on weed cloth, in an open, mowed field to minimize potential edge effects. Average seed weights were derived by isolating 100 seeds 5 times per species, weighing them, and then dividing by 100 (Table 2.1). I created 60 community mesocosms by compositing 40 seeds (by weight) for each species (n = 12) prior to being scattered across the surface of each mesocosm. Initial seed densities approximate those surveyed in the field (Best 2008). Mesocosms were blocked by treatment and arranged in columns (2 x 15) alongside single species mesocosms.

2.2.3 Data Analysis

I estimated the effects of earthworms in germination and establishment phases of the experiment using 12 plant species, four binary plant traits, and conventional ANOVA. Specifically, I recorded seeds as 'germinated' if they had a radical, cotelydons, or other growth visible on surveys conducted between early November to the last snowfall in mid-February. 'Established' seedlings were defined as the number of individuals alive between mid-February and late June, at the termination of the experiment. I refer to 'survival' as the fractional change in the number of plants counted in one census to the next, or the end of the experiment. To visualize temporal variation in survival through time, I plotted the number of plants detected at each survey by fitting a loess regression to survey date (Wickham 2016) (Figure. 2.1). All statistical analyses were performed using R version 3.5.1 (R Core Team 2018).

I also estimated the extent that earthworms influenced the survival of species in experimental communities. To do so, I used survival for each species grown alone or with earthworm in the single species mesocosms as a baseline for expected survival in community mesocosms with and without earthworms added.

To make these comparisons, I first tested for heterogeneity in the effect of earthworms on plants during the germination and establishment periods, and over the entire period for species planted in monoculture using linear mixed effect models and randomized block factorial ANOVA (Kuznetsova et al. 2017). I used species, survey date, and treatment (earthworms present or absent) as fixed effects, and Pot ID as a random effect. I tested for linear and two- and three-way effects using all fixed variables and AICc for model selection.

I next estimated the effect of plant traits on performance by testing for correlations between traits and earthworm presence using linear mixed effects models. Specifically, I denoted treatment and trait as fixed effects, species and date as random effects in monocultures, and by using Pot ID as a random effect in community pots. I test for hypothesized two-way interactions (Table 2.1) for 'earthworm x root' and 'earthworm x seed size' in monoculture mesocosms. I further investigate traits as predictors in the community mesocosms by testing for all two-way interactions between 'earthworms x trait', derive estimated marginal means, and compute Tukey style post hoc tests (Lenth 2019). I use paired t-tests to examine the effects of earthworms on species richness, abundance, Shannon's diversity and Pielou's evenness (hereafter 'biodiversity metrics') in community mesocosms at the final census because weekly tracking of seedlings was impractical (Oksanen et al. 2019).

2.3 Results

Survival in the germination and establishment phases varied by species, treatment and time (Figure. 1). *Colinsia parviflora* and *Grindellia stricta*, both natives, expressed the highest germination and establishment rates (Figure. 2.1). For example, *Rumex acetosella* germinated

well in autumn and survived well into spring, whereas *Hypochaeris radiata* germinated relatively early but exhibited poor tolerance to freezing conditions in mid-February (Figure. 2.1).

Mesocosms with earthworms added varied strongly in the number of germinates detected at each timestep (Appendix A). In particular, I found that earthworms influenced the demography of species most strongly during the germination period, with early differences among them being largely maintained to establishment (Appendix A). However, individual species also varied in their response to earthworms over time, sometimes leading to complex three-way interactions between species identity, time, and the presence or absence of worms (e.g., *Grindellia stricta, Rumex acetosella*).

2.3.1 Predicting survival using traits in monocultures

Species appeared to vary in response to earthworm presence when grouped by root structure and seed size (Appendix A), but no trait predicted survival during the germination period alone (Appendix A). A statistical interaction between seed size and worm presence did suggest an effect of seed size on survival over the entire experiment ($F_{1,6158} = 5.43$, p = 0.02). Similarly, four taxa with taproots (*Grindellia, Plantago, Rumex, and Senecio*) and one with fibrous roots (*Dactylis*) performed differently with earthworms present or absent, they did so in inconsistent ways with respect to time; all other species showed little or no visible response (Figure. 2.1).



Figure 2.1. Monoculture time series by species. Dark purple indicates control groups while light blue denotes earthworm treatments. Colored points show mean establishment for each survey. Observations on the left of the vertical dashed line occur during the 'germination' phase while those on the right side are considered 'established' in analyses. Lines are fitted with a LOESS regression (span = 0.5, SE ± 1).

2.3.2 Predicting establishment using traits in communities

Species also responded differently to earthworm presence when grouped by functional traits (Appendix A). Root morphology, seed size, lifecycle, and an interaction between seed size and earthworm presence were the strongest indicators of establishment in communities, with origin and an interaction between root morphology and earthworm presence also receiving some support.

Seed size and root morphology each interacted with earthworm presence to influence establishment (Figure. 2.2). In comparison with single-species mesocosms, community mesocosms with earthworms had $4.1\% \pm 1.36$ (t = -3.042, df = 373, p = 0.003) fewer plants with small seeds and taproots than expected given controls, and they had $3.4\% \pm 1.56$ (t = 2.216, df = 483, p = 0.027) more large seeded plants with fibrous roots than expected by the performance of those species planted alone. In contrast, species with small seeds and fibrous roots (-1.36% ± 1.00), or large seeds and taproots (0.66% ± 1.20), varied little by treatments. (t = -1.358, df = 147, p = 0.176; t = 0.558, df = 263, p = 0.577; respectively).

Overall, species abundance, richness, evenness, and diversity were all lower in mesocosms with earthworms present as compared to absent (t = 3.49, df = 45.39, p = 0.001; t = 4.39, df = 57.50, p > 0.001; t = 3.49, df = 57.90, p > 0.001; t = 5.61, df = 56.40, p > 0.001; respectively). Moreover, earthworms appeared to have a polarizing effect on community assembly. Specifically, species that performed better in communities than alone (e.g. large seeds, fibrous roots) appeared to benefit from the presence of earthworms, whereas small-seeded species with taproots performed worse with earthworms present in communities (Figure. 2.2).



Figure 2.2. Earthworms amplify differences between seed size and root trait combinations, shown here with 95% confidence intervals. Brodiaea excluded from analysis due to absence in final census.

2.4 Discussion

Although earthworms have diverse effects on seed and seedling survival (Eisenhauer et al. 2010, Dobson and Blossey 2015), how such mechanisms interact with plant traits or affect community assembly remains uncertain (e.g. Frelich *et al.* 2017, 2019). My results indicate that *L. terrestris*, a large, anecic earthworm native to Europe but now widely introduced across the globe (CABI 2019), influenced the germination, survival, and/or establishment of several of the plant species I studied, but that the direction and magnitude of these estimated effects varied temporally and among species (Figure. 2.1). I also found that community mesocosms had lower plant species abundance, richness, evenness, and diversity with earthworms present versus absent, as expected under the hypothesis that non-native earthworms can promote biotic homogenization (Craven *et al.* 2017; Arcese & Rodewald 2019; Frelich *et al.* 2019; Phillips *et al.*

2019). Below, I briefly consider the mechanisms underlying my observations and then speculate about the influence of invasive earthworms on the assembly, composition, and conservation of maritime meadows.

Root morphology and seed size had strong but interacting effects on the survival of germinants and their establishment in the presence or absence of earthworms. For instance, seed size was unrelated to plant survival, except via an interaction with earthworm presence. This finding suggests that small seeds were more often buried, consumed, or harmed with earthworms present, as also found in German grasslands and mixed hardwood plains of eastern Canada (Eisenhauer and Scheu 2008, Cassin and Kotanen 2016). Contrary to my predictions, however, I observed that plants with fibrous roots outperformed those with taproots when worms were present, perhaps because fibrous roots are more able to sequester nutrients associated with earthworm burrows (Cameron et al. 2014). Given the large number of traits potentially affecting plant establishment in the presence or absence of earthworms, experiments with a larger number of species and traits will be needed to reliably predict the effects of non-native earthworm on plant demography and community composition. Nevertheless, my study design would be a viable approach to use for parameterizing such models under *in-situ* conditions by replicating the experiment on islands with and without non-native earthworms (Arcese & Rodewald 2019).

My comparisons of plant performance in solitary versus community mesocosms suggest that non-native earthworms can act as ecological filters in the early stages of invasion by influencing germination and establishment rates of understory plant communities (Figure. 2.2). In contrast, Dobson *et al.* (2020) used a multi-year, field experiment to estimate the direct and indirect effects of deer and earthworms on seedling survival. Finding none, these authors suggested that the species most negatively impacted by earthworms or deer may have been

extirpated prior to establishing the experiment. I also observed heterogeneous responses to earthworm presence, including with and without interspecific competitors (Figure. 2.1, 2.2), leading to mixed support for several hypotheses (Table 2.1). Overall, however, my results are consistent with the hypothesis that non-native earthworms act more as drivers than passengers in ecological change by influencing plant germination, establishment, and community composition (Craven et al. 2017).

Although I am cautious about generalizing these results to management, they do suggest that non-native earthworms may threaten the integrity of Garry Oak and maritime meadow ecosystems, wherein trophic downgrading, fire suppression, and human development have already combined to reduce their extent by >90% (MacDougall et al. 2004, Pellatt and Gedalof 2014). Moreover, because protected area establishment has focused on islands settled more than a century ago by European colonists, many are already invaded (e.g., Arcese & Rodewald 2019). In contrast, because smaller (<10 ha) and more isolated islands in this region tend to support more intact native plant communities, and are more likely to support rare and endangered plants (Bennett et al. 2012; Bennett & Arcese 2013), my results also suggest an increased emphasis on preventing the further invasion of non-native earthworms to islands in this region should be a priority for the conservation of such communities.

Chapter 3: Predictive mapping to identify refuges for plant communities threatened by earthworm invasion

3.1 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 (Mack et al. 2000, Crooks 2002), 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, tend to be facilitated by anthropogenic habitat conversion, migration, and trade (Levine and D'Antonio 2003, Hulme 2009), 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 (MacDougall et al. 2004, Best and Arcese 2009), 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 and Arcese 2013, Keppel et al. 2015).

My overarching goals in this chapter were to: 1) test several hypotheses on the dispersal and persistence of non-native earthworms in a region where native earthworms are absent, and 2) apply my results and spatial modeling techniques to identify refuges likely to support Garry oak

(Quercus garryana) and maritime meadow plant communities in the absence of invasive, nonnative earthworms. Because Garry oak and maritime meadow ecosystems have been prioritized for conservation in many human-dominated, forested, and insular landscapes of the Pacific Northwest of North America (e.g., Parks Canada Agency 2006a, b), I offer a case study with broad application to insular and forested ecosystems (Callaham et al. 2006), but focused on a threatened ecosystem without endemic earthworms. 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 (MacDougal et al. 2004, Schuster and Arcese 2013, Bennett and Arcese 2013, Bennett 2014, Arcese and Rodewald 2019). Here, I use my empirical results on factors limiting the distribution and occurrence of non-native earthworms to develop and test the application of species distribution models 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 (Hendrix and Bohlen 2002, Tiunov et al. 2006, Addison 2009). Such invasions have facilitated reductions in soil carbon, disrupted mycorrhizal associations, and altered plant communities (Bohlen et al. 2004, Frelich et al. 2019a). 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 (Frelich et al. 2006, Migge-Kleian et al. 2006,

Holdsworth et al. 2007, Dobson and Blossey 2015, Arcese and Rodewald 2019). 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. Species distribution models (SDM) 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 and 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). My 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, I 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 and Fender 2007) and many shallow-soil plant communities of high value to conservation still remain extant (MacDougall 2005, Gonzales 2008, Bennett 2014). 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, I addressed two main questions: (1) do natural refuges from earthworm invasion exist in shallow soils 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, I expected to detect earthworms more often nearer to roads or trails, in deeper, wetter soils, and in areas with lower slope and northeastern exposure. I 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, I expected that sites in which earthworms were detected would have less diverse plant communities than expected by habitat type alone.

3.2 Methods

3.2.1 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 (GOERT 2011, Bennett et al. 2013, Bennett 2014). 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 my study site (Reynolds 1977, Addison 2009). 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 and Fender, 2007). My surveys on Sidney Island, BC, cover a range of more and less intact habitats, including endangered maritime meadow plant communities, typically limited to shallow soil (\leq 30 cm) sites near sea level with little overhead canopy (Fuchs 2001, Gonzales 2008, Bennett 2014).

3.2.2 Field sampling

I sampled 300 0.1m^2 quadrats in 100 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 0.1m^2 quadrats were spaced ~ 18m apart, further than the annual dispersal distance, in a triangular orientation (Hale et al. 2005, Cameron and Bayne 2014). At each quadrat, I 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 to the nearest ± 8m (Garmin eTrex® 20x). I used 50gm of mustard powder mixed into a gallon of water, poured slowly over each quadrat to extract earthworms following Gunn (1992), Lawrence and Bowers (2002), and Arcese and Rodewald (2019), identified all adults to species and juveniles to genus before returning them to an area adjacent to the sample quadrat. I also recorded the presence or absence of all plant species in each quadrat prior to extracting earthworm to estimate species richness, as well as canopy cover and dominant tree species over each quadrat.

Table 3.1. Environmental variables tested in species distribution models. Variables are ordered by most to

Variables	Collection and data processing
Soil depth (cm)	Soil depth probe; Derived using gstat.krige function from gstat in R 3.5.1
Landuse	Digitization of air photos with ground truthing
Topographic wetness index	Derived from DEM using basic terrain analysis in SAGA 7.2.0
Heat load index	Derived from DEM using arcpy.aspect and arcpy.slope in ArcGIS 10.6
Slope (rad)	Derived from DEM using arcpy.slope function in ArcGIS 10.6
Distance to road (m)	Digitization of air photos; Derived using arcpy.near function in ArcGIS 10.6
Distance to trail (m)	Digitization of air photos; Derived using arcpy.near function in ArcGIS 10.6

least importance as defined by model ensembles.

3.2.3 Environmental variables

Seven environmental variables were selected for modelling based on *a priori* hypotheses regarding earthworm dispersal (Table 3.1). I 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 measurement at each site to the nearest centimeter. I next estimated soil depth continuously over the island by fitting soil depth data to a semivariogram and interpolating between sample sites using simple kriging (2m² resolution; R package: gstat; Appendix A). The 252 measurements noted above were allocated to 'data deficient' areas identified by the semivariogram.

I used a high resolution, digital elevation model (DEM, 2m² resolution) based on LiDAR data (summer 2006; Terra Remote Sensing Inc., Sidney, BC) collected in the southern Gulf Islands and assembled by (Jones et al. 2010). I 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). I 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 were calculated using the 'Euclidean Distance' tool on a digitized road map in ArcMap 10.6. Landuse classification were acquired from the Islands Trust BC MapIT database 'Terrestrial Ecosystem Mapper' tool. All data were projected into NAD83 UTM zone 10N.

3.2.4 Data Analyses

I used an ensemble approach to species distribution modeling for non-native earthworms in my study area; specifically by combining predictions from randomforest (RF), maxent (MAXENT), boosted regression tree (BRT), and a hierarchical Bayesian generalized linear mixed effects model (BAYES; see Appendix B for model specifications) to construct different SDMs using the dismo (Hijmans et al. 2017) and rstanarm packages (Goodrich et al. 2019) in R version 3.5.1. These models were selected to reduce the likelihood of overfitting my data and to balance model performance and accuracy (Marmion et al. 2009). SDMs were initially built for adults and juveniles separately but later aggregated due to limits on data. Thus, I present SDMs based on all sites with earthworms, casts, or their burrows 'present' versus 'absent'. I did not use pseudo-absences as doing so reduced model fit. However, I 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 taken as the AUCweighted mean of each component model (wherein all models had an average AUC ≥ 0.70).

I used likelihood ratio tests and G-statistics to test if the occurrence of earthworms was correctly predicted by an ensemble model. I delineate refuges from suitable earthworm habitat by applying 30% thresholds to the ensemble model wherein pixels were classified as refuges when the probability of earthworms occurring fell below 30% or was above 70% in the case of suitable habitat. I then calculated the proportion of quadrats surveyed within a predicted refuge that were in fact invaded by earthworms. Likewise, I determined the proportion of quadrats surveyed in suitable habitat that lacked any evidence of earthworm occurrence.

I 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. I 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 landuse as random effects. Finally, I tested for interactions between earthworm occurrence and every fixed effect based on *a priori* hypotheses and present the best model identified by AICc.

3.3 Results

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, I observed 2.2 ± 0.17 earthworms per quadrat in occupied sites (maximum = 9).



Figure 3.1. 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 (Appendix C). On average, the least suitable earthworm habitat occurred in shallow, dry soils on steep terrain.

Earthworms were detected most often in areas with deep, moist soils, low or no slope, nearer to roads and trails, and in forests (Figure 3.1). 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 (Appendix C). 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 3.1A). I found weaker relationships of soil moisture and slope on earthworm occurrence (Figure 3.1B & C). In general, steep terrain promotes soil erosion and surface water run-off. Contrary to predictions (Table 3.1), roads and trails had relatively weak effects on occurrence. These findings imply that earthworms are limited by rugged terrain and is consistent with the hypothesis that natural refuges from invasion exist due to heterogenous habitat.

A weighted ensemble model discriminated among sites best (AUC = 0.93), and suggests a mosaic of suitable habitat for earthworms as well as refuges wherein they are unlikely to occur (Figure 3.2). Implied refuges were most common in the southeastern portion of Sidney Island, as delineated in Figure 3.3. In these predicted refuges, only 2.4% of 123 quadrats had evidence of earthworms, as compared to 96% of 50 quadrats in sites not predicted to be refuges (*G*= 164.81, df = 1, p < 0.001).

Earthworm presence reduced plant species richness across habitat types ($\chi^2 = 5.75$, df = 1, p = 0.017). The number of plant species found 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). Although soil depth and earthworms did interact to affect species richness ($\chi^2 = 4.59$, df = 1, p = 0.032), no clear pair-wise differences were observed between invaded and uninvaded sites. Similarly, I found no differences for heat load and its interaction with earthworms. All other edaphic variables were dropped from the final model.



Figure 3.2. Predicted probability of detecting non-native earthworms on Sidney Island, BC. Lighter, bright shades indicate a lower probability of occurrence. Open black circle are sampling points where I did not detect earthworms while open white circles show positive detections. Solid black lines are road networks and dashed lines are trails.



Figure 3.3. 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 earthworm occur in a light brown color (< 30% predicted occurrence) and where earthworms are most likely to be found in dark, brown (> 70% predicted occurrence).

3.4 Discussion

My results show that non-native earthworms threaten deep soil Garry Oak meadows and emphasize the conservation value of shallow soil savannas that are resistant to invasion. Moreover, because the invasion history of earthworms is closely linked to human development (Arcese and Rodewald 2019), prioritizing remote protected areas on small islands represents one potential strategy to conserve biodiversity in the Georgia Basin. Specifically, I showed that the distribution of earthworms is restricted by shallow, dry soil and steep terrain that characterize refuges. Furthermore, I found that the presence of earthworms reduced plant species richness independent of habitat type. Together these results suggest that earthworms undermine recovery efforts in deep soil meadows by simplifying plant communities, but shallow soil refuges remain intact.

3.4.1 Refuges from invasion

I used species distribution models 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 of the Pacific Northwest of North America. On average, refuges had shallow soil (<12 cm) and were on steep terrain that naturally shed water, such as in broad-leaved savanna and maritime meadow habitats (Figure 3.1). Consequently, these refuges are highly vulnerable to drought-stress during summer months, which is associated with reduced earthworm survival rates (Eggleton et al. 2009). However, connectivity across this depth-moisture gradient is strongly dependent on seasonality; during the rainy season (October – March) the landscape is more connected and earthworms may disperse into or through habitat patches that are unsuitable for long-term persistence (Vasudev et al. 2015). In contrast, deep soil sites (> 12 cm) and those in coniferous forests can protect earthworms from high temperatures and desiccation (Potvin and Lilleskov 2017). Once established earthworms are unlikely to be extirpated from such sites. These results are consistent with my prediction that Garry Oak and maritime meadow habitats occur along a soil depth-moisture gradient that determines their resistance to invasion by earthworms.

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Previous research has shown that earthworm occurrence declines with increased distance to roads and trails but neither feature was strongly associated with earthworm occurrence on Sidney Island (Appendix C; Cameron and Bayne 2009, Paudel et al. 2016). Schneider et al. (2016) cautioned that the performance of distribution models may decline when comparing earthworms across functional groups. Cameron and Bayne (2014) noted that spatial links between earthworms and roads should weaken as invasions 'mature' and non-native species become limited in their distribution by environmental factors or resource limitations. A long history of Non-indigenous colonization, agriculture, and habitat conversion on Sidney Island and empirical findings showing that human settlement is a precondition for detecting earthworms on other islands in the region (Arcese and Rodewald 2019) both indicate that earthworms are likely to have been present on Sidney Island for a century or longer. My results are therefore consistent with the notion that earthworms now occur on Sidney Island in most suitable habitat patches available to them, but remain largely absent from many small but semi-isolated patches of refugial habitat where dispersal limitation or desiccation preclude their colonization or population persistence, respectively (Figure 3.2, 3.3).

3.4.2 Earthworms reduce plant species richness

Plant communities with earthworms present had lower species richness, independent of habitat type (Figure 3.2). 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), and much less intensive surveys of nearby islands (Arcese and Rodewald 2019). Eisenhauer et al. (2010) show that earthworms change the composition of soil seedbanks and that seed and seedling size are defining characteristics affecting a species' vulnerability to depredation by earthworms. Similarly, Dobson and Blossey (2015) found that

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earthworms alter forest plant communities by reducing seedling survival in 12 species. My observation of a decline in species richness where earthworms were present was expected given the analyses above, but they extend those results by demonstrating similar effects in relatively intact deep-soil Garry oak and coastal Douglas-fir (*Pseudotsuga douglasii*) forests of the Georgia Basin (Bohlen et al. 2004, MacDougall et al. 2004).

3.4.3 Implications for conservation planning

Systematic conservation planning has been rapidly adopted by decision scientists to determine the most cost-effect conservation strategies (McIntosh et al. 2017). Spatially explicit SDMs can be excellent tools to predict how species will be distributed based on current or future conditions (Guisan and Thuiller 2005), explore connectivity, and optimize conservation plans (see also Domisch et al. 2019). Applying such tools to non-native earthworms should therefore improve predictions about the dynamics of earthworm invasions in insular and forested habitat globally (Hale et al. 2006). In the Georgia Basin, isolated meadows on small islands harbor more rare and endangered species than do large islands or highly connected landscapes, on average, due largely to their isolation from disturbance by moderns humans and commensal species (Best and Arcese 2009, Martin et al. 2011, Bennett and Arcese 2013). My results demonstrate that shallow soil meadows appear robust to invasion by non-native earthworms, which may therefore represent refuges from their deleterious impacts on species richness and community composition in Garry oak and maritime meadow habitats of high conservation value in Canada (Parks Canada Agency 2006a, 2006b). My results also suggest that deep-soil sites are much more likely to experience invasion and species loss in coastal Douglas-fir and Garry oak forests of the Pacific Northwest of North America. The presence of earthworms in deep-soil Garry oak forests may compound ecological changes caused by pre-existing disturbances including historic fire

exclusion, Douglas-fir encroachment, and overabundant herbivores (Arcese et al. 2014, Pellatt and Gedalof 2014). Systematic conservation plans are unlikely to meet their goals when known threats are left unaccounted, particularly in the case of invasive ecosystem engineers with the potential to alter ecosystem processes and community composition at multiple trophic levels (e.g., Ferlian et al. 2018, Frelich et al. 2019). As a result, the ability to quantify earthworm impacts will be equal to, if not exceeded by, the capacity to predict where they will invade next and to determine whether natural barriers exist that will allow native plant populations to persist.

Chapter 4: Conclusions

4.1 Implications

Non-native earthworms can dramatically alter ecosystem structure and function across Earth's biomes (Frelich et al. 2019). As a result, the invasion of European earthworms into historically earthworm-free territories, such as North American boreal forests and coastal islands, has been identified as an emerging global threat to biodiversity (Sutherland et al. 2011). In these ecosystems, earthworms have been shown to promote CO₂ emissions from disturbed soil, reduce soil organic matter, and lower native plant species diversity. Frelich et al. (2006) showed that the glacial refuges being invaded are among the most important global carbon storages left on earth and harbor some of the last untouched wilderness for biological conservation. Saltmarsh et al. (2016) found that non-native earthworms were often present near roads and boat launches in a relatively undisturbed wildlife refuge in Alaska and suggested prohibiting *Lumbricus* spp. earthworms from being used as bait to limit further spread. As a consequence, there is an urgent need for data on the effects non-native earthworms have on the plant communities they invade, as well as the edaphic limits, or geographic barriers potentially available to limit their spread or influence

In this thesis, I used experimental mesocosms combined with plant and earthworm surveys to elucidate the ways in which non-native earthworms are altering critically threatened Garry oak and maritime meadow plant communities. By combining experimental tests of literature-derived hypotheses with detailed field surveys, I was able to speculate how plants with small seeds and taproots are more susceptible to the negative effects associated with earthworms. Moreover, I showed that species-specific conservation efforts may not be enough to protect Garry oak and maritime meadow plants that are most sensitive to earthworms. Furthermore, I

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show that the presence of earthworms was associated with reduced plant species richness, but some habitats appear to be naturally resistant to invasion. Garry oak meadows that have shallow, dry soil and rugged terrain were effective refuges from the negative effects of earthworms. Overall, this thesis provides evidence that earthworms influence plant community assembly by differentially affecting survival based on seed and root morphology and shows that the shallowsoil meadows most frequently found on small, isolated islands are robust to invasion by nonnative earthworms.

4.2 Key finds, limitations, and future steps

In Chapter 2, I assessed the effect of non-native earthworms on seedling survival for 12 plant species found in threatened Garry oak and maritime meadows. I found that the presence of earthworms reduced seed and seedling survival and those changes translated into simplified plant communities. Earthworms tended to reduce species abundance, richness, evenness, and diversity in multi-species mesocosms. In general, species with large seeds and fibrous roots dominated communities with earthworms present, whereas species with small seeds and taproots only persisted in multi-species mesocosms without earthworms. My findings suggest that earthworms act as ecological filters in the early stages of invasion to shape community composition based on plant morphological traits. Although these results offer insight into some of the plant traits being influenced by earthworms, it is far from comprehensive. This study design could be used as a template for experiments using a larger number of species and traits to develop generalizable predictions of how plant community composition changes as a result of non-native earthworm.

In Chapter 3, I used species distribution models to identify natural refuges in endangered in Garry Oak and maritime meadow plant communities that could resist invasion by non-native earthworms. In general, isolated meadows on small islands have a greater abundance of rare and endangered species than those on large islands or highly connected landscapes in the Georgia Basin due to their insulation from disturbance by moderns humans and commensal species (Best and Arcese 2009, Martin et al. 2011, Bennett and Arcese 2013). I found that shallow-soil meadows reduce the occurrence and distribution of non-native earthworms and so may act as refuges for susceptible plant species from non-native earthworms. In contrast, deep-soil meadows and coastal Douglas-fir forests are much more likely to experience species loss due in part to the effects of non-native earthworms. I also observed that plant species richness was lower in habitats invaded by earthworms, which provides further support for conclusions in Chapter 2. The ability to identify natural refuges is an important advancement for conservation planning, however it remains unclear whether these patterns are found throughout the whole of the Gulf Islands or just where I surveyed. My results and inferences could be improved with a great sampling effort on other islands that vary with size, human colonization history, and land management. Additionally, my results were built using higher-resolution geospatial data than is publicly available which may limit where these inferences can be applied. As higher-resolution spatial data enters the public domain, my results offer a methodology for incorporating the presence of non-native earthworms into conservation planning across North America.

This thesis takes a holistic approach to understanding the causes and consequences for ecosystems invaded by non-native earthworms and provides a framework for improving existing conservation plans in the Pacific Northwest of North America. The highly threatened plant species of the Garry Oak and maritime meadow communities face numerous other socioecological pressures that define and constrain most conservation problems but remain outside the scope of this thesis (Parks Canada Agency 2006a, 2006b). However, this research is the first step

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toward the ability to recognize and proactively account for the invasion of non-native earthworms in threatened plant communities worldwide.

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Appendix A. Model selection tables for chapter 2

Table A.1 Top performing monoculture models vary based on survey phase. Tables are ordered by the experimental phase being tested starting at the top with surveys taking place during the germination phase (A), followed by the establishment phase (B), and for the full experiment (C).

	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)
date	16.55	16.55	1	3,105	6,446.1	>0.001
species	25.73	2.34	11	1,122	910.9	>0.001
earthworms	0.04	0.04	1	1,122	16.7	>0.001
date:species	17.34	1.58	11	3,105	613.8	>0.001
date:earthworms	0.04	0.04	1	3,105	14.3	>0.001

A - Germination (Nov 23-Feb 15)

	Sum Sq	Mean Sq	NumDF	DenDF	F value	e Pr(> F)
date	0.33	0.33	1	2,586	52.3	>0.001
species	13.39	1.22	11	513	194.4	>0.001
earthworms	0.06	0.06	1	214	9.7	0.002
date:species	4.71	0.43	11	2,586	68.4	>0.001
species:earthworms	0.20	0.02	11	214	2.9	0.001

B - Establishment (Feb 15 - Jun 27)

C - Full experiment (Nov 23-Jun 27)

	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)
date	32.20	32.20	1	5,932	3,646.6	>0.001
species	35.50	3.23	11	214	365.5	>0.001
earthworms	0.08	0.08	1	214	9.5	0.002
date:species	22.74	2.07	11	5,932	234.1	>0.001
date:earthworms	0.09	0.09	1	5,932	10.7	0.001
species:earthworms	0.22	0.02	11	214	2.2	0.01
date:species:earthworms	0.43	0.04	11	5,932	4.4	>0.001

Table A.2 Top performing monoculture models predicted by treatment and traits. Tables are ordered by the experimental phase being tested starting at the top with surveys taking place during the germination phase (A), followed by establishment (B), and full experiment (C).

	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)
origin	0.01	0.01	1	7	1.69	0.24
lifecycle	0.02	0.02	1	7	2.26	0.18
root	0.01	0.01	1	7	1.29	0.29
seed size	0.001	0.001	1	7	0.10	0.76
earthworms	0.03	0.03	1	3,332	3.50	0.06

A - Germination by traits (Nov 23-Feb 15)

B - Establishment by traits (Feb 15 - Jun 27)

	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)
origin	0.03	0.03	1	7	3.23	0.12
lifecycle	0.01	0.01	1	7	1.58	0.25
root	0.04	0.04	1	7	5.63	0.05
seed size	0.0000	0.0000	1	7	0.005	0.95
earthworms	0.40	0.40	1	2,814	51.07	>0.001
root:earthworms	0.09	0.09	1	2,814	11.81	0.001
seed:earthworms	0.09	0.09	1	2,814	11.31	0.001

C -	Full	experiment	by	traits	(Nov	23-Jun	27)
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	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)
origin	0.03	0.03	1	7	2.67	0.15
lifecycle	0.02	0.02	1	7	1.94	0.21
root	0.04	0.04	1	7	3.64	0.10
seed size	0.0004	0.0004	1	7	0.03	0.86
earthworms	0.31	0.31	1	6,158	29.42	>0.001
root:earthworms	0.06	0.06	1	6,158	6.12	0.01
seed:earthworms	0.06	0.06	1	6,158	5.43	0.02

Table A.3 Top performing community model predicted by traits during the final census. Traits vary in their ability to predict the relative difference in establishment in community mesocosms.

	v		v			
	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)
origin	571.57	571.57	1	594	8.85	0.003
lifecycle	1,895.08	1,895.08	1	594	29.33	>0.001
root	3,959.18	3,959.18	1	594	61.28	>0.001
seed	1,680.94	1,680.94	1	594	26.02	>0.001
earthworms	11.94	11.94	1	64	0.18	0.67
root:earthworms	252.56	252.56	1	594	3.91	0.05
seed:earthworms	705.76	705.76	1	594	10.92	0.001

Community trait selection by earthworms



Appendix B. Spatial and statistical models for chapter 3

Figure B.1. Soil depth sampling locations marked by open black circles overlaid on the krigged raster surface of soil depth. Gray, hashed areas indicate spaces that were inaccessible during sampling due to property restrictions.

Occurance ~ *Binomial*(1, p_i)

$$\begin{split} logit(p_{i}) &= \alpha + \alpha_{landuse[i]} + \beta_{1}depth + \beta_{2}slope + \beta_{3}twi + \beta_{4}roads + \beta_{5}trails \\ & \alpha \sim Normal(0,1) \\ & \beta_{1 \rightarrow 5} \sim Normal(0,10) \\ & \alpha_{landuse} \sim Normal(0,\sigma_{landuse}) \\ & \sigma_{landuse}, \sim HalfCauchy(0,1) \end{split}$$

Figure B.2. Model specifications for a hierarchical bayesian generalized linear mixed effects model (BAYES). I use a multilevel binomial model to predict the probability of earthworm occurrence with varying intercepts for each landuse class. α is the log-odds of detection across all sample sights. I used a weakly informed normal prior centered at 0 with a standard deviation of 10 for each predictor variable. Last, I specify that the variance for landuse should be allowed to vary based on class, and it does so using a generic weakly informative half cauchy prior with a mode of 0 and scale parameter of 1.



Figure B.3. Variable importance for each machine learning model developed to understand the relationship between earthworm occurrence and environmental conditions. Variable importance was not computed for the bayesian model due to impracticalities. Avg represents a mean-weighted average across models using AUC scores as weights. Importance is scaled between 0-100% to make relative comparisons between component models.

Table B.1. Plant species richness in relation to the presence of non-native earthworms, soil depth, and heat load across Sidney Island (n=300) accounting for habitat and plot-level effects. It appears that non-native earthworms are associated with reduce plant species richness independent of habitat type and plot effect.

	Plant species richness						
Predictors	Beta	std. Error	CI	р			
(Intercept)	1.00	0.31	0.39 – 1.61	0.001			
earthworms	-1.58	0.67	-2.890.28	0.018			
soil depth	-0.04	0.01	-0.060.03	<0.001			
heat load	0.56	0.34	-0.11 - 1.23	0.103			
earthworms x soil depth	0.03	0.01	0.00 - 0.05	0.032			
earthworms x heat load	1.85	0.97	-0.05 - 3.74	0.056			
Random Effects							
σ^2	0.37						
τ ₀₀ plot-level (n=100)	0.04						
τ ₀₀ landuse (n=6)	0.14						
N	300						
Marginal R ² / Conditional R ²	0.137	/ 0.412					




Figure C.1. Individual SDM predictions of earthworm occurrence on Sidney Island, BC. (A) The Bayesian hierarchical model had the highest model accuracy with an AUC of 0.81, (B) Boosted regression tree scored 0.8, (C) Maxent was 0.73, and (D) Random Forest was 0.80