

Predicting spatial extent of invasive earthworms on an oceanic island

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ABSTRACT

Aim Invasions of non-native earthworms into previously earthworm-free regions are a major conservation concern because they alter ecosystems and threaten biological diversity. Little information is available, however, about effects of earthworm invasions outside of temperate and boreal forests, particularly about invasions of islands. For San Clemente Island (SCI), California (USA) – an oceanic island with numerous endemic and endangered plant and vertebrate species – we assessed the spatial extent and drivers of earthworm invasion and examined relationships between earthworms and plant and soil microbial communities.

Location San Clemente Island, southern California, USA.

Methods Using a stratified random sampling approach, we sampled earthworms, vegetation, soils and microbial communities across SCI. We examined the relationship between the presence of invasive earthworms and soil and landscape variables using logistic regression models and implemented a spatial representation of the best model to represent potential site suitability for earthworms. We evaluated the relationship between invasive earthworms and vegetation and microbial variables using ANOVA.

Results We found that the likelihood of encountering earthworms increased close to roads and streams and in high moisture conditions, which correspond to higher elevation and a north-eastern aspect on SCI. The presence of earthworms was positively associated with total ground vegetation cover, grass cover and non-native plant cover; however, there was no significant relationship between earthworms and microbial biomass. These results suggest that the earthworm invasion on SCI is at an early stage and closely tied to roads and high moisture conditions.

Main conclusions Climatic variables and potential sources of earthworm introduction and dispersal (e.g. roads and streams) should be broadly useful for predicting current and future sites of earthworm invasions on both islands and continents. Furthermore, the significant positive relationship between non-native plant cover and invasive earthworm presence raises the possibility of an emerging invasional 'meltdown' on SCI. Additional study of earthworm invasions on human-inhabited oceanic islands is necessary to identify additional invasions and their potential for negative impacts on unique insular biota.

Keywords

invasive earthworms, island, microbial community, moisture, roads, vegetation.

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INTRODUCTION

Earthworm invasion into previously earthworm-free regions has become a major concern for the conservation of rare or otherwise sensitive native species, for plant and vertebrate communities, and for entire ecosystems (Gundale, 2002; Hale *et al.*, 2006; Nuzzo *et al.*, 2009). Because of these effects, Sutherland *et al.* (2011) identified earthworm invasions as a top 15 emerging global issue for biodiversity conservation. Invasive earthworms have substantially altered plant community structure in temperate and boreal forests of northern North America (Hale *et al.*, 2006; Holdsworth *et al.*, 2007a; Nuzzo *et al.*, 2009; Drouin *et al.*, 2016), and population declines and extirpations of sensitive plant species (e.g. the Goblin Fern [*Botrychium mormo*]) have also been linked to these invasions (Gundale, 2002; Hale *et al.*, 2006; Dávalos *et al.*, 2015).

Earthworm-caused plant community change arises from earthworm consumption of the leaf litter layer (Bohlen et al., 2004; Frelich et al., 2006) and alteration of the seed bank (Nuzzo et al., 2015), soil structure, nutrient cycling (Bohlen et al., 2004; Resner et al., 2015) and arbuscular mycorrhizal fungi (AMF; Lawrence et al., 2003; McLean et al., 2006). Changes to soil and plants can cascade to reduce populations of native ground-dwelling amphibians (Maerz et al., 2009) and songbirds (Loss & Blair, 2011). Invasive earthworms may also facilitate invasions of non-native plants (Nuzzo et al., 2009; Clause et al., 2015; Roth et al., 2015), and this parallel invasion could have synergistic ecological impacts (Simberloff, 2011) a characteristic of an invasional 'meltdown' (Simberloff & Von Holle, 1999). Despite the farreaching effects of invasive earthworms, very little information exists about their impacts outside of deciduous and boreal forests of North America. No prior study has systematically quantified the spatial extent and ecological impacts of invasive earthworms in the western United States or on offshore oceanic islands in particular.

Oceanic islands support high rates of endemism and are globally important for biodiversity conservation. Island ecosystems are among the most vulnerable to biological invasions due to the characteristics of the species inhabiting them, including isolation, restricted distribution, reduced competitive ability and few natural predators or disturbances (Elton, 1958; Vitousek, 1988). Invasive non-native species have endangered and/or caused the extinction of many native and endemic species on islands (Simberloff, 1995). On San Clemente Island (SCI), California, the recent discovery of earthworms is a cause for a conservation concern because the island harbours several endemic and endangered plant and animal species. The documented adverse effects of invasive earthworms in other regions suggest the possibility for similar effects on SCI's unique and threatened plants and animals.

We conducted an extensive earthworm survey on SCI to address the following objectives: (1) quantify and model the spatial extent and correlates of invasive earthworm distribution, and (2) assess whether invasions are associated with vegetation and soil microbial communities. Addressing these objectives is useful both for informing conservation efforts on SCI and for contributing to broadened understanding of the introduction modes and impacts of invasive earthworms on other human-inhabited oceanic islands.

METHODS

Study area

Our study area was SCI (118°30' W, 33°00' N), the southernmost of the California Channel Islands, located ~120 km north-west of San Diego, California, USA (Fig. 1). The island is under the management of the U.S. Navy, and several areas of the island including the southernmost portion of the island, the Shore Bombardment Area (SHOBA; Fig. 1), have limited access for research purposes due to naval training operations. SCI is 34 km long from north to south, ranges in width from 2.5 to 6.5 km from east to west and has a maximum elevation of ≈ 600 m a.s.l. The island has complex topography (a central plateau, a steeply sloping eastern side, gently sloping marine terraces on the western side and deep canyons dissecting both sides) and substantial spatial variability in temperature, wind, rainfall and fog (Moody, 2000). The island has no permanent fresh water source and experiences an arid Mediterranean-type climate characterized by wet winters and dry summers, and relatively little temperature variation throughout the year. SCI receives 168 mm of annual rainfall on average with most precipitation (95%) within the wet season of November to April (Yoho et al., 1999). However, the island and most of mainland California have been experiencing a historic drought since 2011 (Seager et al., 2015) and SCI received much lower than average annual precipitation during 2014–2015 (95 mm year⁻¹) (Helen Cox, SCI climate monitoring project, California State University Northridge, pers. comm., November, 2015). Soils are predominantly clayey and fine loamy with Vertisol morphology (Muhs et al., 2007).

The vegetation on SCI is primarily maritime desert scrub dominated by spiny and succulent plants (*Cylindropuntia prolifera*, *Lycium californicum* and *Opuntia littoralis*) and grassland dominated by invasive annuals *Avena barbata*, *A. fatua*, *Bromus diandrus*, *B. madritensis* and native perennial *Nassella* spp. The island harbours a large number of endemic plants (Schoenherr *et al.*, 1999), including federally endangered or threatened plant and animal species: SCI bushmallow (*Malacothamnus clementinus*), SCI Indian paintbrush (*Castilleja grisea*), San Clemente loggerhead shrike (*Lanius ludovicianus mearnsi*) and SCI Bell's Sparrow (*Artemisiospiza belli clementeae*).

Sampling design

In 2014 and 2015, we conducted field sampling during the wet season (between 3 February and 21 April), an expected peak period of earthworm activity. Sampling locations were





selected using a stratified random sampling (SRS) design implemented within ArcGIS (ESRI, 2014). We used a SRS rather than a completely randomized sample because the invasion appeared limited in extent, and we sought to ensure that at least some earthworms were found during the study. Plot locations were stratified based on the a priori assumption that earthworm invasion would be more likely near roads and water courses and in areas with high moisture and shallow slope (Suárez et al., 2006; Cameron et al., 2007; Holdsworth et al., 2007b; Shartell et al., 2013). We conducted stratification of sampling plots based on continuous distances from road edges and stream channel flowlines (distance classes for both variables were 0-25 m, 25-50 m, 50-100 m, and all points were > 5 m apart). Soil texture was an additional grouping factor that was collapsed into two categories (loams or clays) based on taxonomic classifications and physical properties listed in the Soil Survey Geographic soil association database (USDA NRCS, 1995). We excluded plots with slope > 10 degrees because steeper slopes are less likely to have earthworms (Suárez et al., 2006). A topographic wetness index (TWI; Wilson & Gallant, 2000) was calculated at each plot location (using slope, flow direction, precipitation amount and precipitation accumulation) to create a potential soil moisture grid to supplement linear hydrology data. Because low soil moisture reduces earthworm activity and detectability (Edwards, 2000), we excluded plots with TWI values in the lowest quartile. We randomly selected and sampled 336 total plots (n = 236 in 2014; n = 100 in 2015) that were distributed across SCI.

Earthworm sampling

Each sampling location consisted of a 3-m-radius circular plot. At each plot, we established two earthworm sampling subplots (each 33 cm \times 33 cm) within 1 m of the centre of each plot and located 180° opposite of each other at a randomly selected compass orientation. Earthworms were sampled by the hand-sifting approach (Holdsworth et al., 2007a). In each subplot, we removed the top 33 cm of soil and sifted it by hand while carefully searching for earthworms. We also recorded presence/absence of earthworm castings (i.e. droppings) because these generally indicate the actual presence of earthworms (Milcu et al., 2006; Shartell et al., 2013). In this study, unless noted otherwise, earthworm presence is defined as the direct observation of earthworms and/or the observation of earthworm casts. All collected earthworms were initially washed with 70% isopropyl alcohol and then stored in 10% buffered formalin. We used Schwert (1990) and assistance of a taxonomic expert (S. James) to identify all adult earthworms to species, while juveniles could only be identified to genus.

Vegetation and microbial community sampling

Within each plot and 2 m away from the plot centre, we established four $1-m^2$ vegetation sampling subplots (one in each cardinal direction). Within each subplot, we first visually estimated percentage cover of ground-layer vegetation (all plants except woody plants > 50 cm in height), then

estimated percentage cover of all non-native plants and all native plants and then separately estimated percentage cover of herbaceous plants, graminoids (grasses), woody plants < 50 cm and succulents. All percentage cover estimates were independent (i.e. any one plant could be included in multiple percentage cover estimates, as appropriate). Cover estimates were made in 10% increments (e.g. 0–10%, 10–20%, through 90–100%) by two independent observers, and estimates were averaged, first across observers within each subplot and then across subplots. Within a 3-m radius, we also estimated shrub density by counting the number of shrubs (woody stems > 50 cm in height and with diameter at breast height < 5 cm). There were no trees in any of our sampling plots.

To investigate the potential effects of invasive earthworms on relative abundances of microbial functional groups $(gram \pm bacteria and mycorrhizal/saprophytic fungi)$, we collected soil samples adjacent to all earthworm presence plots and an equivalent number of randomly chosen earthworm absence plots; soil types were comparable between earthworm presence and absence plots. At each soil sampling location, four 2 cm diameter × 10 cm deep soil cores were composited. Composited soil samples were stored at ~4 °C and shipped to the laboratory. In the laboratory, soil was freeze-dried, finely ground with a mortar and pestle and five grams of each sample was analysed for neutral lipid fatty acids (NLFAs) and phospholipid fatty acids (PLFAs). Fatty acids are components of cell membranes and generally constitute a relatively constant proportion of the biomass of an organism. NLFAs are the basic storage product of many fungi and serve as the primary energy reserve in fungi (Olsson et al., 1995). Our NLFA/PLFA analyses followed the protocol described in Williams et al. (2012). Individual NLFA/ PLFA data are reported as per cent of the total mole fraction (nmol per gram soil), which can be interpreted as relative abundance. Common non-specific fatty acid biomarkers were included in our analysis to express alterations in overall microbial biomass, although these cannot allow assessment of shifts of specific microbial community groups. Alterations in these profiles represent potential perturbation effects of earthworms on microbial communities, including mycorrhizal fungi (Bååth, 2003).

Derivation of environmental and spatial variables

GIS data were provided by Naval Facilities Engineering Command (NAVFAC) Southwest (SW) for road centrelines, hydrology, soils and buildings. GIS road geometry was redigitized to align with recent imagery and maps. For collateral data for roads, streams and other GIS data, we used 1-m imagery from the U.S. Department of Agriculture (USDA) National Agricultural Imagery Program (USDA, 2012) and GeoPDF 1:24,000 scale topographic maps (USGS, 2012). Water resource data were compared with hydrography data (USGS, 2013) to locate shorelines and stream channels. Landscape characteristics and environmental variables were extracted to sampling locations from grid data sets derived from a high-resolution 3-m digital elevation model (DEM; National Oceanic and Atmospheric Administration, NOAA, 2004). We incorporated average annual precipitation (1981-2010) from grid-based climate data (PRISM Group, 2014) and compared it against available SCI weather station data (California State University Northridge, 2013). Additional spatial data were acquired or derived for other moisturerelated variables, including aspect (i.e. geographic orientation of a slope measured in degrees) and insolation (i.e. amount of solar radiation received). Aspect was transformed (sin $(\theta + 45^{\circ}))$ into a continuous variable that represents an index of north-eastness, a variable that is a proxy for climatic conditions. Other DEM-derived covariates included elevation (metres above sea level) and slope gradient (degrees). Continuous raster surfaces were generated to replace distance class groups (for road and stream variables) used in the original SRS with actual straight-line (Euclidean) distances, and we used these for the following statistical analyses.

Statistical analyses

All statistical analyses were conducted in R (Team RC, 2014). Initially, we checked collinearity among all variables (climatic and topographic), and precipitation and elevation were the only strongly correlated variable pair (Pearson's correlation, r = 0.78). Because elevation data were available at a higher spatial resolution, we only used elevation for analysis. Also, TWI and soil texture classes did not perform well in preliminary analyses of model fit and dropped out during model development. Six final variables were used (Table 1) to estimate patterns of earthworm presence. Logistic regression models were created using the R package 'glmulti' (Calcagno & de Mazancourt, 2010; Calcagno, 2013). We defined a global logistic regression model of earthworm presence/absence that included all six final variables, and we also developed a nested suite of additive candidate models.

We used information-theoretic methods and multimodel inference (Burnham & Anderson, 2002) – specifically

Table 1 Variables used for logistic regression model of theoccurrence of earthworms on San Clemente Island, California,USA.

Environmental variables	Variable code	Unit	Source
Elevation above sea level	ELEV	Metres	NOAA, 3-m DEM
Slope gradient	SLOPE	Degree	NOAA, 3-m DEM
North-eastness	NE	Index	NOAA, 3-m DEM
Distance from streams	STREAM	Metres	NAVFAC SW; USGS NHD
Distance from main paved road	MAINRD	Metres	NAVFAC SW; USGS NHD
Distance from all roads	ALLRD	Metres	NAVFAC SW; USGS NHD

Akaike's information criterion corrected for small sample sizes (AIC_c) – to assess model selection uncertainty and rank the relative likelihood of models. Model support was inferred by evaluating differences in AIC_c values between the model of interest and the best model (Δi) and the relative strength of support for the model (ωi). As a rough rule of thumb, a value of $\Delta i \leq 2$ indicates models with a substantial level of empirical support; models with Δi between 2–4 have less support; Δi models with 4–7 have considerably less support; and models where $\Delta i > 10$ have essentially none (Burnham & Anderson, 2002). We list the ten highest-ranked models by AIC_c, and we implemented a spatial representation of the best model results and interpreted them as a potential site suitability model for earthworms.

To evaluate the relationship between invasive earthworm presence/absence (predictor variable) and vegetation variables (response variables), we performed a series of one-way ANOVA analyses. Due to logistic constraints, we had no vegetation data for five of the 2014 sampling plots and these were removed from ANOVA. Statistical significance was accepted at P < 0.05.

RESULTS

All earthworms found were species not native to continental North America. Eurasian taxa (all in family Lumbricidae; counts in parentheses) included *Aporrectodea caliginosa* (12), *A. rosea* (2), *A. trapezoides*, *Aporrectodea* spp. (66), *Octolasion* spp. (16) and several unidentified juveniles. We also found one South American earthworm taxa, *Microscolex* spp. (28) (family Acanthodrilidae). Non-native earthworms were directly observed in 17 (5.15%) plots and indirectly observed (i.e. observation of castings) in an additional 17 plots. Earthworms were therefore determined to be present in 34 plots (10.30%). Earthworm presence plots were scattered across the island near roads (Fig. 3); however, no earthworms were found in the south-east third of the island (i.e. south of the SHOBA boundary shown in Fig. 1).

When the relative importance of predictor variables over the full 10-model confidence set was estimated, model-averaged support was equally strong for variables related to moisture and distance to roads. All models included elevation and distance from the main paved road. Distance from all roads and distance from streams were in 70% of models, while slope gradient and north-eastness appeared in 40% of models. All variables were contained within the top four models as ranked by AICc (Δi for all ≤ 2 , Table 2). Applying the best-performing model, we created a map of site suitability for earthworms on SCI (Fig. 2).

We found significantly greater cover of total ground vegetation at earthworm presence plots compared to earthworm absence plots ($F_{1, 328} = 15.83$, P = 0.009; Fig. 3a). Likewise, we found greater average grass cover ($F_{1, 328} = 12.45$, P < 0.01; Fig. 3b) and non-native plant cover ($F_{1, 328} = 5.32$, P = 0.02; Fig. 3c) at earthworm presence plots compared to earthworm absence plots. However, earthworm presence was not statistically related to shrub density or herbaceous, succulent, or woody cover (P > 0.05; see Fig. S1). Earthworm presence was not significantly associated with any of the microbial functional groups (gram \pm bacteria, saprophytic/ mycorrhizal fungi) or overall microbial biomass (P > 0.05; see Fig. S2).

DISCUSSION

Spatial distribution and correlates of earthworm invasion

We documented a patchy pattern of earthworm distribution on SCI. We also found that areas close to paved roads and stream channels and characterized by high elevation and north-east orientation are particularly vulnerable to earthworm invasion. Despite the patchy nature of our earthworm observations, incorporating information about the above correlates into a spatially explicit model indicates that a large portion of SCI has the conditions that may facilitate earthworm introduction and/or persistence (i.e. proximity to roads/streams and/or adequate moisture conditions, as captured by high elevation; Fig. 2).

As suggested in studies from previously glaciated northern forests (Cameron *et al.*, 2007; Holdsworth *et al.*, 2007b; Costello *et al.*, 2011; Shartell *et al.*, 2013) and oceanic islands

Model	AIC _c	Δi	ωi	K	Predictor variables
1	230.154	0.000	0.2757	4	STREAM + ALLRD + MAINRD + ELEV
2	231.341	1.187	0.1523	5	STREAM + ALLRD + MAINRD + ELEV + NE
3	231.462	1.308	0.1433	3	ALLRD + MAINRD + ELEV
4	232.197	2.043	0.0992	5	STREAM + ALLRD + MAINRD + ELEV + SLOPE
5	232.675	2.521	0.0782	3	STREAM + MAINRD + ELEV
6	232.692	2.538	0.0775	4	ALLRD + MAINRD + ELEV + NE
7	233.383	3.229	0.0549	6	STREAM + ALLRD + MAINRD + ELEV + NE + SLOPE
8	233.504	3.35	0.0516	4	ALLRD + MAINRD + ELEV + SLOPE
9	234.107	3.953	0.0382	4	STREAM + MAINRD + ELEV + NE
10	234.636	4.482	0.0293	4	STREAM + MAINRD + ELEV + SLOPE

Table 2 Model selection results of earthworm presence on San Clemente Island, California, USA.



in Macaronesia (Talavera, 2011), the relationship of earthworm invasions with roads and water bodies on SCI likely reflects an association with the earthworms' point of original introduction. Invasive earthworms in forests are likely to be introduced and dispersed by vehicle tyre treads along roads and by dumping of fishing bait at the edges of roads and water bodies (Gundale et al., 2005; Tiunov et al., 2006). On SCI, the association between earthworms and roads could reflect a combination of the above vehicle dispersal mechanisms and the favourable soil moisture conditions along roadsides. During occasional heavy rainfall events on SCI, earthworms are likely to be passively dispersed as surface water generally runs off along roadsides until it reaches and runs off into streams. In support of this explanation, we anecdotally (i.e. outside of formal surveys) observed earthworms along gravel shoulders of paved roads in several locations following a heavy rainfall in late February 2014 (S. Paudel, pers. obs.). Because rainwater runs off along roads, in roadside ditches, and ultimately into streams, these features remain wetter for a longer period of time and may be better able to support earthworm persistence and spread once colonization occurs (Edwards, 2000; Costello et al., 2011). The tendency of streams and surrounding areas to provide suitable reservoirs of propagules for future invasions has been previously noted for invasive plants (Parendes & Jones, 2000). The documented affinity of earthworm invasions with moist high elevation areas and north-east-facing slopes in this study and previous studies (Talavera & Perez,



2007; Shartell *et al.*, 2013) further stresses the importance of moisture for supporting introduction and persistence of earthworm invasions. Moisture limitation may be particularly severe on SCI because the island has no permanent fresh water source and has been in severe drought since 2011 (Seager *et al.*, 2015).

Our results suggest that SCI's earthworm invasion occurred recently and is still in its initial stages. Support for this hypothesis is provided by (1) our observation of earthworms at a relatively small number of sampling points in close proximity to streams and roads, both likely points of initial earthworm invasion, (2) a lack of observations of any earthworms during archaeological excavations throughout the island over the last 35 years (Dr. Andy Yatsko, Archaeologist, U.S. Navy; pers comm.) and (3) the very recent first incidental observation of earthworms in Spring 2013 (Emily Howe, Botanist, SCI Botany Program; pers comm.). We are not certain how earthworms from Europe and South America first arrived on SCI. However, we speculate that they may have been introduced in 2008-2009 when topsoil was brought from mainland California to construct the island's paved main road. Consistent with this explanation, all earthworm presence points were located north-west of the SHOBA boundary (Fig. 1), the point south of which the paved road was not constructed. Further, four of the five earthworm species we documented (A. caliginosa, A. rosea, A. trapezoides and Microscolex spp.) have previously been found in mainland California (Fonte et al., 2009; Clause



Figure 3 Comparison of (a) total ground vegetation cover (%), (b) grass cover (%) and (c) non-native plant cover (%) between plots with and without earthworms present on San Clemente Island, California, USA; as indicated by lowercase letters, differences were statistically significant.

et al., 2015), the ostensible source of soil for the roadbed construction in 2008–2009.

Relationships between earthworms and vegetation cover and microbial communities

Our results suggest the possibility for a facilitative interaction between invasive earthworms and non-native plants on SCI. This facilitative relationship may also explain the positive relationships we found between earthworm presence and total ground vegetation cover and between earthworm presence and grass cover. The latter two relationships were surprising in the light of consistent reports of an inverse relationship between invasive earthworms and understory vegetation cover in forested regions (Hale et al., 2006; Holdsworth et al., 2007a; Drouin et al., 2016). Support for the facilitative interaction hypothesis is provided by the strong correlation in our data of non-native plant cover with both overall vegetation cover and grass cover, as well as our observation that several non-native invasive grass species (Avena barbeta, A. fatua and B. diandrus) dominated the vegetative cover at most of the locations where earthworms were found.

Previous research has documented a positive association between invasive earthworms and invasive plants, including a study in a mainland California grassland invaded by *Bromus* spp. and *Festuca* spp. (Clause *et al.*, 2015) and studies of forest ecosystems with non-native buckthorn (*Rhamnus cathartica*; Heneghan *et al.*, 2007; Roth *et al.*, 2015). The direction of causality in our and all previous studies remains largely unclear. However, Nuzzo *et al.* (2009) provided strong evidence that European earthworms are the driving mechanism behind the invasion of three invasive plants (*Alliaria petiolata, Berberis thunbergii* and *Microstegium vimineum*) that substantially change forest understories of the north-eastern USA. Potential explanations for the relationship between earthworms and invasive grasses on SCI include the following: (1) non-native earthworms and their associated changes to the soil and soil microbial community (Lawrence et al., 2003; Dempsey et al., 2013; Paudel et al., 2016) facilitate plant invasions, (2) seed ingestion and subsequent casting by invasive earthworms facilitate germination and establishment of invasive plants (Clause et al., 2015), (3) invasive plants alter the soil or produce nutrient-rich leaf litter in a way that promotes establishment and spread of earthworm invasions (Belote & Jones, 2009) or (4) invasive plants and invasive earthworms are not linked mechanistically, but rather both are associated with high moisture levels and dispersal corridors and therefore tend to occur in the same areas. Consistent with our fourth statement, although results are not presented here, we found substantially higher cover of grasses and non-native plants in close proximity to the areas associated with high moisture and dispersal corridors (S. Paudel, J.C. Benavide, B. Macdonald, T. Longcore, G. Wilson and S.R. Loss, in prep.). Nevertheless, these explanations are not mutually exclusive and multiple mechanisms may be occurring. Additional studies that sample for earthworms at a randomized and replicated sample of wet and dry areas and in areas with and without invasive plants, invasive earthworms and a well-developed litter layer are necessary to disentangle the causal relationships between invasive earthworms and invasive plants.

Our results provide no evidence that non-native earthworms have altered microbial communities on SCI. Previous studies have reported negative effects of invasive earthworms on AMF that likely mediate earthworm-associated changes in plant community structure (Lawrence *et al.*, 2003; Hale *et al.*, 2006; McLean *et al.*, 2006). Lawrence *et al.* (2003) found that the invasion of European earthworms into northeastern U.S. forests disrupts the mutualistic association between AMF and sugar maple (*Acer saccharum*) seedlings and increases prevalence of non-mycorrhizal invasive plants.

In some cases, however, earthworms may assist the dispersal of AMF spores, increase AMF abundance and root colonization (Gange, 1993; Ma et al., 2006) and increase soil bacterial biomass, which can bring about ecosystem-level changes in nutrient cycling (McLean et al., 2006; Dempsey et al., 2013). Here, we provide further evidence of the complex interactions between invasive earthworms and soil microbial communities (Paudel et al., 2016); these interactions likely depend on earthworm life history (i.e. the soil layers inhabited and substrates consumed), soil type, available soil nutrients, time since invasion (McLean et al., 2006) and climate (Edwards, 2000). Notably, drought conditions can alter fungal community structure and diversity (Toberman et al., 2008), reduce AMF colonization to roots (Augé, 2001) and change microbial structure and functions (Hueso et al., 2012). Thus, we suggest that the persistent drought in southern California could have greatly decreased soil microbial activity at all locations we sampled (regardless of earthworm presence). The relatively short history of earthworm invasion on SCI could also mean that noticeable impacts on microbial communities have not yet emerged.

Conservation implications

The positive relationship we document between invasive earthworms and invasive plants is a cause for conservation concern because it could signify the onset of an 'invasional meltdown' (Simberloff & Von Holle, 1999). Such earthworm-involved invasional meltdowns have been previously described (Maerz et al., 2009; Heimpel et al., 2010; Clause et al., 2015). The earthworm invasion on SCI is unique in that it appears to be in an early stage and therefore may be more easily manageable than in other regions that have had invasive earthworms present since European settlement. Experimental research to test and implement environmentally friendly earthworm control and removal methods has produced positive results (e.g. the application of tea seed oil extract at golf courses and airports; Potter et al., 2009; Seamans et al., 2015). However, additional research is needed in natural settings to clarify whether such approaches can be effective over large extents. In most instances, the complete eradication of invasive earthworms is unlikely to be feasible (Hendrix & Bohlen, 2002), and slowing the spread of earthworms, monitoring for effects that only arise after a time-lag period and preventing future invasions are the best available conservation techniques.

The correlates of earthworm invasion we document on SCI suggest potential intervention routes to prevent future earthworm introductions on other oceanic islands and in mainland areas. For example, invasive earthworm dispersal may be preventable by cleaning soil from tyre treads before moving vehicles between locations, especially after heavy rain events when large numbers of earthworms are at the surface. For construction activities that involve the movement of soil between locations (e.g. road building and landscaping), the source soil should be taken from known earthworm-free locations and/or inspected to ensure that no earthworms are present (it should be noted, however, that earthworm detectability rates can be low, especially in dry soil conditions). Monitoring for negative impacts may also be needed for plant and animal species that are in high-risk zones (e.g. areas with moist soil and along and near roads and stream channels). Finally, the distributions and ecological impacts of invasive earthworms should be regularly monitored on islands to avoid unexpected deleterious effects on endemic and endangered island species.

ACKNOWLEDGEMENTS

We thank the United States Navy for facilitating our work on SCI. Research was funded by the U.S. Department of the Navy, Commander Pacific Fleet through Cooperative Agreement number W9126G-13-2-0047 and by the Oklahoma Agricultural Experiment Station. We thank C. Hakseth and C. Mills for field assistance, E. Howe, E. Havstad and D. Mathews for plant identification assistance and B. Snyder and S. James for earthworm identification assistance. J. Rice and M. Booker provided discussion, insight and feedback both during implementation of the field survey and manuscript preparation. J. Coler provided logistic support and A. Yatsko cross-checked earthworm sampling points relative to sensitive archaeological sites. Finally, we are thankful to two anonymous referees for helpful comments on the manuscript.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Comparison of herbaceous, succulent, woody cover, and shrub density between plots with and without earthworms.

Figure S2 Comparison of gram-positive bacteria, gram-negative bacteria, saprophytic fungi, mycorrhizal fungi, and total microbial abundance between plots with and without earth-worms.

BIOSKETCH

Shishir Paudel is a postdoc researcher in the Department of Natural Resource Ecology and Management at Oklahoma State University, focusing on effects of belowground invasions on plant communities. He is a community ecologist, with primary research interest on biological invasion and plant community dynamics in wetland, uplands and islands.

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Editor: Anna Traveset