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Non-native earthworms promote plant invasion by ingesting seeds and modifying soil properties

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ABSTRACT

Earthworms can have strong direct effects on plant communities through consumption and digestion of seeds, however it is unclear how earthworms may influence the relative abundance and composition of plant communities invaded by non-native species. In this study, earthworms, seed banks, and the standing vegetation were sampled in a grassland of central California. Our objectives were i) to examine whether the abundances of non-native, invasive earthworm species and non-native grassland plant species are correlated, and ii) to test whether seed ingestion by these worms alters the soil seed bank by evaluating the composition of seeds in casts relative to uningested soil. Sampling locations were selected based on historical land-use practices, including presence or absence of tilling, and revegetation by seed using *Phalaris aquatica*. Only non-native earthworm species were found, dominated by the invasive European species *Aporrectodea trapezoides*. Earthworm abundance was significantly higher in the grassland blocks dominated by non-native plant species, and these sites had higher carbon and moisture contents. Earthworm abundance was also positively related to increased emergence of non-native seedlings, but had no effect on that of native seedlings. Plant species richness and total seedling emergence were higher in casts than in uningested soils. This study suggests that there is a potential effect of non-native earthworms in promoting non-native and likely invasive plant species within grasslands, due to seed-plant-earthworm interactions via soil modification or to seed ingestion by earthworms and subsequent cast effects on grassland dynamics. This study supports a growing body of literature for earthworms as ecosystem engineers but highlights the relative importance of considering non-native-native interactions with the associated plant community.

1. Introduction

Recent studies have focused on direct impacts of earthworms on plant communities via their ingestion and sometimes digestion of seeds. Earthworms aggregate seeds in their casts, which contain more viable seeds than in the surrounding soil (Decaëns et al., 2003). This ingestion is often species-specific with earthworms selecting seeds according to traits such as size or oil content (Clause et al., 2011; Grant, 1983) or by plant functional groups (Milcu et al., 2006; Zaller and Saxler, 2007). Seedlings that emerge from casts are likely to benefit from their higher nutrient content and physical protection (Bityutskii et al., 2012; Decaëns et al., 2003; Zhang and Schrader, 1993). The outcome in terms of seedling growth and survival should depend on the combination of plant and earthworm species (Eisenhauer et al., 2009a; Milcu et al., 2006). Thus, direct impacts of seed-earthworm interactions through seed ingestion are important for the composition and structure of plant communities (Forey et al., 2011).

Many grasslands are invaded by non-native plant species globally (Seastedt and Pyšek, 2011). Invasion by non-native earthworms can be an important factor of plant invasion because earthworms can negatively affect both soil and plant biodiversity patterns (Hale et al., 2008; Hendrix et al., 2008; Hendrix and Bohlen, 2002; Holdsworth et al., 2007). Non-native (=exotic) species are non-

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native to a region and have been introduced into a region through human activities. Through subsequent dispersal and population expansion, they can cause significant economic or environmental damages to incipient communities, thereby becoming invasive species (IUCN, 2000). One of the most documented ecosystem alterations by non-native earthworms is the modification of the northern American hardwood forests following the colonization by European earthworms (Frelich et al., 2006; Hale et al., 2005). Indirect impacts of earthworms on plant community via soil modifications have also often been reported (Eisenhauer et al., 2009b, 2007; Holdsworth et al., 2007; Nuzzo et al., 2009), but only two studies have focused on the direct impact of non-native, invasive earthworms on plant communities through seed ingestion (Drouin et al., 2014; Eisenhauer et al., 2009b). In the first study, the effects of invasive earthworms, *Lumbricus terrestris* and *Octoaedra tyrtaeum* on seedling emergence in American northern hardwood forests were examined (Eisenhauer et al., 2009b). The presence of the endogeic *O. tyrtaeum* significantly increased the emergence of all seedlings while the presence of the anecic *L. terrestris* increased the emergence of herb seedlings only. The second study showed that invasive earthworms reduce seed germination of seven species and survival of three species of trees in southern Québec (Drouin et al., 2014). Both studies showed an impact of non-native, invasive earthworms on the seed bank and standing vegetation.

Several mechanisms have been identified to explain a positive interaction between non-native earthworms and non-native plants. In disturbed systems, mutualisms and synergisms between non-native plant and non-native animal species impact both plant and animal communities (Catford et al., 2012; Mitchell et al., 2006; Richardson et al., 2000). These facilitative interactions include the predation of native species by generalist non-native predators (Mitchell et al., 2006; Parker et al., 2006) or the modification of the environment physico-chemical properties (Didham et al., 2007; see Mitchell et al., 2006). The interactions between non-native species, and with their physico-chemical environment can lead to positive feedback loops, leading to drastic and irreversible changes in ecosystem functioning and the composition of communities that characterize an ‘invasional meltdown’ (Simberloff and Holle, 1999). Similarly, interactions of invasive earthworms with invaded plant communities favors a decline in native plant species and appears to facilitate plant invasions, at least in American northern hardwood forests (Eisenhauer et al., 2009b; Frelich et al., 2006; Hale et al., 2005). Nuzzo et al. (2009) also suggested that earthworm invasion, rather than non-native plant invasion, was the driving force behind changes in forest plant communities in Northeastern North America.

The general hypothesis of this study is that the abundance of non-native earthworm species is correlated with non-native grassland plant species and that selective ingestion of non-native seeds influences the species composition of seed in casts relative to that in the soil. The following predictions were tested: i) the abundance of non-native earthworms is positively correlated with the abundance of non-native plants, ii) non-native earthworms influence non-native seedling emergence from the seed bank via a facilitative non-native-non-native interaction and, iii) non-native earthworms favor the seedling emergence of herbs and grasses compared to leguminous species due to their preferential selection of seeds.

2. Materials and methods

2.1. Study system

This study was conducted at the Kenneth S. Norris Rancho Marino Reserve (KNRMR) in San Luis Obispo County, California (N 35°32.36–N 35°31.36 and W 121° 05.70–W 121° 04.8). Annual average temperatures range from 2 °C in January to 37 °C in July. Average annual rainfall is 460 mm. Our sampling was done on 26.7 ha of coastal grassland located on Concepcion loam (NCRS Soil Survey USDA, 2013). Concepcion loams are very deep loamy sands with moderate drainage and moderate available water capacity. Soil pH is slightly acidic and increases with depth.

This coastal grassland site was formerly used for agricultural purposes and was tilled until the 1950s (D. Canestro, reserve manager, personal communication). Soil disturbance and tillage are known to promote plant invasion worldwide (MacDougall and Turkington, 2005; Seastedt and Pyšek, 2011). Non-native species such as *Bromus* spp., *Plantago lanceolata*, *Festuca perennis*, and *Erodyum botrys* are categorized as invasive in California grasslands (Calflora, 2012), and are abundant throughout much of the grasslands at KNRMR. However, the area of grassland located along the coastal cliff had never been tilled and harbors native plant species including *Agoseris apargioides*, *Armeria maritima, Calystegia macrostegia, Distichlis spicata* and *Isocoma menziesii*. In addition to tillage, half of the study area, including a portion of the tilled and untilled areas, was sown with the grass *Phalaris aquatica* before the land was taken out of agricultural production (D. Canestro, personal communication). *P. aquatica* is recognized as an invasive species in San Luis Obispo County, although the California Invasive Plant Council classifies its potential impact on native ecosystems as moderate (see Calflora, 2012). We believed that its presence might have affected soil properties and belowground communities, although the relative frequency of the species remained low. Therefore, sown and unsown areas were both sampled.

The KNRMR had never been sampled for earthworms (S. James, personal communication). In Santa Barbara County, Wood and James (1993) identified eight introduced earthworm species (seven European and one South American species) and two native species that were never recorded before (*Ocnerodrilus* sp. and *Argilophilus* sp.). Preliminary sampling at KNRMR (J. Clause measurements) showed 0 to 120 individuals m^{-2} with variation across grasslands and forests. In the study area, only non-native endogeic earthworm species were found and identified: *Aporrectodea trapezoides* (25%), *Aporrectodea caliginosa* (12%), *Allolobophora chlorotica* (0.9%) and *A. rosea* (0.1%). *A. trapezoides* is recognized as an invasive species in Californian grasslands (Hendrix and Bohlen, 2002; Winsome et al., 2006).

2.2. Experimental design

All sampling was done in December 2011 along 20 transects parallel to the coastline running North to South. Five 12 m transects were sampled in each of the following four factor combinations (FC) – invaded/unsown, invaded/sown, uninvaded/unsown, uninvaded/sown. These factor combinations were the result of previous land management and were not the result of manipulation from our part. The presence/absence of the native plant species listed above was the basis of our invaded vs. uninvaded factor (see Section 2.1). The sowing of *P. aquatica* 40 years ago in some areas, but not others, was the basis of our sown vs. unsown factor. Each transect was subdivided into three 4-m plots equaling a total of 60 plots. Standing vegetation, earthworms, casts, and soil were sampled in each plot (Fig. 1).

2.3. Earthworm sampling

The December early rain (not measured) facilitated earthworm sampling. In each plot, a single 50 × 50 × 25 cm^3 hole was dug (Fig. 1). The soil was excavated and earthworms were manually sampled and hand-sorted. This method of sampling has been