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# Competitive interactions between native and exotic earthworm species as influenced by habitat quality in a California grassland

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**Abstract**

Worldwide, anthropogenic disturbance has contributed to reductions in native earthworm abundance and diversity and subsequent establishment of exotic populations. Exotic earthworm species dominate the earthworm community primarily in nutrient-enriched soils characteristic of urbanized and rural areas, while native species persist in less disturbed habitat. We hypothesized that exotic species may displace native species through competitive interactions, but only under conditions of high resource availability. To test this we manipulated both grassland productivity and the presence and density of intra- and interspecific competitors in field and laboratory experiments with two common species, the native megascolecid *Argilophilus marmoratus* Eisen 1893 and the exotic lumbricid *Aporrectodea trapezoides* Dugés 1828.

Overall, *Ap. trapezoides* maintained greater relative growth than *Ar. marmoratus*. The difference in growth between the two species declined with decreasing habitat quality, primarily due to lower relative growth of *Ap. trapezoides* in less productive grasslands. As the competitor species, *Ap. trapezoides* had a negative effect on both itself and *Ar. marmoratus* in all habitat types, while *Ar. marmoratus* as competitor had a more neutral effect. Reproductive development followed the same general pattern, but to become reproductive *Ap. trapezoides* required almost double the amount of relative growth as *Ar. marmoratus*. Both species had a negative effect on potential food resources, including microbial biomass and belowground plant biomass, but *Ap. trapezoides* reduced resources more than *Ar. marmoratus* in all habitat types. *Ap. trapezoides* achieved a greater relative growth than *Ar. marmoratus* in soils with high resource availability, but it lost proportionally more mass as resources declined. Thus, *Ap. trapezoides* attempting to colonize less productive grasslands may simply deplete available resources and fail to achieve sufficient growth for reproductive development. Our results suggest that interspecific competition has the potential to prevent *Ar. marmoratus* from recolonizing pastures dominated by *Ap. trapezoides*. Both species respond to enhanced resources in these pastures, but in resource-rich habitats *Ap. trapezoides* may exclude *Ar. marmoratus* through greater and faster growth per unit resource consumption coupled with earlier onset of reproduction. *Ar. marmoratus* is the weaker competitor of the two, but its negative effect on *Ap. trapezoides* in less productive grassland may exacerbate the role of resource limitation in preventing *Ap. trapezoides* from expanding its range.


*Keywords:* Earthworm; Oligochaeta; Competition; *Aporrectodea*; *Argilophilus*; Species invasion

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## 1. Introduction

The facilitation of biological invasions by human disturbance has been identified as a major component of global environmental change (Vitousek et al., 1997). In many terrestrial systems, important forms of disturbance include land conversion and nutrient amendment, which often occur as a two-stage process (Hobbs, 2000). First, habitat eradication or land conversion eliminates or simplifies native communities and sets the stage for invasion (Kotanen, 1997). Second, nutrient amendment, usually as fertilizer, prevents re-establishment of natives and facilitates establishment of exotic species (Huenneke et al., 1990; Lake and Leishman, 2004). There is a growing body of literature attesting to the difficulty of restoring native communities in these altered habitats, even after decades of abandonment (Berger, 1993; Hobbs, 1999). However, it remains unclear precisely why exotic-dominated communities are so resistant to the re-establishment of native species (Stylinski and Allen, 1999). In a recent review, Byers (2002) proposed that human-modified communities may resist re-establishment by native species because the habitat is so altered by past or chronic disturbance that the native species are more alien to it than are the exotics. Alternatively, the altered community may represent a new stable state, in which species interactions are in fact strong enough to preclude (re-)invasion by native species (Simberloff and Von Holle, 1999). Resources, and competition for resources, are fundamental to both scenarios. However, until fairly recently invasive species were characterized as good colonizers but poor competitors, ''weedy'' species dependent upon environmental change for success in displacing native species (Lodge, 1993). The very concept of competition as an important structuring force in many natural communities remains controversial (Tilman, 1987).

Recent work has shown, however, that biotic interactions that may be slight or transient in undisturbed communities may become important in disturbed systems in which an introduced species interacts in novel ways with native species or with other exotic species, via interspecific competition (Byers, 2000; Juliano, 1998), habitat alteration (Crooks, 2002), and/or apparent competition via shared parasites or predators (Hill and Lodge, 1999). Studies have also shown that the magnitude and outcome of such interactions may shift with respect to disturbance or other habitat modification (D'Antonio et al., 1999; Petren and Case, 1998). Species that maintain strict competitive hierarchies may become equivalent or even switch as environmental conditions change (Suding and Goldberg, 2001; Taniguchi and Nakano, 2000), or a slight competitive advantage may become a major one under changing environmental conditions (Suarez et al., 1998). A loss of refugia or a change in the spatial distribution of resources may force an interaction between an invader and a native species (Kiesecker et al., 2001). Life history traits may also be important to the outcome of some invasions (Kupferberg, 1997; Stohlgren et al., 1999b), where the invading species not only possess a superior capacity to acquire resources but also a more efficient resource conversion capacity, either with respect to reproduction or storage (Byers, 2000; Juliano, 1998). Linking biotic interactions such as competition to environmental change may thus be critical to our understanding of how and why an organism is likely to invade successfully, resist displacement by subsequent invaders, or expand its current range.

To understand how competitive interactions in an ongoing invasion may be mediated by anthropogenic disturbance, here in the form of soil nutrient amendment, we compared interactions between a native and an invading exotic earthworm species in California grasslands under differing management regimes. California supports a diverse earthworm fauna consisting of both native and exotic species. Exotic species include members of the families Lumbricidae, Glossoscolecidae, and Megascolecidae (Reynolds, 1995). The native earthworm fauna of California grasslands belong primarily to a poorly characterized group known as the Argilophilini (Megascolecidae) (Eisen, 1900; Fender and McKey-Fender, 1990). Genera occur in grasslands, oak woodland, and forests throughout the lower Pacific Coast region including Oregon, Idaho and California (Fender, 1995; James, 2000). Exotic earthworm species have largely replaced native species in highly productive soils in urbanized areas, fertilized pastures, and in other human-modified habitats, but native species continue to dominate the community in relatively undisturbed grasslands, oak woodlands, and chaparral (Eisen, 1900; Kalisz and Wood, 1995; Wood and James, 1993).

Similar reductions in native earthworm abundance and diversity and subsequent establishment of exotic populations have occurred worldwide (Bhadauria et al., 2000; Blanchart and Julka, 1997; Callaham and Blair, 1999; Eisen, 1900; Gates, 1982; Hendrix, 1996; Kalisz and Wood, 1995). Although competitive exclusion of native by exotic earthworms was proposed at one time as a possible mechanism to explain the decline of native earthworm populations (Stebbings, 1962), subsequent