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Introduced earthworms in agricultural and reclaimed land: their ecology and influences on soil properties, plant production and other soil biota

G. H. Baker · G. Brown · K. Butt · J. P. Curry · J. Scullion

Abstract Accidental and deliberate introductions of earthworms into agricultural and reclaimed land are natural experiments that provide opportunities to understand the attributes of successful invaders and their impacts on local biota and ecosystem processes. We consider various case studies (e.g., earthworm invasions in agricultural soils in Australia and Brazil) and deliberate introductions of earthworms into reclaimed mine sites, landfills and cutaway peat in the U.K. and Ireland. Invasions of exotic earthworms, such as European Lumbricidae in Australia, have been geographically extensive, but remain very patchy at regional and field scales. Their impacts on soil properties, plant production and other biota are therefore also likely to be patchy. Various methods have been developed to deliberately inoculate exotic earthworms into disturbed lands, with varying degrees of success. The factors controlling success are, in general, poorly understood. A broad range of impacts of invasive earthworms on soil properties (e.g., soil structure, nutrient availability, burial of surface materials, incidence of root diseases) and plant yield and quality have been reported. Less is known of the impacts of invasive earthworms on other soil fauna, but they are likely to occur due to alterations in food availability and habitat structure. Influences on other biota are likely to extend to aboveground communities as well as those belowground. Introductions of earthworms to disturbed lands can yield substantial benefits in agricultural productivity and amelioration of soil degradation. However, the potential impact of the promotion or control of such introductions on non-target biota and ecosystem processes in pristine ecosystems nearby should be considered.

Keywords Disturbed land · Earthworms · Exotic · Plant production · Soil biota · Soil properties

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Abbreviations

EIU	(Earthworm Inoculation Unit) method a technique incorporating adults and their cocoons in a protective soil microenvironment
NT	No-till agricultural practice

Introduction

Invasions of exotic earthworms have significantly damaged pristine, native ecosystems (see other papers in this issue). However, earthworms have also been both accidentally and deliberately introduced to a wide variety of agricultural habitats, with major benefits accruing to land owners (Lee 1985; Edwards and Bohlen 1996). Deliberate introductions have sometimes been part of more extensive restoration programs following habitat degradation (e.g., mining, peat harvesting) or reclamation of land from the sea (e.g., polders) (Hoogerkamp et al. 1983; Curry and Boyle 1987, 1995; Scullion et al. 1988, Scullion and Malik 2000; Butt 1999; Butt et al. 2004). Introductions have been on both a large scale (many hectares) and much smaller scale (enclosures of a few square metres or less) (Stockdill 1982; Baker 2004). Motivation for such earthworm introductions has been driven by needs to improve soil properties (e.g., nutrient turnover, soil structure and water flow, pH, functional biodiversity, food sources for vertebrate predators) and to increase plant production. Frequently, exotic earthworms comprise the majority of the earthworm fauna in agricultural land (e.g., accidental introductions in New Zealand and Australia) and these earthworms provide various beneficial ecosystem services. However, the impacts of introduced earthworms have not always been positive and rates of improvement in site characteristics have frequently been slower than desired following deliberate introductions. Careful site selection and preparation is often paramount for success. “Non-target” effects of exotic earthworms have rarely been considered prior to deliberate introduction, in comparison with some other exotic introductions (e.g., release of biocontrol agents to control agricultural pests).

This paper provides an overview, illustrated with case studies, of accidental and deliberate earthworm introductions to disturbed land, taken from different parts of the world with varying climatic regimes, and reviews the impact that has occurred on soil properties, plant production and the abundance and diversity of other soil biota (both invertebrates and microbes, but native earthworms especially). We also briefly explore the potential of invasive earthworms to influence the abundance of above ground taxa (pests and beneficial species). In addition, studies of the patterns of establishment of introduced earthworm populations and the development of rearing methods for large scale inoculations into farms and reclaimed land have provided insight into the capacity of these invertebrates to disperse, as well as revealing some of the environmental factors that influence their abundance. We will discuss these issues as well as spatial and temporal patterns in establishment that have been observed or predicted in disturbed habitats.

Distributions of exotic earthworms: “Accidental” establishment at different scales, using Australia as an example

Perhaps the best known group of invasive earthworms in agricultural soils are the peregrine members of the European Lumbricidae (Lee 1985), which have colonised all continents of the world, with the exception of Antarctica (see Frelich et al., and Tiunov et al. in this issue). These include several species of *Aporrectodea*, *Allolobophora*, *Lumbricus* and *Octolasion*. Other families, with origins elsewhere in the world, have also contributed frequent invaders, such as *Microscolex*, *Dichogaster* and *Amynthas* (Megascolecidae) and *Pontoscolex* (Glossoscolecidae). For example, all of these genera have invaded Australian agricultural and urban habitats (Mele et al. 1996; Baker et al. 1997a). A similarity in exotic fauna, originating from Europe, could be expected between southern Australia, Canada, USA, southern South America, South Africa and parts of Asia, based on similarities in climate and similar opportunities to colonise through accidental transport (Baker et al. 1994).

Whilst some earthworm species have colonised very broadly on a geographic scale within Australia, others remain very restricted in their distribution (Baker and Barrett 1994; Baker et al. 1997a) (Fig. 1). Factors controlling these distributions are poorly understood. It is quite probable that the potential extent of at least some invasions has yet to be realised, held back thus far through lack of opportunity to colonise (Baker 1998a, 2004). However, ecological boundaries to distribution are occasionally apparent. For example, Baker (1998a) surveyed pastures extensively throughout south-eastern Australia and showed that *Aporrectodea caliginosa* was common at sites receiving >600 mm annual rainfall, but rare where rainfall was less. The closely related *A. trapezoides* was found more commonly at sites with < 600 mm annual rainfall. This apparent difference in tolerance of aridity between the two species accords well with their observed European distributions (e.g., in France where *A. trapezoides* has the more southern distribution of the two) (Bouché 1972). It is perhaps remarkable that the distributions of some exotic lumbricid species are as extensive as they are in Australia, given that the most likely date of introduction was approximately 200 years ago (when European humans first settled Australia and probably brought exotic earthworms with them accidentally in potted plants, ship's ballast, etc). There has been very little deliberate attempt to enhance their distributions since then (Noble et al. 1970; Blackwell and Blackwell 1989; Baker 1998a, 2004).

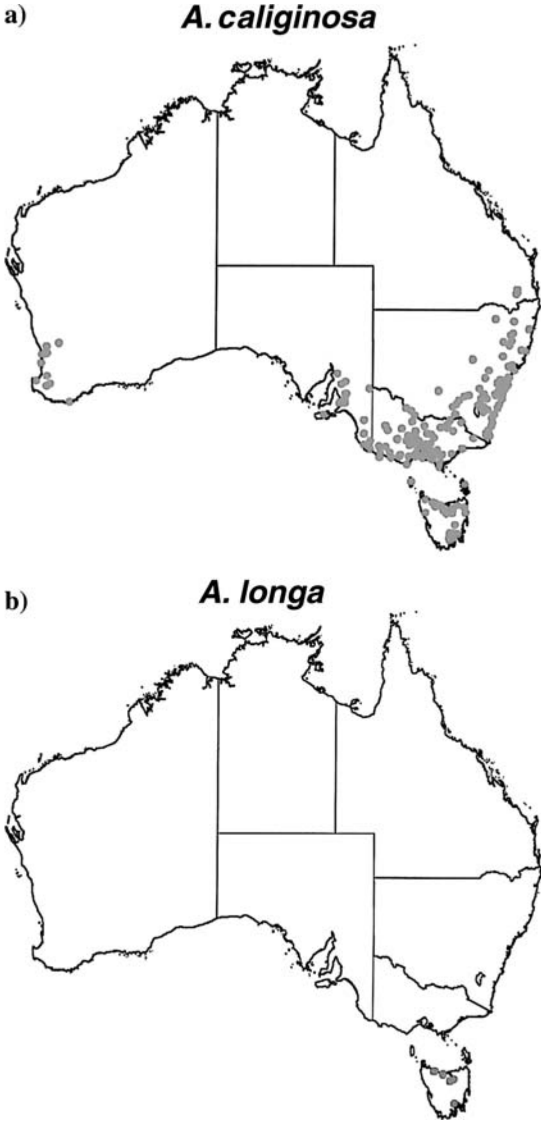

Fig. 1 Distributions of *Aporrectodea caliginosa* and *A. longa* (Lumbricidae) within sites surveyed throughout Australia. Redrawn from Baker et al. (1997a)

At a more regional level, the abundance of exotic earthworms can vary markedly between sites (Baker 2004) (Fig. 2). On some farms, exotic earthworms predominate over native species, and vice versa. Again, lack of opportunity to colonise (and multiply) may explain some of the observed patterns in abundance of the exotic species. Abundance has also been correlated with local rainfall and various soil properties such as carbon content, particle size and pH (Baker et al. 1992b; Baker 1998a). Within individual farms, some fields can contain invasive species, whilst adjacent fields, with apparently similar management and soil type, do not (G. Baker, unpublished data). Within individual fields, invasive earthworms have colonised some soil types more than others (Baker et al. 1993b), and at a finer scale, some exotic earthworms (e.g., *A. trapezoides* and *Microscolex dubius*) aggregate differently under various dung types produced by grazing vertebrates (Scown and Baker, submitted).

The most common invasive earthworms in agricultural soils in south-eastern Australia are *A. trapezoides*, *A. caliginosa* and *A. rosea*, all of

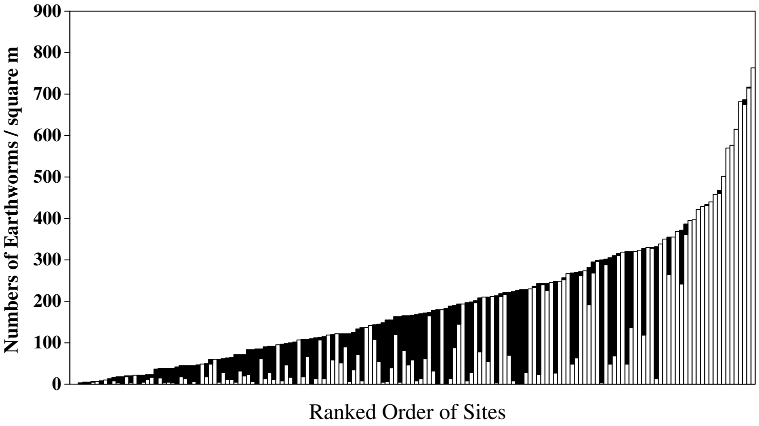

Fig. 2 The abundance of native and exotic earthworms in 163 pastures that were surveyed in late winter-early spring in western Victoria, Australia (see Baker 1998a for more details of survey location). Sites are arranged along the X axis in ascending order of overall population density. Dark bars indicate native species; light bars indicate exotic species. Redrawn from Baker (2004)

which are endogeic species (Baker et al. 1992b; Baker 1998a, 2004). The epigeic species, *M. dubius*, is widespread, but rarely occurs in large numbers. Another epigeic species, *Lumbricus rubellus*, can be locally abundant, but is generally restricted to damp situations. The only anecic invasive species is *A. longa*, but it is mostly restricted to Tasmania. All of these species are only active from early winter to early spring, when soils are cool and moist. Very little is known about the temporal and spatial aspects of the burrowing and feeding of native Australian earthworms, but some marked differences compared with exotic species have been reported. For example, Baker (1996) reported *Gemascolex lateralis* (Megascolecidae) active in leaf litter in the middle of a hot dry summer.

The distribution and abundance of invasive earthworms are thus highly patchy and variable, both at large geographic and local spatial scales, as is the case with earthworms and other soil fauna in general. Earthworm abundance can vary markedly between years as well (Baker 1999). Given this, the influences that invasive earthworms will have on soil properties and other biota will likewise be highly variable. The seasonal activity patterns and particular styles of burrowing and feeding of the invasive species will further determine the nature of these influences (Baker et al. 1992a, 1993a, b; Baker 2004).

Managing deliberate introductions

One of the best known deliberate introductions of earthworms is the case from New Zealand, where lumbricids (most notably *A. caliginosa*) were redistributed to pastures lacking them (Stockdill and Cossens 1966; Stockdill 1982). These managed pastures were sown with exotic plant species. Native earthworms fared poorly under such pastures, leaving a void amongst the soil macrofauna, an accumulation of turf thatch and restricted nutrient cycling. Water infiltration was also impeded. Exotic earthworms were harvested from pastures where they were abundant, using sod-cutting machinery, and then inoculated at regular intervals across pastures devoid of earthworms. Wide-spread establishment within the targeted pastures was achieved within 7 years at economically acceptable costs and with substantial benefits (e.g., increases of 25% in pasture carrying capacity in the long term). Similar strategies have been used in northern Tasmania (Farquhar 1992), with large economic benefits for land-owners and in shorter time frames.

The sod transplantation method might be expected to work better for endogeic compared with anecic earthworms, given the former species' shallower burrowing behaviour, and thus greater potential to be collected in sods. However, information on this topic is scarce. In Tasmanian pastures, where both *A. caliginosa* (endogeic) and *A. longa* (anecic) have been introduced together in sods, the relative success achieved for the two species is not known. Topsoil-dwelling species have established better than deep-burrowing species in reclaimed cutaway peat soils in Ireland following sod transplantation, but this difference is probably better explained in terms of post-introduction survival than by the size of the inoculum (J. Curry, unpublished data). Curry and Schmidt (submitted) noted that the anecic *L. terrestris* was only very sporadic in occurrence in 20–30 year old reclaimed peat, possibly because of insufficient depth of aerobic soil.

The scarcity of anecic earthworms in agricultural soils in southern, mainland Australia has prompted consideration of how the functional diversity of earthworm communities might be improved there (Baker 1998a, 2004). Springett (1985), Temple-Smith et al. (1993) and Baker (1998b) have shown in both field and laboratory experiments in New Zealand and Australia that the addition of *A. longa* to soils already containing *A. caliginosa* and *L. rubellus* can increase pasture production (see other benefits mentioned below). Clearly, there is an additive effect of functional diversity on plant production. Baker (1998a) made a crude prediction of where *A. longa* might establish in Australia if given the chance, based on annual rainfall matching with its known distribution in Europe. Baker and Whitby (2003) have since suggested that the length of time the soil remains sufficiently moist during the year (and hence adequate for cocoon development) may be a better predictor for the successful establishment of *A. longa*. Other edaphic factors, such as soil pH, also need to be considered (Baker and Whitby 2003). Baker et al. (1999a) inoculated *A. longa* in cages into several different soil types in south-eastern Australia and recorded establishment, in the short-term (5 months). *A. longa* survived in all cases. Unencumbered releases have also been made in pastures (Baker 2004). *A. longa* has established and spread at least 7 m from inoculation points within 3 years (with one exceptional individual found at 20 m).

The rate of spread observed for *A. longa* in Australia is similar to those recorded for invasions of lumbricid earthworms in newly formed polders in The Netherlands (Hoogerkamp et al. 1983; Marinissen 1991; Marinissen and van den Bosch 1992; Stein et al. 1992), within land reclaimed following landfill with municipal solid wastes (Butt et al. 2004) (Fig. 3) and on restored surface mine sites in the U.K. (Scullion et al. 1988). Given their different burrowing behaviours and fecundities (hence rates of population growth) (Lee 1985), epigeic, endogeic and anecic earthworms might be expected to disperse and establish away from inoculation sites at different rates, anecic species performing slowest in this regard. Indeed, J. Scullion (unpublished data) showed that the anecic species, *L. terrestris* and *A. longa*, colonised restored mine site soils in the U.K. at slower rates than other more horizontally burrowing species over a 6 year period. Curry and

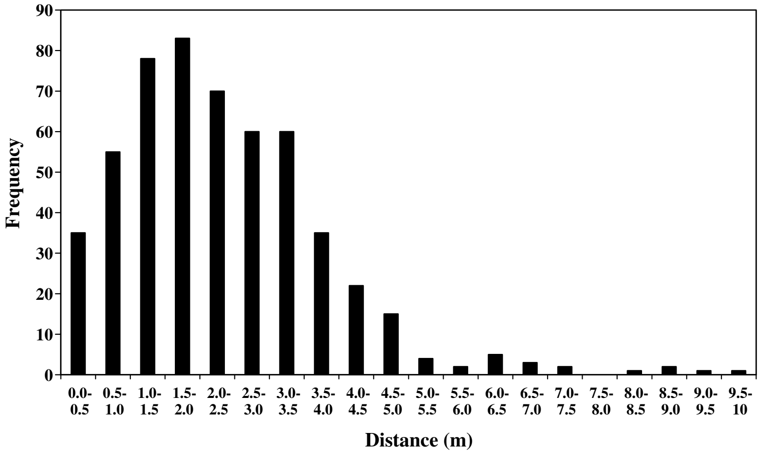

Fig. 3 Distance of casts of *Aporrectodea longa* from point of inoculation, 5 years after introduction to a reclaimed landfill site in the U.K. Data represent total counts of surface casts within 0.5 m radial lengths from the nearest points of *A. longa* inoculation. Redrawn from data in Butt (1999)

Boyle (1987) reported that *A. longa* (and the endogeic *A. rosea*) dispersed more slowly within 1 year from transplanted sods in reclaimed cutaway peat sites than several endogeic and epigeic species (e.g., *A. chlorotica*, *A. caliginosa*, *Dendrodrilus rubidus*, *L. festivus* and *L. rubellus*). Hoogerkamp et al. (1983) found that *A. caliginosa* dispersed at twice the rate of *L. terrestris* in a reclaimed polder in The Netherlands. On the other hand, Butt et al. (2004) recorded *A. longa* at greater distances from inoculation points than *A. chlorotica*, 11 years after introduction to landfill sites. The dispersal of earthworms from release sites can of course easily be confounded by "natural" dispersal from other nearby sites and the finding of individuals at particular distances away from inoculation points also does not necessarily infer successful establishment (i.e., a breeding population). Such data thus need cautious interpretation. Earthworm spread can be enhanced accidentally by agricultural machinery (e.g., cocoons can be picked up in mud clinging to tractor tyres and thus transferred within and between fields, Marinissen, 1991), thus blurring observations of innate capacity for dispersal.

One of the most ambitious introductions of earthworms occurred in Russia, where various lumbricids, most notably *A. rosea* and *A. trapezoides*, were transported 700 km (taking 12 days) from the Zaravshanski Mountains to oases in the Kyzylkum Desert (Ghilarov and Mamajev 1967). Agricultural soils at the inoculation sites were devoid of earthworms and dung from grazing vertebrates was accumulating, until successful establishment occurred and local lucerne production was doubled.

Different methods of inoculation can influence establishment success. At mine sites undergoing rehabilitation in the U.K., several introduction techniques have been used on an experimental basis (Scullion et al. 1988; Scullion and Malik 2000). In one trial, mixed populations of earthworms, collected during cultivation of local undisturbed land, were introduced directly at 2 m intervals into mole plough slits at a newly restored site. In another trial at the same site, strips of topsoil containing viable earthworm populations were placed at 50 or 100 m intervals during replacement of the final soil layer at the restored site. Soil in intervening areas was largely devoid of earthworms. In the direct inoculation trial, observations of casting activity suggested that colonisation was almost exclusively along the mole plough slits during the first 12 months. Colonisation of the soil between slits occurred in the second year of the trial. Then, within 4 years, the population on areas to which earthworms were introduced was similar to that of adjacent and similarly managed undisturbed pasture. At the same time, populations in the inoculation strips had lower numbers of *A. longa* and *L. terrestris* compared with the direct introduction plots, but similar numbers of other numerically dominant species (*L. rubellus*, *A. chlorotica* and *A. caliginosa*). This finding may partially reflect the fairly low residual population of the former species in strip soil.

In another study in the U.K., Butt et al. (1997) reported that the use of a technique incorporating adults and their cocoons in a protective soil microenvironment (The Earthworm Inoculation Unit (EIU) method, Butt 1992) was superior to broadcasting of adults of *A. longa* onto compacted soil at a landfill site (Calvert). A viable population of *A. longa* was recorded over the following decade after using the EIU technique (Butt et al. 2004). This technique was also shown to be of value for endogeic species such as *A. chlorotica* and for mixed species inocula. No earthworms were present at the Calvert landfill site when the capping process was completed in 1991. Butt et al. (1999) recorded the spread of *A. longa* and *A. chlorotica* following their introduction in 1992 and also noted that the abundance of the latter increased in the presence of the former. Natural colonisation of the site by earthworms was recorded after a period of 7 years, when *Eiseniella tetraedra* and *L. rubellus* were located. After a further 4 years, *L. castaneus* and *A. rosea* were also found. At this point (2002), the *A. longa* and *A. chlorotica* still accounted for over 65% of earthworms found on site (Butt et al. 2004). By 2003, dispersal of inoculated species and colonisation of other species meant that distribution patterns no longer equated to inoculation treatments. However, the presence of viable trees (*Alnus glutinosa*), planted at the time of inoculation, led to significantly greater earthworm densities compared to areas where *Acer pseudoplatanus* had been planted and subsequently died (Butt et al. 2004). But the surviving trees (*A. glutinosa*), with associated nitrogen-fixing root nodules, were stunted and only attained a height of 3 m (max) after 11 years, with die back each year. This was attributed to limiting soil factors which were not assisted by the presence of inoculated earthworms.

Other local management practices can influence the establishment of exotic species. For example, in the southern Brazilian state of Paraná, exotic *Amynthas corticis* and *A. gracilis* have extensively colonised croplands in regions with cool, sub-tropical climates (Voss 1986; Tanck et al. 2000; Brown et al. 2003). In these areas, no-tillage (NT) practices have spread widely in the past ten years and now cover 5.5 million ha (25% of the state's land surface). Under NT, organic matter content in the topsoil has increased (Sá et al. 2001). Consequently soil macrofauna, such as earthworms, have increased in abundance (Brown et al. 2001, 2003). The adoption of NT is believed to have encouraged the invasion of *A. corticis* and *A. gracilis*, and build-up of their populations has been rapid. Voss (1986) observed an increase in the abundance of *Amynthas* spp. from 0 to 108 individuals m^{-2} within 4 years of adoption of NT, and Peixoto and Marochi (1996) reported similar increases (0 to >200 individuals m^{-2} in 6.5 years). In addition, several farmers have developed a method of field inoculation which consists of spreading batches of composted manures containing high populations of *Amynthas* spp. at selected sites within their fields (e.g., close to bunds used for erosion control) and at prescribed distances apart to promote earthworm colonisation.

Invasive species often exhibit a ''boom-and-bust'' cycle as they establish (Simberloff and Gibbons 2004). Over-exploitation of resources, disease or arrival of competitors have been suggested as mechanisms for the observed collapses in abundance. However, causes frequently remain poorly understood. Examples for soil fauna are rare in this context (e.g., see Baker 1985 for a millipede example). Although invasive earthworms should offer good opportunities to follow temporal and spatial patterns in abundance following establishment, and the environmental factors which drive such patterns, little data are available. Stockdill (1982) reported that pasture production in New Zealand peaked a few years after the introduction of *A. caliginosa*, and then stabilised at a lower level in subsequent years. This pattern in production may, but need not necessarily, have reflected a ''boom-and-bust'' in earthworm abundance (no data are available). The peak in production may simply have reflected a flush of nutrient release from the decomposing thatch that had accumulated prior to earthworm introduction.

Influences on soil properties and plant production

Earthworms can influence soil properties and plant productivity in several ways (Lee 1985; Lavelle 1988; Curry 1994) and there are many examples in the literature of the contributions exotic earthworms make in this regard in agricultural soils and reclaimed land throughout the world. In southern Australia, for example, several studies have shown the influences of exotic earthworm species in agricultural soils on soil structure (Barley 1959b; Doube et al. 1994b, c; Friend and Chan 1995; Hindell et al. 1994a, b, c, 1997; Hirth et al. 1994, 1996; Chan et al. 1997; Curry and Baker 1998), nutrient availability (Barley and Jennings 1959; Baker et al. 2003a), burial of surface organic matter and lime (Barley 1959a; Baker et al. 1993c, 1998, 1999c; Chan et al. 2004), distribution of beneficial microorganisms (Stephens and Davoren 1994; Stephens et al. 1993b, 1994a, b; Doube et al. 1994a, d), reduction of incidence of root diseases (Stephens et al. 1993a, 1995; Stephens and Davoren 1997), and plant yield and quality (Abbott and Parker 1981; Temple-Smith et al. 1993; Garnsey 1994; Stephens et al. 1994a; Baker et al. 1997b, 1999b, 2003b). Several studies have demonstrated that such influences vary markedly between earthworm species, soil types and plant species (Doube et al. 1997; Baker et al. 1999b, 2003a, Baker submitted; Chan et al. 2004).

In reclaimed polders in The Netherlands, conditions for pasture root growth were improved by earthworm colonisation through increased water infiltration and aeration and decreased compaction of the upper soil layers (Hoogerkamp et al. 1983). Earthworms redistributed surface organic matter throughout the soil, and grass production and pasture quality increased. Stockdill (1982) reported similar benefits from introducing earthworms to pastures in New Zealand. Earthworms however also rendered the soil more liable to damage from treading by domestic animals and invasion of moles as they searched for earthworm prey in the Dutch polders.

Curry and Boyle (1987) studied the impact of earthworms on soil properties and herbage production in a field microplot experiment in central Ireland, where the study site had been reclaimed following industrial peat extraction, and seeded with perennial ryegrass and white clover. The presence of earthworms had little apparent effect on herbage production in the first year, but total herbage yield was 25% greater in the second year and 49% greater in the third year in microplots receiving annual topdressing of cattle slurry, compared with similarly-treated microplots without earthworms. No effect of earthworms on herbage yield was detected in microplots receiving inorganic fertilizer only. However, the control microplots did not remain entirely free of earthworms, and considerable heterogeneity in soil conditions masked any impact that earthworms might have had on soil properties in the field. Glasshouse studies were therefore conducted to assess the role of earthworms under more controlled conditions (Boyle et al. 1997) (Fig. 4). Cumulative herbage yields over a period of 20 months were 89% higher in buckets with earthworms fertilised with cattle manure, and 19% higher in buckets receiving only inorganic fertilizer, compared with comparable treatments without earthworms. Grass growth response to earthworms was most pronounced under conditions of declining fertility (+114% to +222%) when manure and fertilizer applications were discontinued, suggesting that growth response to earthworms was mainly due to enhanced organic matter mineralisation. Soil subsidence rates, hydraulic conductivity, moisture characteristics, bulk density, porosity, fibrosity and soil morphology and micromorphology were all found to be significantly influenced by the presence of earthworms, suggesting that earthworm activity can markedly affect the process of soil maturation and profile development in reclaimed peat soils.

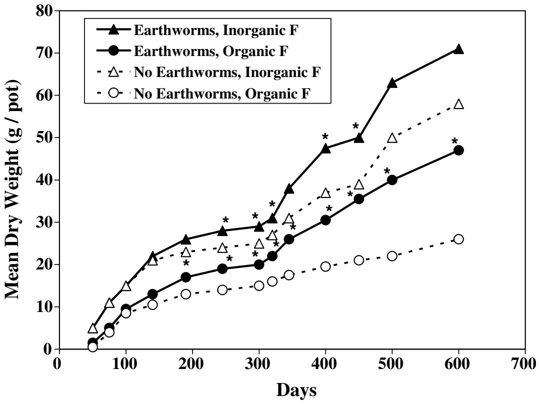

Fig. 4 Cumulative perennial ryegrass (*Lolium perenne*) yields with and without earthworms (mix of *Aporrectodea*, *Allolobophora* and *Lumbricus* spp.) under inorganic or organic fertiliser regimes in glasshouse studies using a mixture of peat and relict degraded mineral soil from reclaimed cutaway peatland. Asterisks indicate significant earthworm effects, within fertiliser treatments. Redrawn from data in Boyle et al. (1997)

In restored mine site soils, Marashi and Scullion (2004) found that inoculation of earthworms increased soil porosity throughout the top 20 cm of soil. However, this increase in porosity was associated with greater soil water-logging, despite the site having been drained and subsoiled. Earthworm activity enhanced water infiltration and artificial drainage was not effective in removing excess water from the soil profile. As a result, the surface of inoculated soils was more prone to treading damage.

Stability of soil aggregates was little influenced by earthworm inoculation in restored mine site soils within 3 years, but by 6 years, aggregation had improved throughout the top 20 cm of soil, especially near the surface (Scullion 1994; Marashi and Scullion 2003). Organic matter content was significantly higher on control compared with inoculation plots to 5 cm depth, but the situation was reversed below this depth. Other work on these soils (Scullion and Malik 2000) showed that increased carbohydrate levels provided the most marked effect of earthworms on organic matter content. Root contents within the soil on inoculated plots were significantly higher than for controls, at all sampling depths (Fig. 5).

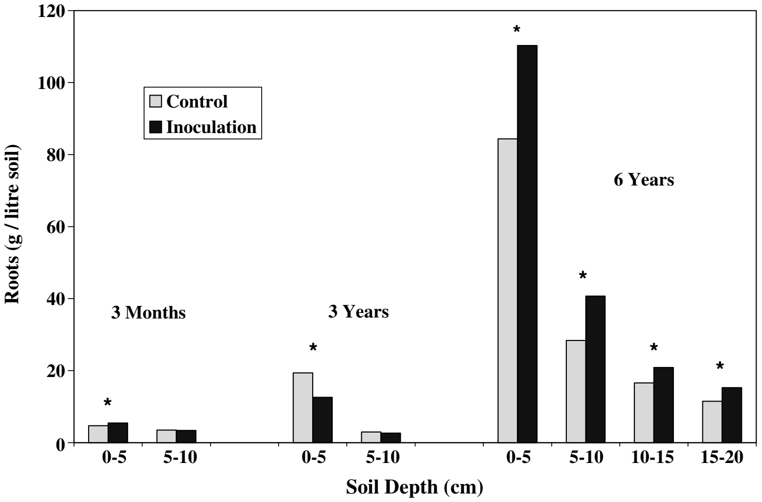

Fig. 5 Root biomass at varying depths, 3 months, 3 years and 6 years after earthworm inoculation to soil at a reclaimed mine site in the U.K. Asterisks indicate significant differences. Redrawn from data in Marashi and Scullion (2003)

Earthworms have an important role in mixing organic matter with mineral soils at reclaimed sites. Ultrasonic dispersion showed that organic carbon was better mixed with clays where earthworms were present (Scullion and Malik 2000). Physical protection of organic matter through close association with mineral components results in a lower decomposition rate.

J. Scullion (unpublished data) has also investigated the influences of earthworm inoculation at mine site rehabilitation sites on % root infection by arbuscular mycorrhizal fungi (same sites as referred to in Fig. 5). Overall, there was no difference in % infection, although total root length infected would have been markedly higher on inoculated sites, given the greater (25–43%) development of roots there.

In Paraná, Brazil, the invasion front of *Amynthas* into NT cropland significantly altered soil structure and water holding capacity (Peixoto and Marochi 1996). Most of the top 10 cm of the soil consisted of earthworm castings, and these had a major effect on increasing water infiltration and the availability of several plant nutrients. In the invaded area, grain yields of wheat and soybean increased by 47 and 51%, respectively, while the dry mass of black oat increased 22%. Similarly, Kobiyama et al. (1994) found enhanced growth of tree seedlings (*Mimosa scabrella*) when *Amynthas* were inoculated in field mesocosms. Earthworms influenced saturated hydraulic conductivity and total soil porosity down to 30 cm depth, especially increasing the number of pores with diameter >0.06 mm. Consequently, soil water holding capacity and plant growth increased (Kobiyama 1994). However, Santos (1995) found few significant differences in soil properties (nutrients, bulk density, water infiltration) and no differences in yields of wheat or black beans (*Phaseolus vulgaris*) when *Amynthas* were inoculated into field mesocosms. Furthermore, Kusdra (1998) observed negative effects of inoculations of *Amynthas* spp. on black bean shoot and root biomass and nodulation by symbiotic *Rhizobia* spp. in greenhouse trials. Santos (1995) and Kusdra (1998) conducted their work in disturbed soils, compared with the undisturbed soils used by the other authors. This difference, as well as the variation in plant type across the studies, may help explain the different results. Brown et al. (1999) have also illustrated how earthworms can have varied (positive and negative) impacts on tropical grain crop yields, but reasons for the variability they observed in plant response are unclear.

Very few studies have compared the impacts of invasive earthworm species with those of native species on soil structure, fertility and plant production in agricultural settings. In Australia, some work (Baker et al. 1996, 2003b; Blakemore 1997; Baker 1998a) has shown that native Megacolecidae, e.g., species of *Spenceriella* and *Gemascolex*, are inferior to exotic lumbricids, such as *A. caliginosa*, *A. trapezoides* and *A. longa*, in improving soil structure and water infiltration, burying surface dung, and improving plant production. In contrast, James (1991) argued that introductions of exotic lumbricids to tallgrass prairie in the USA had negative influences on soil properties through a reduction in the abundance of more useful native species.

Interactions with other fauna

Evidence for interactions (positive or negative) between invasive and native earthworms in agricultural soils is limited, although it seems likely to occur, if only at a small scale (Baker 2004). Probably, the scarcity of native earthworms following agricultural disturbance has stifled scientific inquisitiveness on this topic (see González et al., and Hendrix et al., this issue).

In southern Australia, regional surveys have provided no persuasive evidence of interactions between exotic and native earthworm species. For example, a survey of 104 pastures in southern New South Wales (Baker 2004) provided no correlation between the abundance of native and exotic earthworms. But in a similar survey of 163 pastures in western Victoria, native earthworms were generally absent where exotic abundance exceeded about 400 earthworms m^{-2} (Fig. 2). This is suggestive at first glance of possible competitive exclusion. However, the majority of sites with high numbers of exotic earthworms occurred in dairy or sheep pastures in the higher rainfall portion of the region that was surveyed. The scarcity of the native species may well reflect different responses to management practices compared with the exotic species.

Where native earthworms have been accidentally caged in the field in southern Australia with exotic lumbricids, some reduction in the abundance and/ or biomass of the native species has been observed (Baker et al. 1999a, 2002b). Similarly, the introduction of some exotic lumbricids (e.g., *A. longa*) has reduced the abundance and biomass of other established exotic species (e.g., *A. caliginosa*, *M. dubius*) (Baker 1997; Dalby et al. 1998; Baker et al. 2002a). Possible competitive interactions, such as removal of food and habitat and consumption of cocoons, have been suggested as mechanisms for the effect of *A. longa* on *M. dubius* (Dalby et al. 1998). Similar mechanisms could well operate between invasive and native earthworm species.

In Paraná, Brazil, Brown et al. (in press) found native earthworms at only three of 18 sites with row-crops. Exotic species (mainly *Amynthas* and *Dichogaster* spp.) were found only in secondary vegetation (forests and disturbed grasslands) and agricultural areas (approximately 50 sites sampled in the state). Under well-conserved native vegetation, exotics were absent and native species were common. Some native species (particularly Glossoscolecidae) were also found in disturbed areas such as pine forests, grazed grasslands, introduced pastures and home gardens (low-input). Native earthworms appear not to be well suited to survive under conventional agricultural practices, while exotic or peregrine earthworms may be better suited to the conditions created by cropping. Alternatively, the latter species may be just opportunistic invaders that are occupying empty niches left by native species that disappeared after transformation of the native or former vegetation (e.g., tropical forests) for agricultural uses. Tanck et al. (2000) also found abundant populations of exotic *A. corticis* and *A. gracilis* in long-term NT crops and an adjacent secondary forest, but no exotic earthworms in native grassland.

An exception to these rules in Brazil is *Pontoscolex corethrurus*, a species that has been present in southern Brazil for more than a century (Muller 1857). The origin of *P. corethrurus* is thought to lie further north in the Guyanan Shield area of Brazil (Righi 1984). *P. corethrurus* must be therefore considered an invader in most of Brazil, although it has not been treated as an exotic earthworm in that country and little has been done to reduce its spread to new areas (a phenomenon that has occurred regularly with deforestation and other land transformations). Such invasions of *P. corethrurus* have been associated with negative effects on soil structure (Barros et al. 2004; Chauvel et al. 1999) and perhaps native earthworm communities (Lavelle and Lapied 2003).

Dung from grazing vertebrates represents a resource for which various invertebrates can compete (e.g., dung beetles and fly larvae) (Waterhouse 1974). Earthworms can consume and bury large amounts of dung (Holter 1979; Martin and Charles 1979), thus potentially competing with other dung-dependent fauna. However, we are unaware of any studies that have experimentally explored this possibility in the context of invasive earthworms in agricultural systems. Similarly, negative interactions between invasive earthworms and microarthropods have been demonstrated in forests (e.g., McLean and Parkinson 1998, 2000; see McLean et al. and Migge-Kleian in this issue), and the excreta, burrows, and organic middens that anecic earthworms create at the surface openings of their burrows are known to influence the distribution and abundance of microarthropods and other earthworms (Maraun et al. 1999; Salmon and Ponge 1999; Salmon 2001, 2004; Tiunov 2003); but no similar influences on local fauna have, to our knowledge, been attributed to earthworm invasion of agricultural fields.

The importance of ecological linkages between above and below ground communities is gaining increased recognition (Wardle 2002). A few studies (Scheu et al. 1999; Wurst and Jones 2003; Newington et al. 2004) have recently implicated earthworms as influencing the abundance of above-ground herbivores and their natural enemies, as well as Collembola. The study of earthworms generally, and invasive species in particular, in the dynamics of agricultural pests (e.g., influences on weed seed distribution in the soil [Thompson et al. 1993], or insect pests) seems a particularly fruitful research topic to pursue.

Conclusions

Biological invasions usually invoke serious concerns with respect to negative impacts on the conservation of native biological communities. However, biological invasions also provide opportunities to understand the attributes of successful colonists and their impacts on ecosystem processes (Brown and Sax 2004). Earthworm invasions, especially within disturbed habitats, have thus far provided very fruitful opportunities to demonstrate the influences of these fauna on soil processes and plant production, but their impacts on other fauna have been poorly explored.

Many of the impacts of invasive earthworms on soil processes and plant production, when viewed in an agricultural or land reclamation context, can be viewed positively. But a thorny dilemma is struck when considering the ethics of deliberately redistributing exotic earthworms to achieve additional benefits further afield from where they initially colonise (see also Callaham et al., this issue). A value judgement must be made between the conservation of native fauna and ecosystem function in pristine lands adjacent to the disturbed lands (and thus at risk of invasion) and (re)establishment of ecosystem services that are sorely needed to offset soil degradation that previous management practices have created (Baker 2004). For example, Sharpley et al. (1979) have demonstrated the importance of exotic earthworms in influencing the quality (nutrient content) and quantity of water in runoff from New Zealand pastures. This runoff has the potential to pollute water catchments and represents loss of nutrient resources for farmers. Should these exotic species be further spread to pastures lacking them, and also lacking native earthworms due to habitat destruction, to capture similar benefits? In part, we are particularly hamstrung through our lack of knowledge of the ecology and behaviour of native earthworms in many parts of the world, especially their potential role in ecosystem processes and the management practices that need to be implemented to encourage such species back into disturbed lands.

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