

Chapter 5

Earthworms and Post-Agricultural Succession

Grizelle González, Ching-Yu Huang and Shu-Chun Chuang

5.1 Introduction

Earthworms are the best known and often the most important animals influencing the functioning of soil ecosystems (Hendrix and Bohlen 2002). In mature forests of the Neotropics, earthworms usually dominate the soil food web in terms of biomass (e.g., Odum and Pigeon 1970, Lee 1985, Lavelle, Brussaard and Hendrix 1999). Consequently, they have significant influence on soil structure, nutrient cycling and crop productivity as their activities can increase soil porosity, stimulate microbial activities, and accelerate litter decay and the release of nutrients into the soil (Lee 1985, Lavelle et al. 1999, González and Seastedt 2001, González 2002, Liu and Zou 2002).

Earthworms are classified into endogeic, anecic, and epigeic species to represent soil, soil and litter, and litter feeders, respectively (Bouché 1977). Earthworms can alter soil physical properties and biogeochemical processes (e.g., Edwards and Bohlen 1996) according to their functionality. Through borrowing activities, earthworm may alter soil structure and soil water infiltration rates, thus alter the environmental conditions for microbial growth and biogeochemical fluxes (González et al. 2006). Earthworms also act as inoculators of soil microbes for the freshly fallen plant materials, and consequently accelerate the decomposition of plant materials (González 2002). Endogeic earthworms alter soil properties primarily through changing soil physical and chemical properties and epigeic earthworms mainly affect microbial inoculation and the associated decomposition processes. Anecic earthworm influence soils through both borrowing and inoculation activities (González et al. 2006).

Plant community succession alters the quantity and chemistry of organic inputs to soils (Zou and González 1997). These differences in the organic input influence the patterns of response of the soil biota as do tree species during the process of change from pastures to post-agricultural forests. In addition, land use history and invasions by earthworm exotic species can affect the relative abundance and species composition of a local earthworm fauna distinctly from soil, climate, vegetation, and topography (Hendrix and Bohlen 2002). Regularly in the Neotropics, cosmopolitan earthworm species dominate the pastures at the expense of native ones (Table 5.1). With the conversion of pastures to secondary forests, the richness of earthworm

Table 5.1 Changes of native and exotic earthworm communities along post-agricultural successional stages in the Neotropics

Location	Pattern	Native earthworm	Exotic earthworm	Reference
<i>Brazil</i>				
<i>Manaus</i>	Abandoned plantation of rubber trees	<i>Andiorrhinus</i> sp. 1 <i>An. amazonicus</i> <i>An. venezuelanus tarumanis</i> <i>Rhinodrilus contornius</i> <i>R. priollii</i> <i>R. brasiliensis</i> <i>Tiuba dianaea</i> Data not available Data not available	<i>Pontoscolex corethrurus</i> <i>Dichogaster bolaii</i>	Römbke et al. (1999)
	Secondary forest		None	
	Primary forest		None	
<i>Mexico</i>				
<i>Tabasco</i>	<i>Brachiaria decumbens</i> pasture <i>Cynodon plectostachyus</i> pasture Successional forest	None None None	<i>P. corethrurus</i> <i>P. corethrurus</i> <i>P. corethrurus</i>	Geissen and Gúzman (2006)

(continued)

Table 5.1 (continued)

Location	Pattern	Native earthworm	Exotic earthworm	Reference
Puerto Rico Cayey Mt.	Abandon pasture	None	<i>P. corethrurus</i> <i>Amyntas gracilis</i>	Sánchez-de León et al. (2003)
	Secondary forest	None	<i>P. corethrurus</i>	
	Mature forest	<i>Borgesioa sedecimesetae</i> <i>Estherella</i> sp. <i>Onychochaeta borincana</i> <i>Neotrigaster rufa</i> <i>Trigaster longissimus</i>	<i>P. corethrurus</i>	
		None	<i>P. corethrurus</i> <i>A. rodericensis</i>	
	<i>Pinus caribaea</i> plantation	None	<i>P. corethrurus</i> <i>P. corethrurus</i> , <i>A. rodericensis</i>	
Luquillo Mt.	<i>Swietenia macrophylla</i> plantation	None		González et al. (1996)
	Secondary forest	<i>P. spiralis</i> <i>E. montana</i> <i>E. gatesi</i>		
		None		
Sabana, Luquillo Mt.	Active pasture	None	<i>P. corethrurus</i>	Zou and González (1997)
	Grass-vine-fern	None	<i>P. corethrurus</i>	
	Shrub-small tree	<i>E. gatesi</i>	<i>P. corethrurus</i> <i>A. rodericensis</i>	
			<i>P. corethrurus</i>	
	Forest	<i>E. gatesi</i>	<i>A. rodericensis</i>	

species increases due to the presence of native species (Zou and González 1997). Yet, the exotic earthworms are still dominant in terms of biomass and density (Zou and González 1997, Sánchez-de León et al. 2003). In Puerto Rico, González et al. (1996) found that *Pontoscolex corethrurus* (an exotic earthworm) dominated both plantations and secondary forests but native earthworms occurred only in secondary forests; suggesting that naturally regenerated secondary forests are preferable to plantations for maintaining a high level of earthworm density, biomass and native species in post-agricultural forests. The restoration of secondary forests through natural regeneration on abandoned pastures can promote the recovery of both anecic earthworms and native species (González et al. 1996, Sánchez-de León et al. 2003). Within this context then, in this chapter, we discuss (1) factors that affect the composition of earthworms (soil physico-chemical properties, soil nutrient status, and biotic interactions), (2) habitat disturbance and the invasions of exotic earthworm species, and (3) the physiological mechanisms by which exotic earthworms can successfully invade pastures and disturbed environments. Finally, we highlight gaps in knowledge that might stimulate further studying of native and non native earthworms in natural, agricultural and post-agricultural sites in the Neotropics.

5.2 Discussion

5.2.1 Factors that Affect the Composition of Earthworms

Earthworm communities can be described in terms of numbers, biomass, composition, and diversity of species. These components of earthworm communities are regulated by a combination of environmental factors and biotic interactions. Beyond landscape and regional scales, phylogenetic constraints and geological history determine the distribution and composition of earthworm assemblages. In the North Neotropical region, earthworm communities are mainly constituted of Megascolecidae (Acanthodrilinae and Dichogastrini), then followed by Ocnodrilidae and some Glossoscolecidae (Fragoso et al. 1995). Glossoscolecidae becomes dominant at South America, especially in Brazil, Perú and Colombia (Fragoso et al. 1999a). Earthworm biogeography is also related to past geological history. For example, plate tectonic movements in Caribbean islands might partly explain the differences in earthworm communities and abundance among the Greater Antilles, the Lesser Antilles, and the Bahamas archipelago (Fragoso et al. 1995, James 2004). At the local scale, earthworm community structure may be controlled by a variety of factors such as climate, vegetation, edaphic properties and the biotic interactions in the soil. It has been suggested that these factors affect earthworm communities hierarchically; climate (air temperature) being the predominant factor explaining the variation of earthworm communities, followed by soil nutrient status and seasonal fluctuations of humidity (Fragoso et al. 1999a). However, the predominant factors determining earthworm communities can vary depending on local habitat characteristics. Also, it is difficult to separate the independent effects of environmental

factors as they are often interrelated (e.g., soil temperature and moisture retention) (Lee 1985). Biotic factors may become determinant for earthworm communities, especially in areas invaded by exotic species. Predatory, competitive, or facilitative interactions between native and exotic earthworm species may change the dynamics and composition of the original earthworm community in invaded areas. The community structure we observe in the field is a result of the combined effects from the aforementioned and other factors. We can divide the regulating factors of earthworm communities into two main categories, abiotic and biotic; and the following sections discuss the potential impacts of each on earthworm communities.

5.2.1.1 Abiotic Factors

Soil temperature and moisture. – Edaphic properties have strong controls on earthworm community structure (Fragoso and Lavelle 1992), primarily soil temperature and moisture content, which govern basic requirements for maintaining earthworm activities. Few field studies describe the preferred and/or optimum soil temperatures in relation to earthworm populations due to the difficulty of standardization and concurrently measuring soil temperatures and earthworm activities in natural settings. Generally, the temperature tolerance of earthworms varies depending on the species, collecting site, and the observed conditions (laboratory vs field observation, and methods of experimentation employed) (Lee 1985). However, it has been determined that the optimum temperature range for tropical earthworm growth and activity is between 20–30°C at the surface or sub-surface of the soil in the field (Lee 1985).

Among all environmental factors within the Neotropics, moisture seems to be the principal regulator of earthworm dynamics. Soil moisture content also regulates soil water tension, gas transfer, and other soil fauna activities (i.e. microbial populations), which indirectly affect earthworm communities (Araujo and López-Hernández 1999). In general, total earthworm numbers and biomass increase with an increase in soil moisture content (Garnsey 1994, Araujo and López-Hernández 1999, Schmidt and Curry 2001). Fragoso and Lavelle (1992) found maximum earthworm density and biomass in wet tropical forests with 2,000–4,000 mm annual rainfall. Beyond this range, the soils were either too wet or too dry for sustaining an optimum earthworm community. Nevertheless, once soil moisture content meets the basic requirement for earthworm activities, this factor may have less influence on earthworm dynamics. In Puerto Rico, González et al. (1999) found that soil water content, which ranged 40 to over 100%, in wet (tabonuco) forests had no influence on earthworm communities and *Pontoscolex corethrurus* densities.

Soil moisture content usually closely relates to soil temperature fluctuations. The rise of soil temperature due to removal of litter floor or loss of canopy may also result in an increase in soil evapotranspiration rates; which in turn decrease the soil water content. Both soil moisture and temperature fluctuations cause spatial and temporal (seasonal and annual) heterogeneity in earthworm communities at a variety of ecosystems within the Neotropics. Araujo and López-Hernández (1999)

found that soil temperature and moisture were positively correlated to earthworm densities in a natural savanna of Venezuela. In the east Mexican tropics, soil temperature and moisture significantly affected the relative dominance of endogeic and epigeic groups of earthworm communities in different types of forests (Fragoso et al. 1995). In the tropics, earthworms can either become inactive or migrate into deeper soil when confronting extremely low soil moisture conditions like during droughts (Lavelle 1988). In Colombian pastures and savannas, earthworms showed uniform vertical distribution in the top 20 cm of the soil profile during the rainy season; while during the dry season, most worms moved to deeper soils responding to the decline of soil moisture at the top 20 cm of soil (Jiménez and Decaëns 2000). Seasonal or frequent droughts may convert earthworm communities from mixed species with different ecological strategies to the dominance of some specific species, which are more likely to be opportunistic poly-humic species (Lavelle 1988). Earthworm species richness is negatively correlated to the quiescent period of earthworm population in tropical regions (Lavelle 1988). However, other edaphic characteristics and biotic regulating factors may become more predominant than soil temperature and moisture when the climate factors remain relatively constant, such as in some tropical wet and rain forests.

Soil pH and texture. – Soil properties may be useful predictive variables of earthworm communities, particularly soil pH and texture. Some studies have showed a strong correlation between soil texture and earthworm communities in the Neotropics. Hubers et al. (2003) suggested that “severe” soil physicochemical conditions in Nipe soils of Maricao State Forest, Puerto Rico, resulted in lower diversity and abundance of earthworm communities as compared to Mexico, Venezuela, and other sites in Puerto Rico. These factors included lower soil pH, lower organic matter, and higher exchangeable iron (Fe), magnesium (Mg) and aluminum (Al) concentrations in Nipe soils. However, in the Luquillo Mountains of Puerto Rico, soil pH alone could not explain the distribution and biomass of earthworm communities (González et al. 1996, González et al. 1999, González and Zou, 1999b). The correlation between soil texture and earthworm communities should be explained with caution, since the casting and burrowing activities of earthworms result in the modification of soil texture (silt, clay, and sand contents), soil pH, and bulk density (Lee 1985, Edwards 2004).

Soil nutrients. – Depending on the feeding strategies of earthworms (epigeic, endogeic and anecic groups), earthworms can utilize litter, soil organic matter, plant roots, root exudates and microbes as food resources. Litterfall input (quantity) and quality are more important determinants of the presence and abundance of epigeic and anecic than endogeic earthworm species because of direct consumption of litter by the former groups. Fragoso and Lavelle (1992) showed that earthworm biomass increased with an increase in litter quantity among 14 localities of tropical rain forests. Further, the reduction of litter inputs in most agroecosystems via forest clearing and aboveground crop harvest, which is detrimental to epigeic and anecic species, have resulted in the dominance of endogeic earthworm species in the tropics (Fragoso et al. 1999a). Earthworm abundance is often positively correlated to litter quality (such as litter nitrogen, or phosphorus) and is negatively related to litter polyphenol content (Lee 1985). In the Luquillo Experimental Forest of

Puerto Rico, González and Zou (1999) described a correlation between litter N and phosphorus (P) contents and the biomass of anecic earthworms in both *Dacryodes* and *Heliconia* tree communities. Fragoso and Lavelle (1987) found that litter quality and soil organic matter explained the aggregated distribution of earthworm communities in a Mexican tropical rainforest.

Soil organic matter is considered an important food source for endogeic earthworm species (Lavelle 1988). Earthworms are always found in soils with higher soil organic matter (Lee 1985, Hubers et al. 2003). Hubers et al. (2003) found the density of *P. corethrurus* was higher in sites with soil organic matter above 6.5%. Fragoso and Lavelle (1992) showed that the soil nutrients status, including N, calcium (Ca), and Mg, accounts for 28% of the variation of earthworm communities, which is the second most important factor after soil moisture (45%), in tropical rainforests of Central America, South America, South Africa and Asia. The improved soil fertility status in the soil, either due to increased litterfall inputs and/or the applications of organic and inorganic fertilizers, can enhance earthworm biomass, density and diversity (Zou and González 1997, López-Hernández et al. 2004). Plant living and dead roots, root exudates and associated microbes which form the "rhizosphere", provide alternative food resources for earthworms (Lee 1985, Brown et al. 2000). Aggregated earthworm communities are usually found near the rhizosphere and dominated by endogeic species, because of higher soil carbon input in this zone as compared to the surrounding soil. For example, direct and indirect evidence showed that endogeic earthworm, *P. corethrurus*, fed in and aggregated around the rhizosphere (Brown et al. 2000, Sánchez-de León et al. 2003). *P. corethrurus* was shown to assimilate root-derived carbon of maize plants and sugar cane by directly observing the ^{13}C shift in worm tissues from an originally lower ^{13}C value (from C3 vegetation) to a higher ^{13}C content (from C4 plants) (Brown et al. 2000). Indirectly, Sánchez-de León et al. (2003) suggested that grass roots can be an important food resources for endogeic earthworms, *P. corethrurus*, because root biomass affected the earthworm community and distribution in a chronosequence of pastures in the Cayey Mountains of Puerto Rico. Moreover, Zou and González (1997) suggested root quality as an important factor explaining the difference on earthworm communities between pastures and woody plantations in Puerto Rico. Still, few studies deal with the potential effects that root exudates or microbial-earthworm interactions in the rhizosphere might have on earthworm community patterns. More research is needed in this area; as both microorganisms and root exudates are believed to be favorable food for earthworms. Generally, energy (food quality) and nutrient availability in the soil are good indicators of earthworm communities and their distributions.

5.2.1.2 Biotic Factors

Decaëns and Rossi (2001) investigated the spatio-temporal structure of earthworm communities and its relationship with soil heterogeneity in Colombian pastures; and found that the spatial and temporal variations of soil heterogeneity at regional scales could not completely explain the variability of earthworm distributions (Decaëns

and Rossi 2001). Further, they argued that soil properties explained a small portion of the spatial and temporal structure of earthworm distribution, suggesting that earthworm communities themselves were at a non-equilibrium state, which was possibly caused by biotic interaction, such as competition exclusion (Decaëns and Rossi 2001) or predatory pressure.

Predatory pressure. – The earthworm tissue is enriched with proteins and thus earthworms are favored food for many animal species, which include birds, mammals, amphibians, reptiles, beetles, flatworms and some other invertebrates (Macdonald 1983, Lee 1985, Judas 1989, Blackshaw 1995). Most studies on earthworm predation focused either on the effects of predators on a single earthworm species or on the predator behavior. Lee (1985) argued that few studies have gathered data on amounts of earthworms captured or eaten by the predators, how predators affect earthworm populations, or the significance of earthworms in the energy flow of the food web. Yet, some studies had been done on the potential impacts of predatory pressure (mostly birds) on the structure of earthworm communities in temperate forests (Bengtson et al. 1976, Barnard and Thompson 1985, Judas 1989, Blackshaw 1995). For example, Bengtson et al. (1976) found twice the abundance and biomass of earthworms in protected plots than in the plots exposed to predation of golden plovers (*Pluvialis apricaria*) in an Icelandic hayfield. Judas (1989) found the average mortality of earthworms that were exposed to the predators (chilopod, *Strigamia acuminata*) was two times higher (64%) than the control (chilopod-excluded; 31%) in a 2-month field microcosm experiment. However, he did not find any significant effects of predatory pressure from macro-predators (birds, carabids, rodents, and shrews) on earthworm populations and vertical distribution in exclusion and control plots in another 7.5 mo field exclusion experiment in a beech forest (Judas 1989). The predation pressure may not always play a significant role on earthworm communities, and its inconsistent influence may depend on the seasons and certain situations (such as changes in vegetation and invasion of new predators). Shifts of vegetation types due to anthropogenic factors can result in the presence and/or absence of litter floor and canopy, which in turn may change the intensity of predatory pressure on earthworm communities though predatory efficiency and/or as related to different assemblages of earthworm predators. Blackshaw (1995) investigated the population sizes of invasive predatory flatworm, *Artioposthia triangulata*, and its impacts on earthworm communities in grasslands of Ireland. With the presence of predatory flatworms, he found a reduction in earthworm species richness (Blackshaw 1995). However, potential relationships between earthworms and their predators due to vegetation changes have not been intensively explored. In the Neotropics, many tropical pastures have been gradually converted to grasslands or secondary forests following the abandonment of agricultural practices due to soil degradation and changes in economic strategies (e.g., Brazil and Puerto Rico, see Buschbacher 1986, Helmer 2004). This post-agricultural succession provides great opportunities to investigate the dynamics of earthworms and their potential predators along the successional stages.

Intra- and inter-populations interactions. – Three ecological groups of earthworms (epigeic, endogeic, and anecic groups) represent different abilities to utilize resources (niche partitioning), including space and nutrients (Bouché 1977). Epigeic

species are litter-dwelling and mostly feed on surface litter, while endogeic species live in the soil and consume organic residues and soil. Anecic species, which live in permanent vertical burrows, eat and bury surface litter (Lee 1985). When the niche of different earthworm species overlap, significant competition would be expected due to the use of similar resources. Since 1980s, several researchers have been interested in the competitive interaction among earthworms. Competition intensities are found to vary among different earthworm species from many laboratory studies (Abbott 1980, Hamilton et al. 1988, Butt 1998, Dalby et al. 1998, Baker et al. 2002, Lowe and Butt 2002). For example, Abbott (1980) showed persistent competition for food between *Eisenia foetida* and *Microscolex dubius*, but not between *E. foetida* and *Allolobophora trapezoides*. In a laboratory study by Butt (1998), the decrease of growth rates and cocoon production of *Allolobophora longa* resulted from both intra-specific competition and inter-specific competition with *Lumbricus terrestris*. Winsome et al. (2006) described that *Argilophilus marmoratus* had lower growth and reproduction rates in the presence of *A. trapezoides* in different habitats in a California grassland. They attributed this to the competition for exploiting similar food resources (particularly microbes) (Winsome et al. 2006). In contrast to the abovementioned studies from temperate ecosystems, few studies have focused on the competitive relationships between native and exotic earthworm species in the tropics (Hendrix et al. 1999, Lachnicht et al. 2002). Hendrix et al. (1999) examined earthworm resource utilization under field conditions in three different forest ecosystems (elfin forest, tabonuco forest, and a pasture) in Puerto Rico by using the natural abundance of ^{13}C and ^{15}N . The differences in ^{15}N fractions within native and exotic earthworm species when they co-exist in the soil indicated that there might be resource competition between native and exotic species (Hendrix et al. 1999). Also in Puerto Rico, Lachnicht et al. (2002) set up a 19-day incubation experiment to evaluate the interactive effects of *P. corethrurus* (an exotic earthworm) with native *Estherella* sp. by using stable isotopes. *P. corethrurus* and *Estherella* sp. were found to inhabit different soil layers when incubated together. In addition, *P. corethrurus* assimilated different nitrogen resources in the presence of *Estherella* sp. (Lachnicht et al. 2002). In the field, habitat disturbance and invasion of exotic earthworm species usually trigger or enhance competitive exclusion within earthworm communities due to the shortage of food resources. Nevertheless, it is still not clear how competitive exclusion and its intensity affect the structure of earthworm communities in different ecosystems; especially in the tropics.

Although environmental (abiotic) and biotic factors are determinants on earthworm communities, earthworm activities can reversibly affect their environments. Earthworms, as ecological engineers, have significant impacts on the soil abiotic and biotic environment and can regulate the availability of resources for other species by directly or indirectly modifying their habitats (Lee 1985, Edwards 2004). Soil moisture, soil texture, organic matter distribution, and soil nutrient cycling can be modified by earthworm activities, e.g. casting and building burrows (Lee 1985, Edwards 2004). Hence, unique earthworm assemblages are generally believed to reflect not only their specific adaptations or preferences to the local surroundings, but also the habitat they build.

5.2.2 *Habitat Disturbance and the Invasion of Exotic Earthworm Species*

Habitat disturbance can modify biotic and abiotic factors, which in turn can have significant effects on the composition of earthworm communities as discussed earlier. Natural disturbances, such as flooding and landslides caused by hurricanes, can result in temporal changes of earthworm communities through the alteration of litter inputs and soil properties in localized areas. However, anthropogenic disturbances, like forest clearing, human inhabitation and land-use management, can occur more frequently than natural disturbances and have more permanent and devastating influences on earthworm communities. For instance, large areas of tropical moist forests had been converted into savannas and pastures in Asia, Africa, South America, and Central America (Buschbacher 1986). Tropical trees in the original forests of Central America have been replaced with shrubs, annual/perennial crops or grasses (Nations and Komer 1983). This transformation of vegetation types causes a reduction of litter quality/quantity, alteration of root distribution and availability, and modification of soil properties. As a result, these abrupt fluctuations on soil physical/chemical conditions and food resource availability from habitat disturbance can modify the original composition and distribution of earthworms taxonomically and functionally (Abbott 1985, González et al. 1996, Sánchez-de León et al. 2003, Sánchez-de León and Zou 2004). Often, there is a significant decline of earthworm diversity, with endogeic earthworm species becoming dominant after vegetation conversion from forests to agroecosystems in most tropical countries (Blanchart and Julka 1997, Fragoso et al. 1999b, González et al. 2006). However, the alteration of earthworm communities will vary with the nature of land-use management and as it relates to the intensity and frequency of the disturbance (Abbott 1985, Fragoso et al. 1999a). For example, the dominance of earthworm ecological groups can be modified from the endogeic species in natural savannas (*Glossodrilus* n. sp.; 80%) to anecic species (88%) in the man-made pastures in Eastern Colombia (Jiménez et al. 1998).

Recently, it has been found that anthropogenic habitat disturbance can enhance the introduction of exotic earthworm species (Fragoso and Lavelle 1992, González et al. 2006). The invasion of exotic earthworm species can alter local native earthworm communities (Kalisz 1993, Kalisz and Wood 1995). The success for exotic earthworms to invade novel areas or their potential impacts on native earthworm communities depends greatly on population characteristics of both exotic and native earthworms and the local environmental and soil properties. Hendrix et al. (2006) illustrated the possible sequences of invasion depending on degree of habitat disturbance and invasion success by exotic earthworms invading ecosystems inhabited by native earthworms (Figure 5.1). They hypothesized that the intensity of habitat disturbance (severe, moderate or minimal) would influence native earthworm communities in the natural ecosystems differentially. Exotic species can occupy disturbed areas, exclusively or by coexisting with native earthworm species where competition displacement could happen in the later case (Hendrix et al. 2006). Hendrix et al. (2006) also proposed three main mechanisms (propagule pressure, habitat match

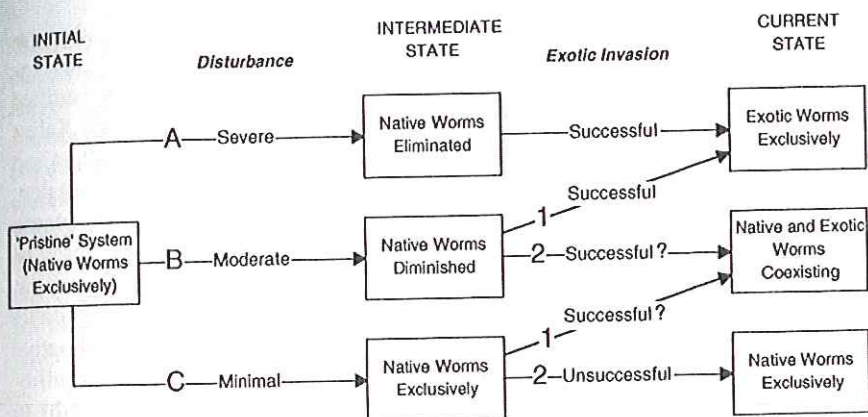


Fig. 5.1 Hypothesized sequences of invasion depending on degree of habitat disturbance and invasion success by exotic earthworms invading ecosystems inhabited by native earthworms (reproduced with kind permission of Springer Science and Business Media from Fig. 1 of Hendrix et al. 2006)

and biotic resistance) to determine invasion success or failure of exotic earthworm species during the invasion processes. Propagule pressure relates to the magnitude of the exotic earthworm introduction into the invaded soils, in terms of the frequency of the introduction and size of the introduced population (Hendrix et al. 2006). Repeated introductions and more individuals involved during each introduction can enhance the success of exotic earthworm populations to establish, proliferate and disperse. Hence, population characteristics (such as life history and reproduction strategy) of the invasive species become determinant elements at this initial stage of invasion. For example, high fecundity and parthenogenesis can boost certain exotic earthworm species to build their populations in a relative short time (Hendrix et al. 2006). Nevertheless, even with the advantage of the propagule pressure, exotic earthworm species still have to adapt to the local environment that they attempt to invade, which may encompass different plant communities, food resource availability, and soil properties. As noted earlier, these abiotic environmental factors are basic requirements for earthworm populations and significantly affect earthworm communities and distributions. Hendrix et al. (2006) called this "adaptation" step to the invaded environment as the "habitat matching" mechanism, which is relevant for distribution, growth and reproduction of exotic earthworms. The characteristics of higher tolerance and flexible plasticity to the environment can make exotic earthworm species more competitive than other earthworm species, especially when they invade into the disturbed areas. Superior adaptation ability to new environments and reproduction biology (e.g., parthenogenesis and *r*-selected strategy) are generally attributed to the success of exotic earthworm species, e.g. *Pontoscolex corethrurus*, a pan-tropical distributed invasive earthworm species (Fragoso et al. 1999a, González et al. 2006, Hendrix 2006). The third mechanism, "biotic resistance", hypothesized the potentially resistant forces from local native communities to impede the invasion of exotic earthworms. Predatory pressure, parasitism, and competition with indigenous earthworm species for resources can retard the establishment of exotic

earthworms even when they are able to overcome the challenges of propagule pressure and habitat matching (Hendrix et al. 2006). Biotic resistance gives a reasonable explanation for the lack of invasion of exotic earthworms in some undisturbed forests adjacent to areas they have invaded (Lavelle and Pashanasi 1989, Kalisz 1993). In addition, recognition systems on exotic earthworms by new predators and parasites may not develop in a relative short time at the beginning of the invasion. Competition relationships with local native earthworm communities may play a more important role for invasion success of exotic earthworm at the early stage of invasion. The resistance to the invasion from the native earthworm communities can be weakened by habitat disturbance. The shortage of food availability and unsuitable soil conditions from habitat disturbance are usually detrimental to the local native earthworms. As a result, habitat disturbances devastate the integrity and equilibrium of local earthworm communities and can curtail their resistance strengths to impede the invasion of exotic species. In disturbed areas, the mechanisms for exotic earthworms to become the dominant species include not only the two advantages discussed above (adaptation plasticity and reproduction biology), but also the lack of competition stress from local native earthworm communities (Fragoso et al. 1999a, González et al. 2006).

Consistent with Hendrix et al. (2006), González et al. (2006) showed different pathways by which exotic earthworms can establish populations in natural and disturbed ecosystems (Figure 5.2). In natural ecosystems with no or minor disturbance,

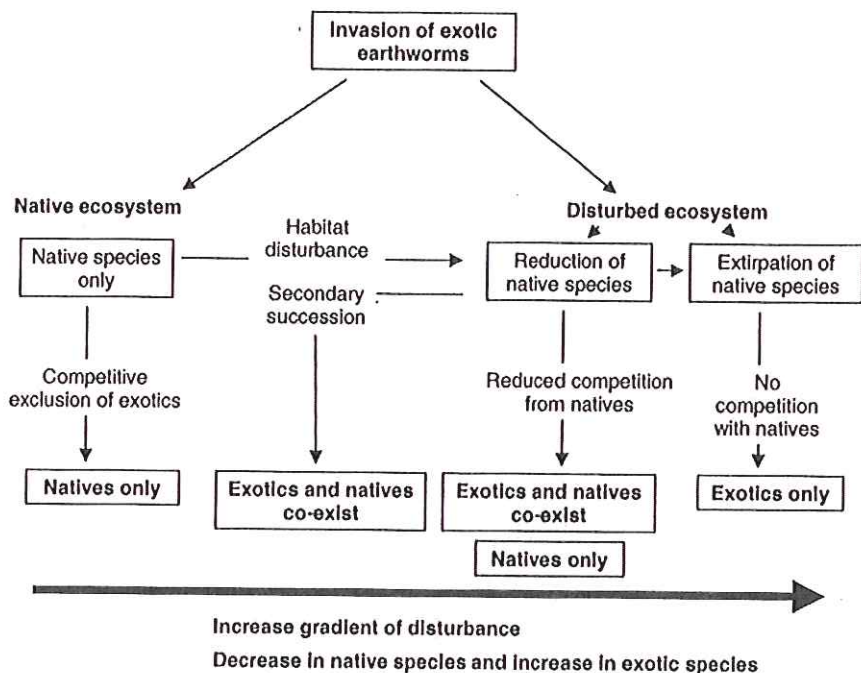


Fig. 5.2 Model illustrating the paths by which invasion of exotic earthworms affect native earthworm species in undisturbed and disturbed ecosystems (reproduced with kind permission of Springer Science and Business Media from Fig. 1 of González et al. 2006)

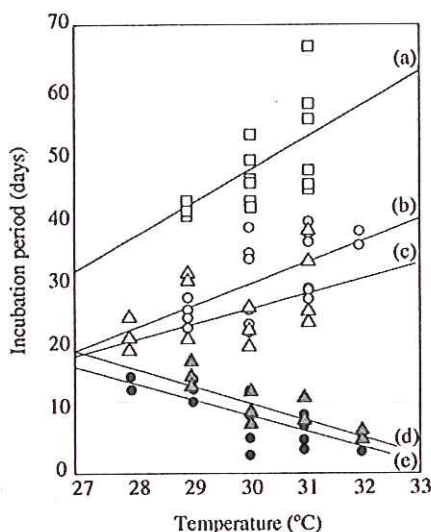
the integrity of local native earthworm communities gives few chances for exotic earthworm species to invade. Once native earthworm communities are excluded and/or disrupted by habitat disturbance in the disturbed areas, exotic earthworm species can occupy the empty niches released by native earthworms to build their populations. The intensity and frequency of disturbance will significantly affect the completeness of native earthworm communities (biotic resistance), therefore the invasion success for exotic earthworm species (González et al. 2006). In reality, these three mechanisms (propagule pressure, habitat matching, and biotic resistance) correlate to one another when explaining the invasion success of exotic earthworms. More efforts are needed to test and clarify each of these mechanisms. The relative importance of each mechanism may be diverse in the different ecosystems.

5.2.3 The Physiology of Exotic Earthworms: Mechanisms for Successful Introductions in Pastures and Disturbed Environments

The reproductive biology of exotic species is an important characteristic to deem in the context of invasion (González et al. 2006). Tropical peregrine earthworms (e.g., *P. corethrurus*, *Perionex excavatus*, *Dichogaster modigliani* and *Polypheretima elongata*) are often considered to be continuous breeders with high fecundity (Bhattacharjee and Chaudhuri 2002). So that on the basis of response to selection pressure, high fecundity, short incubation period with high hatching success are probably adaptative strategies of *r*-selected organisms that enables them to survive drastic environmental changes, especially heat, drought and predation in the soil (Pianka 1970, Bhattacharjee and Chaudhuri 2002). Up until now, endogeic earthworms are more frequent invaders of disturbed tropical pastures than epigeic species. Interestingly, exotic endogeic species (e.g., *P. corethrurus*, *P. elongata* and *Drawida nepalis*) have been shown to increase their rate of cocoon production and incubation period with increased temperature (Figure 5.3) while epigeics decreased their reproductive capabilities (Bhattacharjee and Chaudhuri 2002). Thus, the interactions between the characteristics of the exotic earthworm species—particularly their functionality and activities—could determine their potential for establishment (González et al. 2006).

Animals have physiological adaptations to the environment, and earthworms are no exception. Efficient adaptations to the environment by earthworms ensure the survival of species, particularly that of non-natives. How can *P. corethrurus* adapt and distribute widely in tropical areas around the world? The physiological adaptations of this species may be very important to consider when answering this question. For example, some earthworm species, such as *Lumbricus terrestris*, *Amyntas gracilis*, *A. robustus*, and *Metaphire schmardae*, crawl out of the soil after a heavy rain exposing themselves to predation (Chuang et al. 2004, Darwin 1881, Tsai 1964). Other earthworm species do not. In tropical and subtropical Taiwan, *P. corethrurus* is a common exotic worm; where it has

Fig. 5.3 Relationship between temperature and incubation period in different earthworm species (a) *Polypheretima elongata*, (b) *Drawida nepalensis*, (c) *Pontoscolex corethrurus*, (d) *Dichogaster modiglianii*, and (e) *Peryonix excavatus*. Endogeic species are represented with open symbols and epigeic species are represented with filled symbols (modified from Bhattacharjee and Chaudhuri 2002)



not been observed to crawl out of the soil after a heavy rain. To understand why some earthworms crawl out of the soil, Chuang et al. (2004) and Chuang and Chen (in press) investigated the respiration physiology of *A. gracilis* (a native earthworm to Taiwan) and *P. corethrurus* by placing earthworms in open and sealed bottles filled with air-saturated water. They found the mean survival time of *A. gracilis* in water was 5.4 ± 1.34 h in a sealed bottle and 13.4 ± 6.95 h in an open bottle. A control earthworm remained alive for more than 72 h (end of testing) in a humidity box. However, *P. corethrurus* survived five to ten times longer than *A. gracilis* under the same conditions, surviving in water for 45.4 ± 3.58 h in a sealed bottle and to the end of the test (76 h) in an open bottle and for at least 96 h (end of test) in a humidity box (Figure 5.4). When *A. gracilis* was classified as dead, the residual oxygen concentration in the sealed and open bottle was 1.87 or 1.5 $\mu\text{g/ml}$, respectively. However, *P. corethrurus* could survive until the oxygen concentration in the sealed and open bottles fell to 0.73 or 0.64 $\mu\text{g/ml}$, respectively (Figure 5.5). Therefore, it is reasonable to infer that *P. corethrurus* might use anaerobic respiration in oxygen-shortage conditions. *Amyntas gracilis* was found to have a diurnal rhythm of oxygen consumption, using more oxygen at night than during the day. However, *P. corethrurus* lacked a diurnal rhythm (Figure 5.6). *P. corethrurus* consumed similar amounts of oxygen at different time periods and temperatures. In addition, the cocoon and juveniles of *P. corethrurus* are easily found on the soil surface throughout the entire year unless the soil is extremely dry (Chuang et al. 2004). If the soil humidity is too low, then *P. corethrurus* will go into torpor. They twist their body into a coil and secrete mucus to maintain moisture (Chuang et al. 2004). This phenomenon was also described for *Glossoscolex paulistus* (Abe 1985), and they are both classified as Glossoscolecidae. Thus, *P. corethrurus* has lower oxygen consumption, tolerates poor oxygen concentrations in the environment and adapts to a wide range of soil temperatures. These physiological adaptations could well

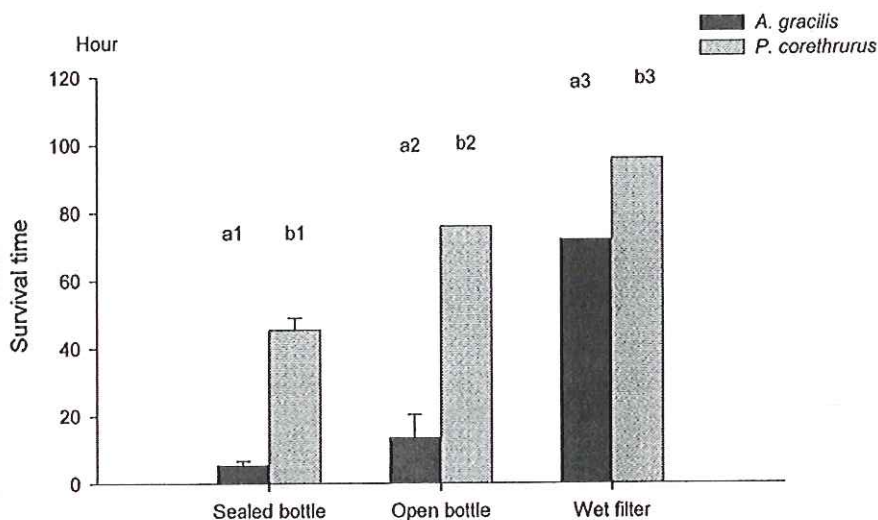


Fig. 5.4 Survival times of submerged earthworms. Earthworms were kept in an open or sealed bottle filled with artificial spring water (ASW) at 25°C. Different letters indicate significant differences. The data are the mean \pm SD ($n = 20$) for the survival time (Chuang et al. in press).

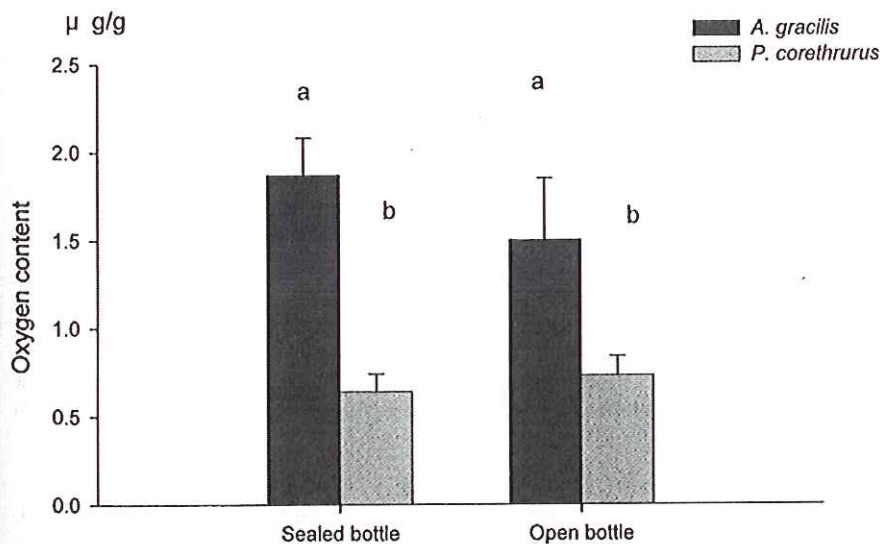


Fig. 5.5 Oxygen remaining in artificial spring water-containing bottle at 25°C. The value was measured immediately after the worm was found to be dead. Different letters for different treatments indicate significant differences. The data are the mean \pm SD ($n = 20$) for the residual oxygen content (Chuang et al. in press)

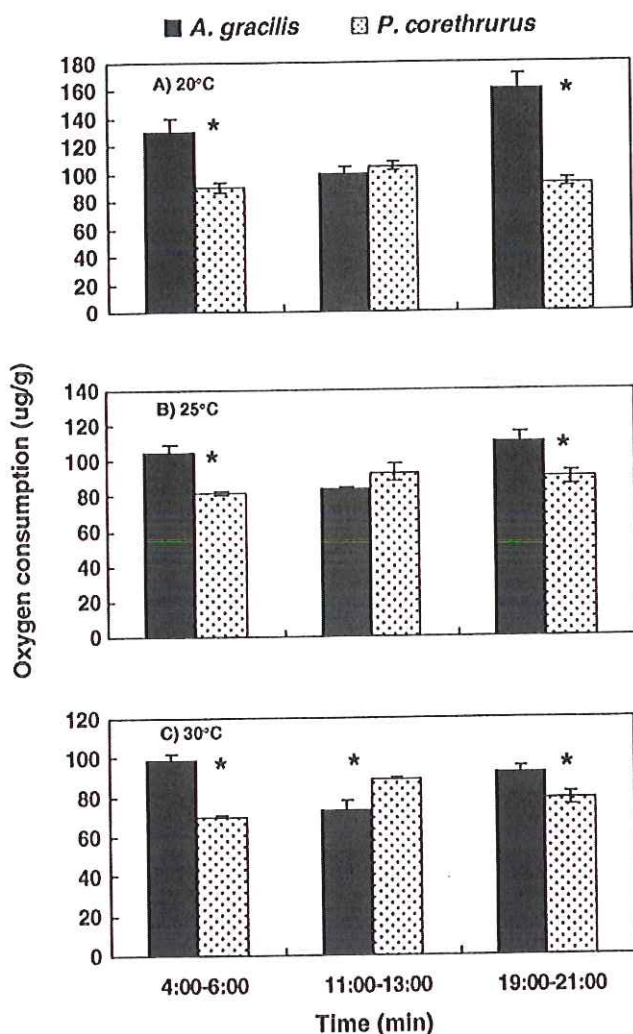


Fig. 5.6 Total oxygen consumption of two species of earthworms at different temperatures. The oxygen consumption of *A. gracilis* was significantly higher than *P. corethrurus*, regardless of being at the different temperature ($P < 0.001$). The asterisks indicate significant difference (from Chuang et al. 2004)

explain why *P. corethrurus* is widely distributed in the tropics around the world. On the other hand, the high oxygen demand of *A. gracilis* (especially at night), causes it to expose its body on the soil surface to exchange for air, consequently making them more susceptible to predation. This behavior is not observed in *P. corethrurus* (as it is an endogeic species), which might be another explanation as to why *P. corethrurus* can be a successful exotic earthworm (Chuang et al. 2004) in pastures and disturbed sites with a non continuous canopy cover. Another characteristic that makes *P. corethrurus* a hard-hitting invader is the ability that the juveniles

have to enter diapause and regenerate after amputation independent of soil moisture (Fragoso and Lozano 1992). This phenomenon and the fact that parthenogenesis is common for most tropical exotics (Fragoso et al. 1999b) could well be adaptive strategies of tropical exotic earthworms to avoid predation pressure in a climatically harsh environment; making them without doubt strong invaders and competitors (González et al. 2006).

In addition to the respiration adaptation to water-saturated environments, *P. corethrurus* exhibits other traits that help them survive in severe environments. *P. corethrurus* has high tolerance to ultraviolet radiation (UV) (Chuang et al. 2006). Chuang et al. (2006) tested UV effects on the behavior and physiology of three species of earthworms: *A. gracilis*, *M. posthuma* and *P. corethrurus*. They found that *P. corethrurus* would crawl slowly after UV (Figure 5.7), but surprisingly, they would not die or have tissue damage even after 24 h of ultraviolet radiation (Figure 5.8). The influence of UV to *P. corethrurus* may be temporary, as UV influences their crawling activity, but these earthworms may have some mechanism to protect themselves. It is known that the development of pigment is an important

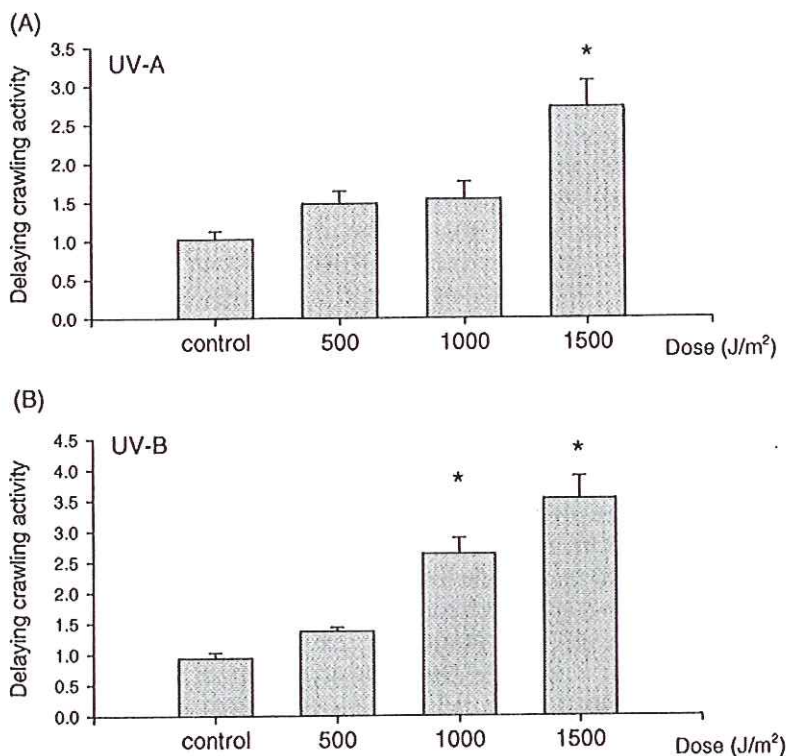


Fig. 5.7 Relative crawling time of earthworms after exposure to either UV-A and UV-B. A) The crawling time of *Pontoscolex corethrurus* exposed to $1,500\text{ J/m}^{-2}$ of UV-A was significantly increased compared to controls (ANOVA, $N=6$, $*P<0.01$) B) After UV-B exposure, *P. corethrurus* show a significantly increased crawling time compared to controls (ANOVA, $N=6$, $*P<0.01$) (from Chuang et al. 2006)

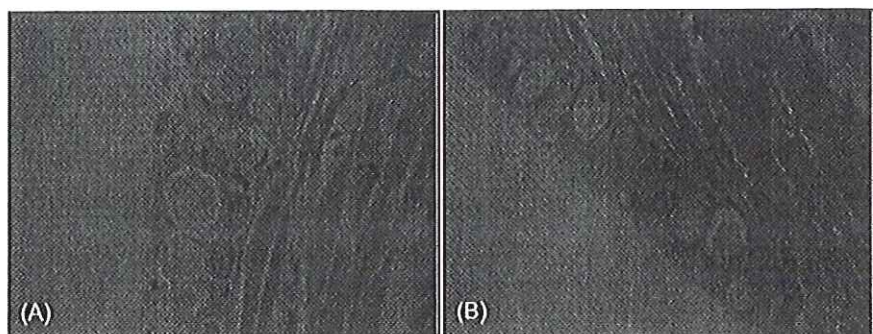


Fig. 5.8 Cross section photographs of *Pontoscolex corethrurus* tissue A) with no UV radiation (control) and B) as exposed to UV radiation at a dose of $1,500 \text{ J/m}^2$ after 24 h. No changes in the epidermis were observed after 2, 12 and 24 h (as shown in B) of UV radiation. Also note the many granular cells in the epidermis by which *P. corethrurus* can secrete more mucus than *A. gracilis* or *M. posthuma* (photographs taken by Shu-Chun Chuang)

adaptation against solar radiation. However, *P. corethrurus* does not show much pigmentation in the epidermis. Yet, the mucus and epidermis of *P. corethrurus* is thicker than other species of earthworms (Chuang, personal observation). In addition, *P. corethrurus* mucus may contain chemicals that help absorb UV and protect their skin. Experimentation with earthworm mucus is problematical given difficulties in the extraction of mucus from the earthworm skin surface (Chuang, personal communication). Accordingly, Chuang et al. (2006) proposed that *P. corethrurus* might utilize substances such as mycosporine-like amino acid (MAA) or flavonol quercetin, and/or some enzymes like photolyase to protect itself. Chuang et al. (unpublished data, not shown), showed that *P. corethrurus* has a high activity of Protein kinase before and after UV radiation. Protein kinase activity is related to the release of acetylcholine, which is an important hormone in neuromuscular junction. Earthworms can have better movement behavior with higher acetylcholine activity. On the other hand, oxidative stress and lipid peroxidation after ultraviolet radiation may be lethal for earthworms because the final product of lipid peroxidation is lipid peroxide (LOOH). LOOH will lead to the accumulation of malondialdehyde (MDA) in the earthworm muscle/skin tissue. When MDA reacts with thiobarbituric acid (TBA), it forms TBA-reactive substances (TBARS). Therefore, we can extract MDA from earthworm skin/muscle tissue to react with TBA and test the level of lipid peroxide. The higher TBARS means the higher LOOH. Therefore, TBARS can be good indicators of lipid peroxidation. For example, when *P. corethrurus* is exposed to $1,000 \text{ J/m}^2$ UV-B, the concentration of TBARS increased after 2 hr, however, at other doses of UV-B radiation, the concentration of TBARS did not change; meaning that *P. corethrurus* did not have much lipid peroxidation after UV-B exposure (Table 5.2, unpublished data).

Chuang et al. (unpublished data) also found that the anti-oxidant enzyme activity of other earthworm species decreased after UV radiation, but in *P. corethrurus*, it remained high after UV radiation (Table 5.2, unpublished data). Girotti (2001) classified the photo-oxidative damage into four degrees and according to these

Table 5.2 MDA level and catalase activity in muscle/skin tissue (Chuang et al. unpublished data)

Dosage (J/m ²)	Time (min)	TBARS (mmol/g) ¹	Catalase activity (mU/mg) ²
Control		15.029±1.91	4.67±0.94
500	15	17.57±1.38	5.62±0.36
	120	15.07±3.92	5.52±0.62
	240	14.88±2.24	5.04±0.52
1,000	15	20.12±2.85	5.65±0.38
	120	23.45±1.22 (* ³)	5.07±1.13
	240	14.53±1.01	4.94±0.24
1,500	15	22.12±3.97	5.95±0.27
	120	23.31±3.58	4.79±0.87
	240	17.74±2.68	5.30±0.37
3,000	15	16.06±4.27	5.69±0.38
	120	21.40±2.52	5.53±0.38
	240	14.78±1.12	4.87±0.21

¹The MDA level of muscle/skin tissue depended on minutes expose and doses of UV-B radiation. The concentration of MDA was used to estimate the extent of lipid peroxidation.

²Effect of UV-B radiation on catalase activity in muscle/skin tissue. The activity meant the ability of anti-oxidative stress.

³Asterisk (*) meant significant differences compare to control treatment (Two way ANOVA test, $p < 0.05$).

results from *P. corethrurus*; it should be classified into secondary degree. It means that epidermal cells of *P. corethrurus* have been influenced slightly after ultraviolet radiation, but the increase of lipid peroxidation also turned on the anti-oxidative mechanism and further protected the epidermal cells. In the aforementioned study, the anti-oxidative enzyme of *P. corethrurus* was also found to be kept at a high activity after UV radiation and the reasons for this are unknown. Therefore, *P. corethrurus* still had enough protection from UV and did not die. The oxidative stress relates not only to the effects of ultraviolet radiation but also to other stresses such as heavy metal pollution and an adversely compromised physiology. Therefore, if *P. corethrurus* has high tolerance to oxidative stress, they would better survive in a harsh environment. Certainly, we also argue that this mechanism can help *P. corethrurus* invade successfully disturbed sites throughout in the tropics.

5.3 Summary

In the Neotropics, large areas of pasture have been gradually converted to grasslands or secondary forests following the abandonment of agricultural practices. These areas covered with the secondary succession are expected to expand in the near future because of the adjustment of economic strategies and soil degradation problems in these tropical countries (e.g., Brazil and Puerto Rico, Buschbacher 1986, Birdsey and Weaver 1987, Helmer 2004). For now at least, these post-agricultural succession processes boost the recovery of natural landscapes and vegetations and help the restoration of natural ecosystems. Natural succession (no attempted management) evolved from these post-agricultural lands provides an

opportunity to observe the dynamics of vegetation communities, the re-colonization sequence of soil fauna, and further the interactive relationships among plants, soil fauna, and microbes within considerable areas along the continuum of successional forests. These areas also represent an excellent opportunity to explore the linkage between aboveground communities (forest types, vegetation cover) and belowground soil fauna (especially earthworm communities) in post-agricultural lands. In addition, the variety of exotic and native earthworm communities observed in post-agricultural fields provide for good opportunities to test the mechanisms of invasion biology. The case study from post-agricultural pastures and secondary forests of Puerto Rico showed that native earthworm communities are gradually re-colonizing the forests as aboveground plant communities mature. We can test the three mechanisms (propagule pressure, habitat matching, and biotic resistance) proposed by Hendrix et al. (2006) by monitoring dynamics of exotic and native earthworm populations and/or conducting field experiments along post-agricultural/succession gradients. Comparisons between different ecosystems and geographic regions are also possible by using earthworms as an experimental model for invasion biology.

5.4 Future Research Directions

The history of the introductions of non-native flora and fauna is much more complex in the Neotropics than in temperate North America; as it is related to the complex human history of migration and use of the landscape, water barriers and island ecosystems. An interdisciplinary approach (i.e., history and ecology) can help elucidate the spreading of non-native species in the tropics and the development of sustainable land management practices (González et al. 2006). Landscape scale dynamics of earthworm distributions within changing landscapes; and physiological and other mechanisms controlling community dynamics are important areas of future study on earthworm ecology in the Neotropics. As discussed above, *P. corethrurus* shows better physiological adaptations than other earthworms in terms of oxygen utilization, oxygen consumption, ultraviolet tolerance and high anti-oxidative enzyme activities. These physiological traits can be powerful and effective competitive adaptations when non native earthworms invade new areas. Yet, many questions related to the physiological adaptation of exotic earthworms like *P. corethrurus* remained unanswered. For example, why can *P. corethrurus* survive in oxygen-shortage conditions? Why does *P. corethrurus* have high tolerance to ultraviolet radiation? Why does it have higher anti-oxidative stress in its body? The hemoglobin of earthworms (mega-hemoglobin) is different from vertebrates. Thus, is the high oxygen binding affinity of *P. corethrurus* hemoglobin that can help worms survive in anoxia condition? Also, although we do know that *P. corethrurus* is tolerant to UV; we still do not understand the mechanism by which it can protect itself from the radiation. *P. corethrurus* mucus is thick and sticky and we infer it has some protective chemicals. MAA is a chemical which can absorb ultraviolet in sea hare (Carefoot et al. 1998) and photolyase is an enzyme known to repair DNA damage in frogs (Blaustein et al. 1998). To date, it is unknown whether or not

earthworms have these chemicals, but these topics merit study. On the other hand, heavy metals, pesticides or chemical fertilizers are also harmful to earthworms, but their toxicity to *P. corethrurus* is not well understood. Exactly how species such as *P. corethrurus* can survive in pastures and / or agricultural fields requires further investigation.

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References

- Abbott, I. 1980. Do earthworms compete for food? *Soil Biol. Biochem.* 12:523–530.
- Abbott, I. 1985. Distribution of introduced earthworms in the Northern Jarrah Forest of Western Australia. *Aust. J. Soil Res.* 23:263–270.
- Abe, A. S. 1985. Oxygen uptake of active and aestivating earthworm *Glossoscolex paulistus* (Oligochaeta, Glossoscolecidae). *Comp Biochem Physiol* 81A(1):63–66.
- Araujo, Y., and López-Hernández, D. 1999. Earthworm populations in a savanna-agroforestry system of Venezuelan Amazonia. *Biol. Fertil. Soils* 29:413–418.
- Baker, G., Carter, P., Barrett, V., Hirth, J., Mele, P., and Gourley, C. 2002. Does the deep-burrowing earthworm, *Aporrectodea longa*, compete with resident earthworm communities when introduced to pastures in south-eastern Australia? *Eur. J. Soil Biol.* 38:39–42.
- Barnard, C. I., and Thompson, B. A. 1985. *Gulls and Plovers: The Ecology of Mixed-species Feeding Groups*. New York: Columbia University Press.
- Bengtson, S.-A., Nilsson, A., Nordström, S. and Rundgren, S. 1976. Effects of bird predation on lumbricid populations. *Oikos* 27:9–12.
- Bhattacharjee, F., and Chaudhuri, P. S. 2002. Cocoon production, morphology, hatching pattern and fecundity in seven tropical earthworm species: a laboratory-based investigation. *Journal of Biosciences* 27:283–294.
- Birdsey, R. A., and Weaver, R. W. 1987. Forest area trends in Puerto Rico. Research Note SO-331, USDA Forest Service, Washington, D.C., USA.
- Blackshaw, R. P. 1995. Changes in populations of the predatory flatworm *Artioposthia triangulata* and its earthworm prey in grassland. *Acta Zoolog. Fennica* 196:107–110.
- Blanchart, E., and Julka, J. M. 1997. Influence of forest disturbance on earthworm (Oligochaeta) communities in the Western Ghats (South India). *Soil Biol. Biochem.* 29:303–306.
- Blaustein, A. R., Kiesecker, J. M. D., Chivers, P., Hokit, D. G., Marco, A., Beloden, L. K., and Hatch, A. 1998. Effect of ultraviolet radiation on amphibians: field experiments. *Am. Zool.* 38:799–812.
- Bouché, M. B. 1977. Ecologie et paraecologie: peut-on apprécier le rôle de la faune dans les cycles biogéochimiques? *Soil Organism as Components of Ecosystems* 25:157–163.
- Brown, G., Barois, I., and Lavelle, P. 2000. Regulation of soil organic matter dynamics and microbial activity in the drilosphere and the role of interactions with other edaphic functional domains. *Eur. J. Soil Biol.* 36:177–198.
- Buschbacher, R. 1986. Tropical deforestation and pasture development. *BioScience* 36:22–28.

- Butt, K. R. 1998. Interactions between selected earthworm species: a preliminary, laboratory-based study. *Appl. Soil Ecol.* 9:75–79.
- Carefoot, T. H., Harris, M., Taylor, B. E., Donovan, D., and Karentz, D. 1998. Mycosporine-like amino acids: possible UV protection in eggs of the sea hare *Aplysia dactylomela*. *Mar. Biol.* 130:389–396.
- Chuang, S. C., Lee, H., and Chen, J. H. 2004. Diurnal rhythm and effect of temperature on oxygen consumption in earthworms, *Amyntas gracilis* and *Pontoscolex corethrurus*. *J. Exp. Zool.* A Comp. Exp. Biol. 301:731–744.
- Chuang, S. C., Lai, W. S., and Chen, J. H. 2006. Influence of ultraviolet radiation on selected physiological responses of Earthworms. *J. Exp. Biol.* 209:4304–4312.
- Chuang, S. C., and Chen, J. H. In press. Diurnal rhythm of oxygen consumption may cause earthworms to crawl out of the soil at night after heavy rain. *Inverte. Biol.* (in press).
- Dalby, P. R., Baker, G. H., and Smith, S. E. 1998. Competition and cocoon consumption by the earthworm *Aporrectodea longa*. *Appl Soil Ecol.* 10:127–136.
- Darwin, C. 1881. *The Formation of Vegetable Mould Through the Action of Worms, with Observation of Their Habits*. London: John Murray.
- Decaëns, T., and Rossi, J.-P. 2001. Spatio-temporal structure of earthworm community and soil heterogeneity in a tropical pasture. *Ecography* 24:671–682.
- Edwards, A. L. 2004. *Earthworm Ecology*. Boca Raton: CRC Press.
- Edwards, C. A., and Bohlen, P. J. 1996. *Biology and Ecology of Earthworms*. New York: Chapman & Hall.
- Fragoso, C., and Lavelle, P. 1987. The earthworm community of a Mexican tropical rainforest (Chajul, Chiapas). In *On Earthworms*, ed. A. M. Bonvicini-Pagliai and P. Omodeo, pp. 281–295. Mucchi: Modena.
- Fragoso, C., and Lavelle, P. 1992. Earthworm communities of tropical rain forest. *Soil Biol. Biochem.* 24:1397–1408.
- Fragoso, C., and Lozano, N. 1992. Resource allocation strategies imposed by caudal amputation and soil moisture in the tropical earthworm *Pontoscolex corethrurus*. *Soil Biology and Biochemistry* 24:1237–1240.
- Fragoso, C., James, C., and Borges, S. 1995. Native earthworms of the North Neotropical Region: current status and controversies. In *Earthworm Ecology and Biogeography in North America*, ed. P. F. Hendrix, pp. 67–115. Boca Raton, FL: Lewis Publishers.
- Fragoso, C., Lavelle, P., Blanchart, E., Senapati, B. K., Jiménez, J. J., Martínez, M. Decaëns, T., and Tondoh, J. 1999a. Earthworm communities of tropical agroecosystems: origin, structure and influence of management practices. In *Earthworm Management in Tropical Agroecosystems*, ed. P. Lavelle, L. Brussaard and P. Hendrix, pp. 27–56. New York: CAB International.
- Fragoso, C., Kanyonyo, J., Moreno, A., Senapati, B. K., Blanchart, E., and Rodríguez, C. 1999b. A survey of tropical earthworms: taxonomy, biogeography and environmental plasticity. In *Earthworm Management in Tropical Agroecosystems*, ed. P. Lavelle, L. Brussaard, and P. Hendrix, pp. 1–26. New York: CABI Publishing.
- Gamsey, R. B. 1994. Seasonal activity and aestivation of Lumbricid earthworms in the Midlands of Tasmania. *Aust. J. Soil Res.* 32:1355–1367.
- Geissen, V., and Gúzman, G. M. 2006. Fertility of tropical soils under different land use systems - a case study of soil in Tabasco, Mexico. *Appl. Soil Ecol.* 31:169–178.
- Girotti, A. W. 2001. Photosensitized oxidation of membrane lipids: reaction pathways, cytotoxic effects and cytoprotective mechanisms. *J. Photochem. Photobiol. B Biol.* 63:103–113.
- González, G. 2002. Soil organisms and litter decomposition. In *Modern Trends in Applied Terrestrial Ecology*, ed. R. S. Ambashit and N. K. Ambashit, pp. 315–329. New York: Kluwer Academic / Plenum Publishers.
- González, G., and Seastedt, T. R. 2001. Soil fauna and plant litter decomposition in tropical and subalpine forests. *Ecology* 82:955–964.
- González, G., Zou, X., and Borges, S. 1996. Earthworm abundance and species composition in abandoned tropical croplands: comparison of tree plantations and secondary forests. *Pedobiología* 40:385–391.

- González, G., Zou, X., Sabat, A., and Fetcher, N. 1999. Earthworm abundance and distribution pattern in contrasting plant communities within a tropical wet forest in Puerto Rico. *Caribb. J. Sci.* 35:93–100.
- González, G., and Zou, X. 1999. Plant and litter influences in earthworm abundance and community structure in a tropical wet forest. *Biotropica* 31:486–493.
- González, G., Huang, C.-Y., Zou, X., and Rodríguez, C. 2006. Earthworm invasions in the tropics. *Biological Invasions* 8:1247–1256.
- Hamilton, W. E., Dindal, D. L., Parkinson, C. M., and Mitchell, M. J. 1988. Interaction of earthworm species in sewage sludge-amended soil microcosms: *Lumbricus terrestris* and *Eisenia fetida*. *J. Appl. Ecol.* 25:847–852.
- Helmer, E. H. 2004. Forest conservation and land development in Puerto Rico. *Landsc. Ecol.* 19:29–40.
- Hendrix, P. F. 2006. Biological invasions belowground- earthworms as invasive species. *Biological Invasions* 8:1201–1204.
- Hendrix, P. F., and Bohlen, P. J. 2002. Exotic earthworm invasions in North America: ecological and policy implications. *BioScience* 52:801–811.
- Hendrix, P. F., Lachnicht, S. L., Callahan, M. A., and Zou, X. 1999. Stable isotopic studies of earthworm feeding ecology in tropical ecosystems of Puerto Rico. *Rapid Comm. in Mass Spectrom.* 13:1295–1299.
- Hendrix, P. F., Baker, G. H., Callahan, M. A., Damoff, G. A., Fragoso, C., González, G., Winsome, T., and Zou, X. 2006. Invasion of exotic earthworms into ecosystems inhabited by native earthworms. *Biological Invasions* 8:1287–1300.
- Hubers, H., Borges, S., and Alfaro, M. 2003. The Oligochaetofauna of the Nipe soils in the Maricao State Forest, Puerto Rico. *Pedobiologia* 47:475–478.
- James, S. W. 2004. Planetary processes and their interactions with earthworm distributions and ecology. In *Earthworm Ecology*, ed. C. A. Edwards. Boca Raton: CRC press.
- Jiménez, J. J., and Decaëns, T. 2000. Vertical distribution of earthworms in grassland soils of the Colombian Llanos. *Biol. Fertil. Soils* 32:463–473.
- Jiménez, J. J., Moreno, A. G., Decaëns, T., Lavelle, P., Fisher, M. J., and Thomas, R. J. 1998. Earthworm communities in native savannas and man-made pastures of the Eastern Plains of Colombia. *Biol. Fertil. Soils* 28:101–110.
- Judas, M. 1989. Predator-pressure on earthworms: field experiments in a beechwood. *Pedobiologia* 33:339–354.
- Kalisz, P. J. 1993. Native and exotic earthworms in deciduous forest soils of Eastern North America. *Biological Pollution: the control and impact of invasive exotic species. Proceedings of a Symposium held at the University Place Conference Center, Indiana University-Purdue University, Indianapolis, October 25 & 26, 1991*:93–100.
- Kalisz, P. J., and Wood, H. B. 1995. Native and exotic earthworms in wildland ecosystems. In *Earthworm Ecology and Biogeography in North America*, ed. P. F. Hendrix, pp. 117–126. Boca Raton, FL: Lewis Publishers.
- Lachnicht, S. L., Hendrix, P. F., and Zou, X. 2002. Interactive effects of native and exotic earthworms on resource use and nutrient mineralization in a tropical wet forest soil of Puerto Rico. *Biol. Fertil. Soils* 36:43–52.
- Lavelle, P. 1988. Earthworm activities and the soil system. *Biol. Fertil. Soils* 6:237–251.
- Lavelle, P., and Pashanasi, B. 1989. Soil macrofauna and land management in Peruvian Amazonia. *Pedobiologia* 33:283–291.
- Lavelle, P., Brussaard, L., and Hendrix, P. 1999. *Earthworm Management in Tropical Agroecosystems*, p. 300. New York: CABI Publishing.
- Lee, K. E. 1985. *Earthworms, Their Ecology and Relationships with Soils and Land Use*. New York: Academic Press.
- Liu, Z. G., and Zou, X. M. 2002. Exotic earthworms accelerate plant litter decomposition in a Puerto Rican pasture and a wet forest. *Ecological Applications* 12:1406–1417.
- López-Hernández, D., Araujo, Y., López, A., Hernández-Valencia, I., and Hernández, C. 2004. Changes in soil properties and earthworm populations induced by long-term organic fertilization of a sandy soil in the Venezuelan Amazonia. *Soil Sci.* 169:188–194.

- Lowe, C. N., and Butt, K. R. 2002. Growth of hatchling earthworms in the presence of adults: interactions in laboratory culture. *Biol. Fertil. Soils* 35:204–209.
- Macdonald, D. W. 1983. Predation on earthworms by terrestrial vertebrates. In *Earthworm Ecology: From Darwin to Vermiculture*, ed. J. E. Satchell, pp. 393–414. London: Chapman and Hall.
- Nations, J. D., and D. I. Komer. 1983. Central America's tropical rainforests- positive steps for survival. *Ambio* 12:232–238.
- Odum, H. T., and Pigeon, R. F. 1970. A tropical rain forest: a study of irradiation and ecology at El Verde, Puerto Rico. S.S. Atomic Energy Commission, National Technical Information Service, Springfield, VA.
- Pianka, E. R. 1970. On r and K-selection. *American Naturalist* 104:459–466.
- Römbke, J., Meller, M., and García, M. 1999. Earthworm densities in central Amazonia primary and secondary forests and a polyculture forestry plantation. *Pedobiologia* 43:518–522.
- Sánchez-de León, Y., and Zou, X. 2004. Plant influences on native and exotic earthworms during secondary succession in old tropical pastures. *Pedobiologia* 48:215–226.
- Sánchez-de León, Y., Zou, X., S. Borges, and Ruan, H. 2003. Recovery of native earthworms in abandoned tropical pastures. *Conservation Biology* 17:999–1006.
- Schmidt, O., and Curry, J. P. 2001. Population dynamics of earthworms (Lumbricidae) and their role in nitrogen turnover in wheat and wheat-clover cropping systems. *Pedobiologia* 45: 174–187.
- Tsai, C. F. 1964. On some earthworms belonging to the genus *Pheretima* Kinberg collected from Taipei area in North Taiwan. *Q. J. Taiwan Mus.* 17:1–35.
- Winsome, T., Epstein, L., Hendrix, P. F., and Horwath, W. R. 2006. Competitive interactions between native and exotic earthworm species as influenced by habitat quality in a California grassland. *Appl. Soil Ecol.* 32:38–53.
- Zou, X., and G. González. 1997. Changes in earthworm density and community structure during secondary succession in abandoned tropical pastures. *Soil Biol. Biochem.* 29:627–629.