

Original article

Land use change affects earthworm communities in Eastern Maryland, USA

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Abstract

We assessed earthworm species composition and abundance during secondary succession at the Smithsonian Environmental Research Center, Maryland, USA. Land use history is well known at this site. Adjacent forest stands of different ages and other vegetation patches were sampled in 1998–99 and in 2006. Out of the 12 species three (*Eisenoides loennbergi*, *Bimastos palustris*, *Diplocardia caroliniana*) were native, the rest were European peregrine earthworms. Native species were mainly found in mature forests, otherwise the species composition of mature and successional stands was similar. Earthworm density and biomass was significantly higher in the successional forests, than in the mature forests, and this pattern appears to be stable at a decadal time scale. Two smaller stands that have never been clearcut did not harbor any earthworms. The forest floor on these sites had a thick organic layer, moder humus and low pH. Bulk density was highest in the youngest (50–70 years) forests. It appears that as the forests enter to a late successional stage (150 years), they no longer can support high abundance of litter feeding earthworms.

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1. Introduction

It has been estimated that prior to European settlement 95% of Maryland was covered with forests [2]. In the Chesapeake Bay region land clearing peaked in the late 1800s, when over 80% of the land was used for agriculture. By the 20th century much of this land has grown back to forest [27]. Today urban and suburban development is the major reason for loss of the remaining forests and agricultural land.

Earthworm invasion in North America has become a major ecological, conservation and management issue [4,14,16,23]. Converting forests into agricultural fields has facilitated exotic earthworm establishment and further dispersion. The steps of earthworm colonization in forests and disturbed sites have been demonstrated in several studies [19]. Much less is known of the reverse process, i.e. how earthworm assemblages change when abandoned disturbed sites, such as agricultural fields are left for forest regrowth [20]. The objective of our study was to compare species composition and abundance in physically adjacent forest stands of various stages of old field succession. We expected high species richness and abundance in the

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successional stands, because of the age of these forests is closer to the initial disturbance. However, it is not known whether these assemblages can maintain high abundances over time, as the forests mature.

2. Methods

2.1. Study site

The Smithsonian Environmental Research Center (SERC hereafter) lies in the Rhode River estuary along the western shore of Maryland. This 2886-hectare watershed is 62% forest, 23% croplands, 12% pasture, and 3% freshwater swamp. The watershed is underlain by relatively impermeable clay layer. Soils at all study sites are fine sandy loams of the Collington–Monmouth series that have formed on sedimentary soils from the Pleistocene Talbot formation [8,28]. The 160-year average rainfall is 1080 mm. Precipitation is evenly distributed throughout the year (<http://www.serc.si.edu/>). The watershed was settled by Europeans in the 1650s and cleared for agriculture. Prior to that time, it was occupied intermittently by Indian villages for several thousand years. Most sites have gone through several land uses including tobacco farming, cultivation of corn wheat and alfalfa, and, prior to abandonment, cattle grazing. The current landscape of SERC is a patchwork of several stages of old field succession and other land cover such as grass and buildings. Forests at SERC have been classified into the Tulip poplar association [6,7,18]. The most common tree species include tulip poplar (*Liriodendron tulipifera*), sweetgum (*Liquidambar styraciflua*), red maple (*Acer rubrum*), several oaks (*Quercus* spp.), hickories (*Carya* spp.) and beech (*Fagus grandifolia*). In successional (50–70 years old) forests spicebush (*Lindera benzoin*) is also common, whereas in mature forests (150+ years old) ironwood (*Carpinus caroliniana*) and dogwood (*Cornus florida*) occur. The herb layer is more diverse in mature forests. Chestnut oak and black gum also occur on the two uncut sites.

2.2. Sampling

We collected earthworms using a variety of techniques. For density and biomass estimates we used formalin extraction [21] on 50 cm × 50 cm quadrats. Sampling took place in summer and fall of 1998, spring 1999, and again in late spring 2006. Seven forest stands (two mature forests, three successional forests, and two sites that were never clear cut) were sampled regularly. An additional sixteen were quantitatively sampled in 1999. A variety of habitats, such as riparian areas,

dried-up beaver ponds and lawns surrounding buildings were included in this sampling.

Earthworms were killed in ethanol and preserved in 4% formalin. Species names are used according to Csuzdi and Zicsi [10]. Most immature individuals could be identified only to genus or family level. These immature earthworms were included in the biomass and density analyses (Fig. 1), but were excluded from the community structure discussion (Table 1, Fig. 3).

For soil and forest floor analysis composite soil samples were collected using a stainless steel coring device with a 5 cm diameter and included at least six subsamples. Forest floor thickness and soil horizons are very different depending on the age of the forest, and earthworm abundance, thus sampling focused on depth rather than on horizons. After coarse leaf litter layer was removed, 0–5 and 5–10 cm cores were taken. Soil pH was determined by glass electrode using a Barnart 20 digital pH/mV/ORP meter kit. Total organic matter content was determined by loss on ignition (470 °C for 24 h) and calculated as a percent initial weight.

2.3. Statistical analysis

The biomass and density values were not normally distributed thus we analyzed the data by Kruskal–Wallis ANOVA. For pairwise comparisons Mann–Whitney test with sequential Bonferroni correction was used [29]. Earthworm community composition was analyzed by cluster analysis (Sorensen index of similarity and Ward's method of separation).

3. Results

The 1651 specimens collected belonged to 12 species (Table 1). With the exception of the native *Diplocardia caroliniana* (Acanthodrilidae) all species belong to the family Lumbricidae. *Bimastos palustris* and *Eisenoides loennbergi* are native North American lumbricids, the rest are of European origin. Surprisingly, the common anecic *Lumbricus terrestris* has not been found at SERC. However, *L. friendi*, recently recorded for the first time in North America [9], proved to be fairly common in the sampled forests. *Dendrodrilus rubidus rubidus* was the only species not collected with formalin extraction, only by qualitative sampling. All species but *L. friendi* have been known from Maryland [22–24].

A total of eight and nine species were found in the mature and successional forests, respectively (Table 2). Plots on the average yielded 2–3 species with the exception of site D, the youngest of the successional stands with five species. It is the only plot where

Table 1
Vegetation, forest floor and soil characteristics of seven forest stands at the Smithsonian Environmental Research Center

Site	Vegetation	Age (years)	Soil/forest floor		
			Bulk density (g/cm ³)	pH	Total organic matter (%)
A	Mature forest	150+	0.44 ± 0.09 0.85 ± 0.14	6.1	6.80 ± 0.02
B	Successional forest	50–70	0.81 ± 0.08 0.93 ± 0.08	5.6	5.73 ± 0.14
C	Uncut forest	200+	0.30 ± 0.28 0.47 ± 0.22	4.2	14.78 ± 0.12
D	Successional forest	50–70	1.00 ± 0.17 1.09 ± 0.06	5.8	6.13 ± 0.31
E	Mature forest	150+	0.63 ± 0.04 0.82 ± 0.18	4.7	6.04 ± 0.32
F	Successional forest (Virginia Pine)	50–70	0.89 ± 0.12 1.23 ± 0.05	4.6	6.00 ± 0.06
G	Uncut forest	200+	0.32 ± 0.02 1.01 ± 0.15	4.5	9.17 ± 0.43

Only sites where earthworm samples were taken multiple times are listed here. Upper and lower bulk density values mean 0–5 cm and 5–10 cm depth, respectively. Total organic matter was determined for 0–10 cm depth.

A. chlorotica was found. This site was a dairy farm until abandonment about 50 years ago, and it is still fairly open with grassy patches. The presence of *A. chlorotica*, which does not occur in forests, could be a legacy of the dairy operation.

Both species composition and dominance structure are different in the successional and mature forests. The native *E. loennbergi* and *Bimastos palustris* occur almost exclusively in the mature forests, whereas *Diplocardia caroliniana* was found in a variety of habitats, although in very low abundances. In the mature forest *E. loennbergi* and *L. rubellus* dominated whereas in the successional forests *A. caliginosa* and *L. friendi* dominated (Table 1).

Kruskal–Wallis ANOVA showed significant differences in both density and biomass (Fig. 1, Tables 3

and 4). The effect of stand, i.e. successional status, was significant both for density and biomass. Effect of sampling date was significant for biomass, but not for density. This is primarily due to the very low numbers in November 1998, which followed the driest summer in the decade. Overall, a consistent pattern emerges: successional forests (B, D) harbor a more abundant earthworm community, mature forests (A, E) have lower abundance, and there are no earthworms on the two uncut sites (C, G).

It is remarkable the spring biomass in 1999 and 2006 are very similar on all sites except E. Here in 2006 we recorded an unusually high abundance of *E. loennbergi* (over 80% of the individuals). Site F is unique, in that although it is relatively young, in 1998–99 the plot was dominated by Virginia Pine. Virginia Pine is an

Table 2
Species list of earthworms at SERC

Species	Successional forest	Mature forest	Other habitats
<i>Allolobophora chlorotica</i> (Savigny, 1826)	1.3	0.0	
<i>Aporrectodea caliginosa</i> (Savigny, 1826)	51.3	12.9	
<i>Aporrectodea rosea</i> (Savigny, 1826)	0.7	0.0	Wetland
<i>Bimastos palustris</i> Moore, 1895	0.0	6.5	Wetland, pine stand
<i>Dendrobaena octaedra</i> (Savigny, 1826)	0.0	0.0	Forest edge
<i>Dendrodrilus rubidus rubidus</i> (Savigny, 1826)	0.0	0.0	Wetland
<i>Eisenoides loennbergi</i> (Michaelsen, 1894)	0.7	35.5	Wetland, pine stand
<i>Lumbricus friendi</i> Cognetti, 1904	29.6	16.0	Wetland, grass, pine stand
<i>Lumbricus rubellus</i> Hoffmeister, 1843	6.6	19.4	
<i>Octolasion cyaneum</i> (Savigny, 1826)	4.6	6.5	Wetland, grass
<i>Octolasion lacteum</i> (Örley, 1881)	4.6	3.2	Grass
<i>Diplocardia caroliniana</i> Eisen, 1899	0.7	0.1	Wetland, grass

Numbers refer to percentages of each species found in successional and mature forests. Only adult and subadult individuals were included in the calculation. The third column refers to other habitat types where the species was found either by quantitative or qualitative sampling.

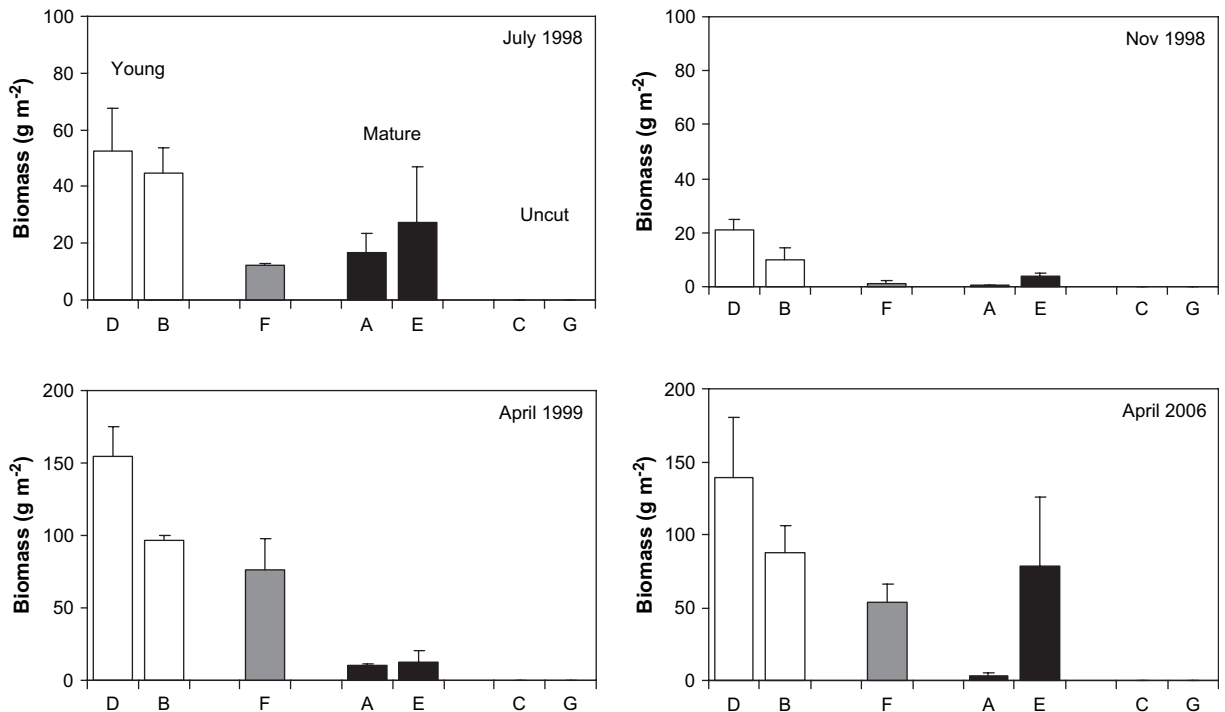


Fig. 1. Earthworm biomass (mean \pm SE) in seven forest stands that were repeatedly sampled. A and E are mature forests; B, D and F are successional forests (F mixed with Virginia pine); C and G are uncut sites. Note that the y axes for July and November 1999 data are at a different scale reflecting the driest summer of the decade.

early successional species in the mid-Atlantic. By 2006 most of the trees were dead or dying and are being replaced by broadleaved trees. Although coniferous stands are generally less suitable habitats for earthworms due to low palatability of needle litter, here a mixture of deciduous and pine litter seems to provide enough resources for the earthworms, which appears to be increasing over time (Fig. 1).

Cluster analysis (Fig. 2) reveals four main groups. In the first the two successional forests are together with one mature stand. Even though the abundances are

different, species composition appears to be the same, and the dominance of *Aporrectodea caliginosa* is the determining factor. Three sites (13, 14, and 15) in the second group are grassy areas around buildings. These are the sites where *Diplocardia caroliniana* was found. In three and two out of the four sites in the third cluster *Eisenoides loennbergi* and *Bimastos palustris*, respectively, occur. The fourth group is eclectic in terms of land cover, but similar in that *Lumbricus* is the dominating genus. We have to be very cautious when interpreting these results. Sampling was done in only one season,

Table 3

Density (ind m^{-2}) of earthworms (mean \pm SE) in seven forest stands, that were repeatedly sampled

Site	June 1998	November 1998	April 1999	April 2006
A ^a	46.7 \pm 15.4	4.0 \pm 2.3	60.0 \pm 12.2	4.0 \pm 2.3
E ^a	34.7 \pm 22.7	5.3 \pm 1.3	20.0 \pm 6.9	72.0 \pm 27.2
B ^b	78.7 \pm 25.3	25.3 \pm 9.3	173.3 \pm 23.1	222.7 \pm 39.3
D ^b	145.3 \pm 35.1	64.0 \pm 14.4	433.3 \pm 70.6	324.0 \pm 28.1
F ^{ab}	22.7 \pm 8.7	1.3 \pm 1.3	50.7 \pm 11.6	89.3 \pm 26.0
C ^c	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0
G ^c	2.7 \pm 2.7	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0

A and E are mature forests, B, D and F are successional forests (F mixed with Virginia pine), C and G are uncut sites. Superscript letters are the results of pairwise comparisons (Mann–Whitney test with sequential Bonferroni correction). Different letters indicate significant ($P < 0.05$) differences.

Table 4
Effects of sampling date and forest stand on biomass and density by two-way Kruskal–Wallis ANOVA

		Biomass	Density
Total	Sum of ranks	44230.3	44833.3
	df	27	27
	<i>H</i>	74.3	75.4
	<i>P</i>	<0.001	<0.001
Date	Sum of ranks	5435.3	4618.8
	df	3	3
	<i>H</i>	9.1	7.8
	<i>P</i>	<0.05	n.s.
Stand	Sum of ranks	33424.3	35056.8
	df	6	6
	<i>H</i>	56.2	58.9
	<i>P</i>	<0.001	<0.001
Date × Stand	Sum of ranks	5370.7	5157.8
	df	18	18
	<i>H</i>	9.0	8.7
	<i>P</i>	n.s.	n.s.

and we likely missed some of the species occurring at a particular site. Moreover, the majority of earthworms are often juveniles, meaning that we are forced to lump together juveniles of *Lumbricus friendi* and *L. rubellus*, which are two ecologically different species. The overall species richness is not too high (although comparable to data from deciduous forests) therefore not much separation can be expected. Overall, apart from the native species mainly occurring in the mature stands, species composition of different age forests overlap considerably. To see if the earthworm assemblages ecologically differ, we compared the relative abundance of epigeic, endogeic and anecic earthworms (for simplicity we used only the three categories by Bouché [5] in the successional and mature forests (Fig. 3). While the proportion of endogeic species does not change, there is a decrease in the proportion of anecic earthworms in the mature stands, and an increase in the epigeic species.

4. Discussion

Non-native earthworms in North America have received a lot of attention both in the scientific literature and in the media (e.g. [4,14,16]). The concern is that exotic earthworms modify forest floor structure, soil characteristics and element cycling [3,15], which results in change in other soil biota and loss of native rare understory plant species [12,13,19].

Most of the experiments and observations are reported from the Northern-Northeastern region that has lacked native earthworms since the last glaciation.

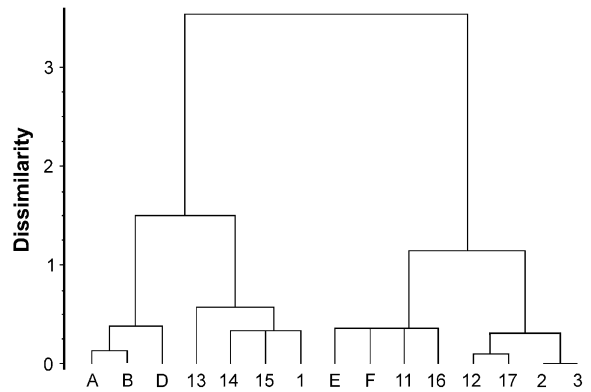


Fig. 2. Hierarchical cluster analysis (Sorensen index of similarity, Ward separation) of earthworm assemblages at various land use types. Only 1999 spring sampling is included. Sites repeatedly sampled are indicated by letters, sites with numbers were sampled only in 1999. Sites with no earthworms were excluded.

Our study site represents a more complex situation because (1) in the Mid-Atlantic region a mixture of native and non-native species occurs, and (2) here we are observing not the steps of invasion following disturbance, but the reverse process, i.e. change in earthworm assemblages in a previously clearcut, then heavily managed area, which has been going through secondary succession for many decades. For studying animal succession the “space for time” approach is more challenging, since animals actively move, and their populations is more dynamic. Moreover, although the land use history of SERC is well known, we can only speculate what the earthworm community might have been two hundred years ago, when most of the area was in agricultural land use. We can safely assume that the land clearing accelerated spread of non-native earthworms [3], and we also know that earthworms can be abundant in cropfields [11]. Even if at the time of abandonment initial earthworm density is low due to intensive tilling, earthworms

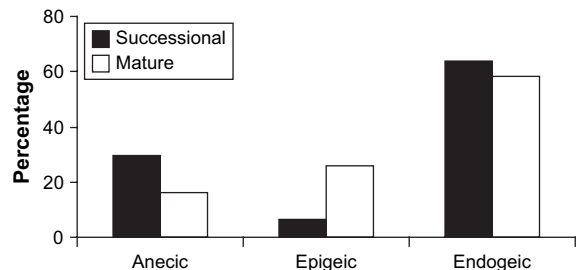


Fig. 3. Percentage of earthworm ecological categories in young successional and mature forests. Only adult individuals were included. Data are from 11 forest sites (five mature and six successional stands). Only 1999 data were used for the calculation.

can quickly colonize the site and reach very high densities within a few years [20]. The observed patterns in earthworm abundance are therefore driven by a combination of land use change and shift in plant composition over time.

Why are earthworms less abundant in older forests at SERC? One possibility is lack of high-quality resources. Most soil detritivores, including earthworms, favor more nutritious leaf litter types such as maple, ash, tulip poplar, linden over oak and beech, at least in the initial stage of decomposition. This has been shown for earthworms in numerous studies (e.g. [26,30]). During succession tree composition changes from palatable to less palatable foliage. This shift in resource quality contributes to the shift in earthworm species composition and abundance. Mature oak forests with moder humus can no longer support large populations of anecic earthworms with high demand of palatable leaf litter [25]. Epigeic species also depend on leaf litter, but they also consume decomposed organic matter, and endogeic species are less affected by the types of surface leaf litter. Preliminary studies by McCormick and Whigham (pers. commun.) showed that leaf litter disappears much faster in successional forest plots than in the mature plots. The type and abundance of soil organic matter also influences earthworm abundance and vice versa [17].

Earthworms do not occur on the two uncut sites. Characteristics of the forest floor and soil upper layers (low bulk density, high organic matter content, lower pH, thick organic layer, mor humus) at these sites are typical to earthworm-free conditions (Table 1). Why the earthworms have not colonized these two patches is not clear. While one site (C) is somewhat separated from the surrounding forests by a tidal wetland, this barrier does not exist on site G. Here the adjacent successional forest harbors abundant earthworm assemblages. There is also considerable traffic (researchers, visitors), since one of the hiking trails leads through site C which should facilitate earthworm colonization. Other soil macroinvertebrates, such as isopods and ants are extremely abundant on both sites (Szilávecz, unpublished).

Pižl [20] followed changes in earthworm species composition and biomass during secondary succession in Central Europe. Similar results of his and our study are: (1) similar species richness regardless of successional stage; (2) decrease of earthworm biomass in the subclimax plant community; (3) increase in the proportion of epigeic species; (4) stable abundance in a short (5 year) period in the forest earthworm community; and (5) species associated only with oldest forests. Earthworm abundance was also lower in later stages of succession of an alpine spruce forest in France [1].

In conclusion, the present study shows that on previously disturbed sites non-native earthworms may not maintain high abundances over long periods of time. At the Smithsonian Environmental Research Center secondary forests of different age have different earthworm assemblages, i.e. younger, successional forests have higher earthworm abundance, than mature, older forests. In the short term this pattern is robust, i.e. independent of seasons, and does not change within a decade. We expect that in the long term this pattern will change along with changes in the plant composition and soil microbial community. Future studies will reveal how this complex interaction of below- and aboveground biota affects ecosystem processes such as carbon and nitrogen cycling.

Acknowledgements

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References

- [1] N. Bernier, J.F. Ponge, J. Andre, Comparative study of soil organic layers in two bilberry spruce forest stands, *Geoderma* 59 (1993) 89–108.
- [2] F.W. Besley, *The forests of Maryland*, Maryland State Board of Forestry, Baltimore, 1916.
- [3] P.J. Bohlen, P.M. Groffman, T.J. Fahey, M.C. Fisk, E. Suárez, D.M. Pelletier, R.T. Fahey, Ecosystem consequences of earthworm invasion of north temperate forests, *Ecosystems* 7 (2004) 1–12.
- [4] P.J. Bohlen, S. Scheu, C.M. Hale, M.A. McLean, S. Migge, P.M. Groffman, D. Parkinson, Non-native invasive earthworms as agents of change in northern temperate forests, *Frontiers in Ecology and the Environment* 8 (2) (2004) 427–435.
- [5] M.B. Bouché, *Strategies lombriciennes*, in: U. Lohm, T. Persson (Eds.), *Soil Organisms as Components of Ecosystems*, *Ecological Bulletin*, vol. 25, 1977, pp. 122–132 Stockholm.
- [6] M.K. Brown, G.G. Parker, Canopy light transmittance in a chronosequence of mixed-species deciduous forests, *Canadian Journal of Forest Research* 24 (1994) 1694–1703.

- [7] G.S. Brush, C. Lenk, J. Smith, The natural forests of Maryland: an explanation of the vegetation map of Maryland, *Ecological Monographs* 50 (1980) 77–92.
- [8] D.L. Correll, Soil sampling and nutrient analyses in forest ecology sites, in: D.L. Correll (Ed.), *Environmental Monitoring and Baseline Data, Compiled Under the Smithsonian Institution Environmental Sciences Program. Temperate Studies, Volume III*, Chesapeake Bay Center for Environmental Studies, Edgewater, MD, 1974, pp. 1099–1112.
- [9] Cs. Csuzdi, K. Szilávecz, *Lumbricus friendi* Cognetti, 1904 a new exotic earthworm in North America, *Northeastern Naturalist* 10 (1) (2003) 77–82.
- [10] Cs. Csuzdi, A. Zicsi, Earthworms of Hungary. (Annelida: Oligochaeta, Lumbricidae), Hungarian Natural History Museum Publ., Budapest, 2003, 271 pp.
- [11] C.A. Edwards, P.J. Bohlen, D.R. Linden, S. Subler, Earthworms in agroecosystems, in: P.F. Hendrix (Ed.), *Earthworm Ecology and Biogeography*, Lewis Publ., Boca Raton, 1995, pp. 185–214.
- [12] M.J. Gundale, Influence of exotic earthworms on the soil organic horizon and the rare fern *Botrychium mormo*, *Conserv. Biol.* 16 (2002) 1555–1561.
- [13] C.M. Hale, L.E. Frelich, P.B. Reich, Exotic European earthworm invasion dynamics in northern hardwood forests of Minnesota, USA, *Ecological Applications* 15 (3) (2005) 848–860.
- [14] P.F. Hendrix, P.J. Bohlen, Exotic earthworm invasions in North America: Ecological and policy implications, *BioScience* 52 (2002) 801–811.
- [15] S.W. James, T.R. Seastedt, Nitrogen mineralization by native and introduced earthworms: effects on big bluestem growth, *Ecology* 67 (1986) 1094–1097.
- [16] S.W. James, P.F. Hendrix, Invasion of exotic earthworms into North America and other regions, in: C. Edwards (Ed.), *Earthworm Ecology*, CRC Press, Boca Raton, 2004, pp. 75–88.
- [17] P. Lavelle, F. Charpentier, C. Villenave, P.P. Rossi, L. Derouard, B. Pashanasi, J. Andre, J.F. Ponge, N. Bernier, Effects of earthworms on soil organic matter and nutrient dynamics at a landscape scale over decades, in: C. Edwards (Ed.), *Earthworm Ecology*, CRC Press, Boca Raton, 2004, pp. 145–160.
- [18] G.G. Parker, J.P. O’Neill, D. Higman, Vertical profile and canopy organization in a mixed deciduous forest, *Vegetatio* 89 (1989) 1–12.
- [19] D. Parkinson, N.A. McLean, S. Scheu, Impacts of earthworms on other biota in forest soils with some emphasis on cool temperate montane forests, in: C. Edwards (Ed.), *Earthworm Ecology*, CRC Press, Boca Raton, 2004, pp. 241–261.
- [20] V. Pizl, Succession of earthworm populations in abandoned fields, *Soil Biol. Biochem* 24 (1992) 1623–1628.
- [21] F. Raw, Estimating earthworm populations by using formalin, *Nature* 184 (1959) 1661–1662.
- [22] J.W. Reynolds, The earthworms of Maryland (Oligochaeta: Acanthodrilidae, Lumbricidae, Megascolecidae and Sparganophilidae), *Megadrilogica* 1 (11) (1974) 1–12.
- [23] J.W. Reynolds, Status of exotic earthworm systematics and biogeography in North America, in: P.F. Hendrix (Ed.), *Earthworm Ecology and Biogeography in North America*, Lewis Publ., Boca Raton, 1995, pp. 1–29.
- [24] J.W. Reynolds, 1995. The distribution of earthworms (Annelida, Oligochaeta) in North America, in: *Advances in Ecology and Environmental Sciences*. Ashish Publ. House, New Delhi, pp. 133–153.
- [25] J.E. Satchell, Earthworm ecology in forest soils, in: J.E. Satchell (Ed.), *Earthworm Ecology: from Darwin to Vermiculture*. Chapman and Hall, London, pp. 161–170.
- [26] J.E. Satchell, D.G. Lowe, Selection of leaf litter by *Lumbricus terrestris*, in: O. Graff, J.E. Satchell (Eds.), *Progress in Soil Biology*, North Holland Publ. Co., Amsterdam, 1967, pp. 102–119.
- [27] D.W. Schneider, Effects of European settlement and land use on regional patterns of similarity among Chesapeake forests, *Bulletin of the Torrey Botanical Club* 123 (1996) 223–239.
- [28] USDA, *Our Soil, Our Strength: Soil Survey Maps of Anne Arundel County Maryland*, Soil Conservation Service, College Park, Maryland, 1968.
- [29] J.H. Zar, *Biostatistical Analysis*. Prentice Hall, New Jersey, p. 718.
- [30] A. Zicsi, Earthworm ecology in deciduous forests in Central and Southeast Europe, in: J.E. Satchell (Ed.), *Earthworm Ecology: from Darwin to Vermiculture*, Chapman and Hall, London, 1983, pp. 171–177.