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Patterns of Abundance and Habitat Associations of Earthworms in Remnant Forests of the Willamette Valley, Oregon

Abstract

Among the most pervasive introduced animal taxa in North America are earthworms in the family Lumbricidae. Understanding their patterns of abundance is important in evaluating their potential impact on the native earthworm fauna. We examined the relationship of the abundance of introduced and native earthworm species, and compared soil and vegetative attributes associated with their abundance in five remnant forests within the Willamette Valley, Oregon. We detected two genera of native earthworms, *Toutellus* (78.5% of native earthworms) and *Argilophilus* (21.5%), collectively, in 7% of the excavated soil samples. We detected non-native lumbricids at all five remnants, in 86% of the samples, and we estimated an average of 1,136 kg of lumbricids/ha in the top 25cm of soil. We found a positive association between counts of lumbricids and the percent of organic matter and moisture content. Greater depth of surface organic matter and sloped terrain were associated with the presence of *Toutellus.* We found a positive association between abundance (counts/sample) of lumbricids and *Toutellus.* We found no direct evidence that the introduced earthworm fauna was impacting native earthworm species, although we failed to detect numerous native species that are presumed to be present in the Willamette Valley. We recommend an experimental approach, coupled with field observations that allow the estimation of species-specific detection probabilities, for future research into the potential impacts of introduced earthworms on the native fauna. This topic deserves further attention given the ubiquity of introduced earthworms in North America.

Introduction

Although unknown to most ecologists, there is a diverse earthworm fauna in North America (Fender 1995). Earthworms in North America are divided into two families, Lumbricidae and Megascolecidae. The Lumbricidae includes most of the introduced earthworm species in the western United States and are native to Europe. The Megascolecidae are distributed in the southern hemisphere and in northwestern North America, and include most native western North American species. The native earthworm fauna of the western United States contains at least 9 genera and 28 species, with many still undescribed (Fender and McKey-Fender 1990, Fender 1995). Over 20 introduced species have been described in this region (Fender 1985).

Three factors likely have influenced the biogeography of western earthworms. The Pleistocene glaciation eradicated many native earthworms over much of the continent although several species survived in glacial refugia (Fender 1995). Physical barriers to dispersal, including the arid region east of the Cascade Range and the Sierra Nevada, may also have been important. Finally, human migration introduced various European species onto the continent through ship ballasts, potted plants, and the fishing industry (Gates 1966, Fender 1995, Dymond et al. 1997).

Observations of native earthworms in a wide range of conditions led Fender (1995) to suggest that native species may have a much higher tolerance than introduced species for soils with high clay content and low pH, an avoidance for sandy soils, and a preference for compacted soils along game trails. Contrary to this view, Piearce (1984) found a negative relationship between compaction and occurrence of native earthworms, and suggested that reduced soil porosity would impede movement. Spiers et al. (1986) found higher abundance of the native earthworm genus *Arctiostrotus* in soils with pH of 2.6 to 6.2. This limited understanding of earthworm ecology, obtained from only a few studies, forms our current understanding of the relationships between native and introduced earthworms in North America.

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We used this existing research to formulate our hypotheses on the patterns of abundance and habitat associations of introduced and native earthworms in the Willamette Valley of western Oregon. Western Oregon is well suited for investigations on the potential impact of introduced earthworms on the native earthworm fauna because of the abundance and diversity of earthworms in the region. We predicted (1) a negative relation between abundance of introduced and native earthworm species; (2) that native species would be more selective of soil and vegetative characteristics than would introduced species; and (3) that native species would increase in abundance in response to the density of conifer trees, soil compaction, and percent clay in the soils.

Study Sites

We conducted our study in the Willamette Valley of western Oregon, located between the Cascade Range and the Coast Ranges. The climate of the Valley is typically mild with wet winters and warm, dry summers (Franklin and Dyrness 1973). We selected five remnant forests from twelve sites in which the Oregon giant earthworm (*Driloleirus macelfreshi*) was previously found. Three sites were excluded due to development and four sites were excluded because of restricted access. All five sampled sites were adjacent to farmed land, rivers, creeks, ponds, or sloughs, were ~70 m elevation, and ranged from 3 - 12 ha (Table 1). The dominant overstory consisted of Douglas-fir (*Pseudotsuga menziesii*), bigleaf maple (*Acer macrophyllum*), Oregon white oak (*Quercus garryana*), red alder (*Alnus rubra*), and Oregon ash (*Fraxinus latifolia*). Understory species included English ivy (*Hedera helix*), Himalayan blackberry (*Rubus discolor*), dull Oregongrape (*Berberis nervosa*), Pacific blackberry (*Rubus ursinus*), snowberry (*Symphoricarpos albus*), and western swordfern (*Polystichum munitum*).

Methods

Sampling

Within each of the five sites (remnant forests) we established an array of points from which we sampled earthworms and habitat characteristics. We sampled each of the five sites twice, from February-April 2000, when soils were moist and above freezing. For each of the two sets of samples, we randomly selected a distance and direction for the initial sample point. Each subsequent sample point (n=45 - 61 per site) was selected systematically, and spaced at 10-30 m depending on the size of the site. At each sample point, we excavated an area of 22 x 22 x 25 cm (~12,000 cm^3 soil removed) below the soil surface, following methods described by Zicsi (1962) and Dickey and Kladivko (1989). We counted the number of individuals of each earthworm taxon detected by hand-sorting the excavated soil (Dickey and Kladivko 1989, Callaham and Hendrix 1997). Fragments of worms were counted as one-half worm (Dickey and Kladivko 1989). We identified earthworms to the level of family for Lumbricidae or genus for native species.

TABLE 1. Characteristics of remnant forests sampled in the Willamette Valley, Oregon, Winter 2000.

Remnant	Size (ha)	Soil Type(s)	% Slope	Dominant Overstory	Dominant Understory
Alderman	12.1	Woodburn silt loam, Woodburn silt clay loam	0-20	Douglas-fir, bigleaf maple	Western swordfern, blackberry, snowberry
Belleview	8.1	clay, silty clay, clay loam	0-10	white oak, red alder	Himalayan blackberry, ivy
Helmick	6.1	loam, clay loam, silty clay loam, sandy clay loam	<5	Douglas-fir, bigleaf maple	Western swordfern, snowberry
Mallard	3.2	McBee silt loam	0	Douglas-fir, white oak	blackberry
Mission Bottom	5.7	silt loam, silty clay loam	20-40	Douglas-fir white oak	Western swordfern, blackberry

Habitat Characteristics

We estimated habitat characteristics at every third sample point and for all points in which we found native earthworms. We estimated basal area of coniferous and deciduous trees >12.5 cm diameter at breast height (dbh), percent of shrub cover (plants >1m in height and <12.5 cm dbh), percent of ground cover (< 1m in height), soil characteristics, and classified sample points into two slope classes: hillside or flat.

Basal area of trees within a 5 m radius of the center of the sample point was estimated from dbh measurements. Shrub cover was estimated separately for woody and herbaceous vegetation (e.g., large ferns) using the line-intercept method (Higgins et al. 1994), with cover recorded at each cardinal direction along a 5 m transect from the sample point. Percent ground cover was estimated by using the quadrat plot method with ocular estimates (Higgins et al. 1994), placing 0.25 m^2 plots 1 m from the sample point at each cardinal direction. Depth of surface organic matter (duff) was measured by inserting a ruler into the layer of organic matter on top of the soil, 1 m from the sample point at each cardinal direction.

Soil samples were collected from the A horizon using a bulk density sampler with a volume of approx. 100 cm^3. Moisture content was calculated after oven-drying 10 g of sample at 105° C for 24 hr. Samples were later air-dried for 3 d at 33° C and sieved (4 mm). Soil aggregates >4 mm, including roots, stones, and sticks, were excluded from all analyses. Percent organic matter was estimated by mass loss on ignition. Each air-dried sample (10 g) was dried in a 100° C oven for 3 hr to obtain the base weight. The sample was then placed in a muffle furnace at 550° C for 5 hr and reweighed. Textural classification (sand and clay content) was estimated by the hydrometer method (Gee and Bauder 1986). Soil pH was estimated in the field using a field dye indicator kit.

Statistical Analyses

We used simple linear regression to estimate the association between abundance of *Toutellus* spp. and lumbricids, given that *Toutellus* were present. Because we were interested in the potential effects of lumbricids on native species, we considered lumbricid counts as the explanatory variable and counts of *Toutellus* as the response variable. We used only sample points in which we located *Toutellus* spp. and thus only the Alderman site was included in analyses. Counts for different dates of sampling were pooled after finding no weather effect. To normalize the distribution of abundance data, counts were square-root transformed prior to analysis.

We used regression analyses to estimate habitat associations. Because the number of *Toutellus* detected were distributed in an almost binary form, we used logistic regression to evaluate habitat characteristics associated with probability that *Toutellus* was present (and detected) in the earthworm samples. We modeled the association of the number of lumbricids detected and habitat characteristics with linear regression. Because of the lack of independence among samples (due to short distance intervals) within a site, we retained site as a covariate in all models. Soil samples were not collected at nine of the *Toutellus* sample points. We excluded these samples when conducting analyses that included soil characteristics in any of the models considered. After finding that soil characteristics were not included in our best models (see Results), we conducted a separate analysis without soil variables in the models considered to allow all sample points with *Toutellus* to be included in the analyses. Analyses were conducted with Proc Logistic and Proc GLM (SAS Institute 1994). We report means and estimated regression coefficients ± 1 SE.

Prior to conducting analyses, we developed 19 (*Toutellus*) to 27 (lumbricids) models of the relationship between habitat and worm abundance (Table 2). Each model allowed us to estimate effects of a different set of habitat characteristics that potentially influenced habitat selection. Evaluation of only the most biologically realistic models reduces the risk of incorrect inference from spurious correlations that often result when many models are evaluated (Burnham and Anderson 1998). Rather than using conventional methods of testing statistical significance of null hypotheses, we used an information-theoretic approach, which ranks models and provides a means of assessing the strength of evidence for one model over another (Burnham and Anderson 1998). The focus of our analysis was to identify the appropriate models for estimating model parameters and their uncertainty (Johnson 1999). We used Akaike's Information Criteria, with small-sample (second-order) bias adjustment (AICc) as the basis for model selection (Burnham and Anderson 1998).

TABLE 2. Comparison of models of the habitat associations of lumbricids and *Toutellus* spp. All five remnant forests were included in analyses of lumbricids and only the Alderman remnant included for *Toutellus*. Sample sizes (n) indicate number of 22 x 22 x 5 cm excavations included in analysis.

				Toutellus spp.[3]			
	Lumbricids[2] (n = 73)			All measurements (n = 25)		Without soil measurements (n = 34)	
Model variables[1]	r^2	ΔAICc[4]	w[5]	ΔAICc[4]	w[5]	ΔAICc[4]	w[5]
pH, org, pH*org, silt, clay, moist, den, basalH, basalC, groundv, wood, shrubW, shrubH, slope	0.35	27.1	0.00				
Above model, without slope	0.35	23.6	0.00				
BasalH, basalC, groundv, shrubW, shrubH	0.19	13.6	0.00				
Basal, groundv, shrubW, shrubH	0.15	14.8	0.00				
BasalH, basalC, groundv, shrub	0.13	16.4	0.00				
Basal, groundv, shrub	0.13	13.8	0.00	5.6	0.01	9.4	0.01
Groundv, shrub	0.12	11.4	0.00	3.4	0.18	6.5	0.01
Groundv	0.11	9.7	0.00	0.9	0.06	4.0	0.04
Basal	0.12	9.5	0.00	1.3	0.05	4.8	0.03
Shrub	0.12	9.0	0.01	2.2	0.03	4.8	0.03
pH, org, pH*org, silt, clay, moist, den	0.26	12.7	0.00				
pH, org, pH*org, clay, moist, den	0.26	10.1	0.00				
pH, org, pH*org, moist	0.24	6.7	0.01				
pH, org, moisture	0.23	4.3	0.04	3.9	0.01	8.2	0.01
pH, org, den	0.23	4.4	0.04	4.5	0.01	9.2	0.01
pH, org	0.22	3.3	0.07	1.9	0.04	6.3	0.01
pH(log), org(log)	0.21	3.7	0.06	1.8	0.04	6.3	0.01
Org(log)	0.21	1.5	0.17	1.1	0.06	4.7	0.03
pH(log)	0.11	9.9	0.00	0.4	0.08	4.0	0.04
Org	0.21	1.0	0.21	1.4	0.05	4.7	0.03
pH	0.11	9.9	0.00	0.3	0.08	4.0	0.04
Moist	0.22	0.0	0.36	2.2	0.03	4.5	0.03
Clay	0.14	7.6	0.01	2.3	0.03		
Den	0.12	9.1	0.01	0.9	0.06	4.6	0.03
Duff	0.12	8.9	0.01	0	0.10	0.3	0.26
Slope	0.11	9.7	0.00	0.5	0.08	0.0	0.31
No effects	0.11	7.4	0.01	0.03	0.10	2.6	0.08

[1] Site (remnant) was included as a categorical covariate in all lumbricid models. Variable acronyms: basalH = basal area of hardwood species, basalC = basal area of coniferous species, basal = basalH + basalC, den = soil density, groundv = ground cover by vegetation, moist = soil moisture, org = organic matter, shrubH = cover of herbaceous "shrubs," shrubW = shrub cover of woody species, shrub = shrubH + shrubW, wood = wood debris ground cover. Models without values were not evaluated for the given taxa.

[2] Includes species within the Lumbricidae.

[3] Soil measurements were not taken on nine sample points. Analyses with n = 25 included soil variables in models whereas analyses with n = 34 excluded soil variables.

[4] Akaike's Information Criteria (with a small sample size correction, AICc) difference between the model with the lowest AICc and the respective model. Lower AICc indicates a better model from which to make inferences.

[5] Akaike's Information Criteria weights (*w*) estimate the relative likelihood of the given model being the best within the set considered (Burnham and Anderson 1998).

We used AICc weights to compare the relative likelihood of a model being the best (Burnham and Anderson 1998). For the linear regression models we computed AICc with the least-squares method described by Burnham and Anderson (1998). Because at least one model will always be identified as best, we included models that we treated as no-effects models. The model with only the intercept term served as the no-effects model for *Toutellus;* for lumbricid analyses, the model with only site effects served as the no-effects model.

Results

Vegetative characteristics varied among the five sites, particularly with the relative density of coniferous and deciduous tree species (Table 3). There was little variation of pH and soil density within or among sites. Soil texture varied considerably among sites but there was little within-site variation (Table 3).

We counted a total of 1790.5 earthworms in the five sites (Table 4). Most (97.4%) were lumbricids; we detected 36.5 *Toutellus* and 10 *Argilophilus*. Lumbricids were found in all sites, with percent occurrence ranging from 61.7 to 98.3% of the excavated samples (Table 4). Mean number of lumbricids/sample among sites ranged from 2.8 to 7.8 (6.1 ± 0.41), corresponding to a mean density (individuals/m^2) of 126.3 ± 8.5 (Table 4). Within sites there was high variability in the number of individuals detected (Table 4); a maximum of 21 - 59 individuals/sample were counted among sites. Based on our finding of a mean mass

TABLE 3. Habitat characteristics in remnant forests sampled in the Willamette Valley, Oregon, February–April 2000. Mean and SE were computed from measurements made at sampling points within each remnant.

	Alderman		Belleview		Helmick		Mallard		Mission Bottom	
Habitat Characteristic	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Conifer stems >12.5 cm dbh (no./ha)	1062.2	151.7	0	0	492.6	230.9	785.8	319.0	341.0	252.4
Deciduous stems >12.5 cm dbh (no./ha)	22.5	0.9	335.1	148.6	479.4	101.1	124.6	83.3	172.2	90.3
Woody shrub cover (%)	63.4	7.2	94.8	2.4	46.4	7.5	31.3	16.2	58.8	11.7
Herbaceous shrub cover (%)	3.1	2.3	0	0	17.9	6.8	20.0	13.3	9.5	9.1
Ground vegetation (%)	74.9	3.6	82.3	4.0	70.1	4.1	89.1	4.2	80.1	5.7
Woody debris cover >10 cm (%)	1.4	1.0	0.9	0.5	3.5	0.9	2.3	1.9	0.4	0.4
Woody debris cover <10 cm (%)	19.2	3.6	8.8	2.1	10.5	2.5	8.6	4.0	18.3	5.4
Bare ground (%)	3.5	1.0	8.0	3.1	15.8	4.3	0	0	1.1	0.6
Duff depth (cm)	4.4	0.6	3.0	0.9	7.6	0.9	4.7	1.7	5.2	0.8
Soil pH	6.0	0.1	6.3	0.1	6.2	0.1	5.9	0.1	6.3	0.1
Soil organic matter (%)	9.4	0.4	12.6	0.9	8.5	0.7	9.1	0.4	8.2	0.3
Sand (%)	16.9	0.5	23.5	2.3	41.6	3.4	23.6	0.9	14.6	0.6
Silt (%)	58.3	0.6	41.1	1.2	31.1	1.7	56.8	0.9	57.9	0.7
Clay (%)	24.8	0.5	35.4	1.5	27.3	2.1	19.6	0.4	27.5	1.0
Moisture content (%)	37.5	1.5	55.9	3.2	38.8	2.0	39.0	2.1	30.4	1.8
Density (g/cm^3)	0.67	0.02	0.62	0.02	0.70	0.02	0.64	0.03	0.71	0.02

TABLE 4. Earthworm abundance in five remnant forests, Willamette Valley, Oregon. Each remnant was sampled twice during February–April 2000.

		Lumbricids			*Toutellus*			*Argilophilus*		
		Percent	Abundance^2		Percent	Abundance^2		Percent	Abundance^2	
Remnant	Total no. of sampling point	Occurrence^1	$\bar{x}$	SE	Occurrence^1	$\bar{x}$	SE	Occurrence^1	$\bar{x}$	SE
Alderman	61	93.4	6.7	0.79	26.2	0.6	0.18	8.2	0.1	0.04
Belleview	60	98.3	7.0	0.63	0	0	0	0	0	0
Helmick	45	88.9	6.4	1.04	0	0	0	2.2	0.1	0.09
Mallard	60	61.7	2.8	0.52	0	0	0	0	0	0
Mission Bottom	60	88.3	7.8	1.30	0	0	0	0	0	0

[1] Percent of samples (22 x 22 x 5 cm excavation) in which a given taxa was detected.

[2] Mean and SE of the number of earthworms of the given taxa counted in each sample.

of 1.6 g/individual lumbricid, we estimated an average biomass of 1,136 ± 76 kg/ha of lumbricids for the upper soil surface.

In contrast, native species were only found at two sites, with frequencies at these sites ranging from 2.2% to 26.2% (Table 4). Mean number of individuals/sample ranged from 0 to 0.6 (0.16 ± 0.04) among sites, with a maximum number of 8 *Toutellus* and *4 Argilophilus*. Despite the much lower detections of native earthworms than lumbricids, we found a positive association (b= 0.34 ± 0.14; $r^2 = 0.33$) between lumbricids and *Toutellus* (Figure 1).

Few habitat characteristics that we measured were associated with the abundance of earthworms. Only models of habitat selection that contained variables associated with soil moisture and organic matter were preferable to the no-effects model. For lumbricids these models were twice as likely as the no-effects model to be the best among the set we considered (Table 3). Soil moisture and organic matter were highly correlated (r = 0.81). Counts of lumbricids were positively associated with soil moisture (b= 0.05 ± 0.02) and percent organic matter (b= 0.17 ± 0.06). Presence of *Toutellus* was associated with a similar characteristic, depth of surface organic matter (duff). The model with this single variable was identical in AICc weights to the no-effects model, and not convincingly more likely as the best model compared with other one-variable models that included either soil pH, organic matter, soil density, or slope (Table 3). To further investigate *Toutellus* habitat models, we used all of the sampled areas within the Alderman site, and thus excluded soil texture variables which were not measured at all sample points. From this larger sample, the single-variable model with duff depth and that with slope were the most likely, and were greater than three times more likely than the other models (Table 3). Duff depth tended to be greater at sample points in which we detected *Toutellus* (5.7 ± 1.0 cm) than where they were not detected (3.8 ± 0.4 cm). Of the 34 points sampled for both

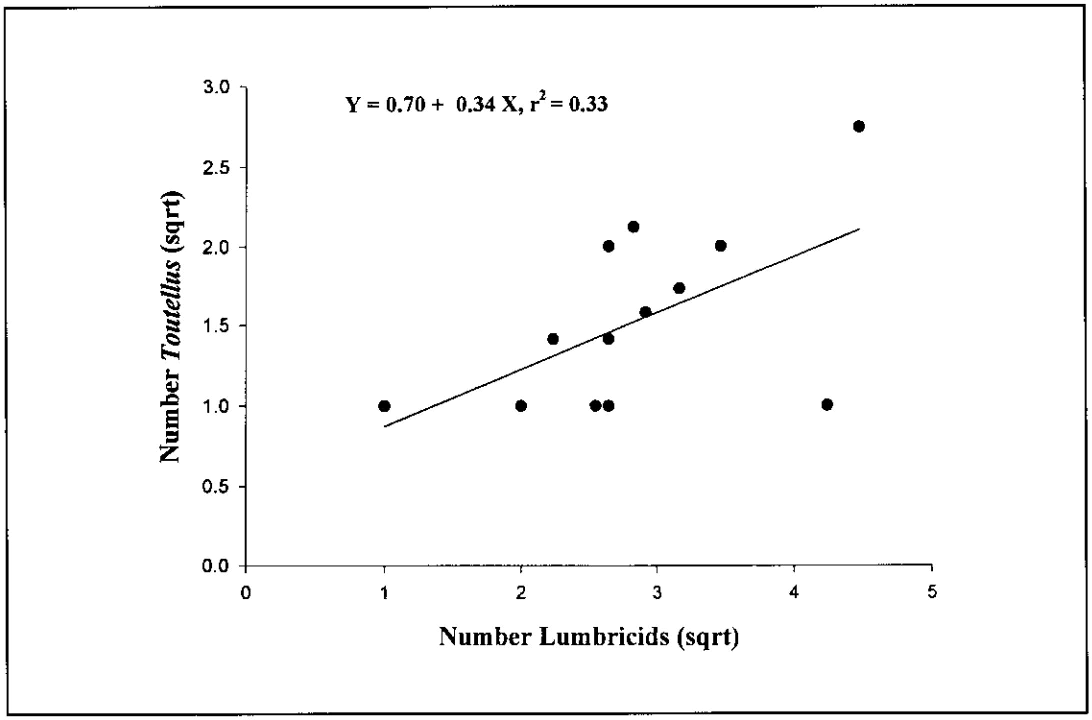

Figure 1. Relationship between the number of *Toutellus* and lumbricid earthworms counted within fourteen 22 x 22 x 5 cm excavations centered on the sampling points within the Alderman site, Willamette Valley, Oregon, February - April 2000. Only excavations within which both lumbricids and *Toutellus* were found were included. Counts were square-root transformed prior to analysis.

earthworms and habitat characteristics in the Alderman site, we detected *Toutellus* in 67.7% (8 of 12) of the sloped sample points and in 27.3% (6 of 22) of those relatively flat. Duff depth was similar between the sloped (4.6 ± 0.5) and flat (4.6 ± 0.7) sample points, demonstrating that the two habitat characteristics associated with the presence of *Toutellus* were not simply correlated with one another.

Discussion

Our results are consistent with previous findings (Kalisz and Dotson 1989, Kalisz and Wood 1995) that introduced lumbricid earthworms are ubiquitous and native species are uncommon in disturbed forests. That we estimated a biomass of >1100 kg/ha of lumbricids from the top 25 cm of the soil surface suggests that they constitute a major component of the animal biomass of these forests. In contrast, native earthworms, comprising two genera (*Toutellus* and *Argilophilus*), were found at only two of five of these remnants and in much lower densities than the lumbricids. Unfortunately, there are no published studies to evaluate abundance of native earthworms in the Willamette Valley prior to the presence of lumbricids.

Contrary to our prediction of a negative effect of introduced taxa on abundance of natives, we found a positive association. As abundance of lumbricids increased, so did abundance of *Toutellus*, suggesting that habitat conducive for introduced earthworms may also be conducive to *Toutellus*. However, because we failed to detect several native species that are presumed to be present in the Willamette Valley, the potential impact of lumbricids on the native earthworm fauna may be great. That we found few individuals of only two native species and high densities of lumbricids in most of the sites warrants further investigation of the potential impact of lumbricids on the native earthworm fauna.

Although native earthworm species may have different ecological requirements from introduced species (Fender 1995) and thus reduce the potential for competition (Kalisz and Wood 1995), little work has been conducted to test hypotheses on these differences. Fender's (1995) work helped form our predictions that native species would predominate in natural forest soils with high clay content, low pH, and along compacted trails, and that native species would be more selective of habitat characteristics than the introduced species of lumbricids. We found no evidence to support these predictions. Habitat variables associated with greater abundance of *Toutellus* were increasing depth of the duff layer and sloped terrain, although effects were weak. Abundance of introduced species (lumbricids) increased as soil moisture and percent organic matter increased, two factors that were highly correlated with each other. These may have been the only factors of statistical importance in our models simply because lumbricids are more likely to be near the surface as soil moisture increases (Edwards and Lofty 1976). We may have failed to detect habitat associations for several of the variables, such as acidity and soil compaction, because of the narrow range of conditions within and among the five sites. Furthermore, that we identified few characteristics associated with earthworm counts may be partially due to increased variation of counts arising from the unknown but likely variable detection rates of earthworms among sample points, sites, and species.

All of our study sites have been fragmented over the past century. Habitat fragmentation often leads to modification of microclimate (Saunders et al. 1991). Blanchart and Julka (1997) noted the possibility that earthworm communities are also affected by the size and shape of habitat patches, and their position in the landscape. Kalisz and Wood (1995) suggested that microclimate, edge effects, influx of introduced taxa, and input of toxic chemicals may reduce the ability of native earthworms to survive or compete with introduced species. Indeed, native species dominated the earthworm fauna in large, undisturbed forests of the southern Appalachians (Kalisz and Dotson 1989). Further work exploring patterns of earthworm diversity and abundance, and landscape factors influencing such patterns would greatly aid our understanding of native and introduced earthworm interactions.

Future research should focus on a broad set of vegetation types to further determine characteristics important to native earthworms in western North America. An experimental approach, coupled with comparative field observations, may be the most fruitful means of understanding the potential impacts of introduced earthworms to the native fauna. Earthworms tend to be clustered (Dickey and Kladivko 1989, Wood and James 1983) and the likelihood that an individual, although present, may be undetected may be very high for some species. It thus will be important to incorporate estimated detection probabilities into analyses of patterns of earthworm abundance. This, combined with intensive sampling in a broad array of habitats, should increase our knowledge of the impressive diversity of native earthworms, and our ability to evaluate factors that may affect their future existence within highly modified ecosystems.

Acknowledgements

We thank the landowners and managers that allowed us access to the sites: Glen Ford, Scott Hamilton, Vicki Perrett, Bill and Susan Usrey, and Rob Westberg. We are grateful to Jeff Rosier for locating sites; to Cheron Ferland, Jason Adams, Autumn Bauwens, Kale Haggard, and Stephanie Lamb for their dedication in conducting field work; to Will Austin and the Central Analytical Laboratory (Dept. of Crop and Soil Science, Oregon State Univ.) for assistance with soil analyses; to Jim Kagan and the Oregon Natural Heritage program for collaboration and assistance with identifying potential study sites; and to Mary Fauci and Stewart Wuest for helpful reviews of earlier drafts of this manuscript. This work was made possible by funds provided by the Biological Resources Division of the U.S. Geological Survey, the U. S. Fish and Wildlife Service, and through collaborative agreements with the Oregon Cooperative Fish and Wildlife Research Unit. Cooperators of the Unit included the U. S. Fish and Wildlife Service, Oregon State University, Oregon Department of Fish and Wildlife, the Wildlife Management Institute, and the Biological Resources Division of the U. S. Geological Survey. Publication of this paper was supported, in part, by the Thomas G. Scott Publication Fund.

Literature Cited

Blanchart, E., and J.M. Julka. 1997. Influence of forest disturbance on earthworm (Oligochaeta) communities in the Western Ghats (South India). Soil Biology & Biochemistry 29:303-306.

Burnham, K.P., and D.R. Anderson. 1998. Model Selection and Inference: A Practical Information-theoretic Approach. Springer-Verlag, New York.

Callaham, M.A. Jr., and P.F. Hendrix. 1997. Relative abundance and seasonal activity of earthworms (Lumbricidae and Megascolecidae) as determined by hand-sorting and formalin extraction in forest soils on the southern Appalachian Piedmont. Soil Biology & Biochemistry 29:317-321.

Dickey, J.B., and E. J. Kladivko. 1989. Sample unit sizes and shapes for quantitative sampling of earthworm populations in crop lands. Soil Biology & Biochemistry 21:105-111.

Dymond, P., S. Scheu, and D. Parkinson. 1997. Density and distribution of *Dendrobaena octaedra* (Lumbricidae) in aspen and pine forests in the Canadian rocky mountains (Alberta). Soil Biology & Biochemistry 29:265-273.

Edwards, C. A., and J. R. Lofty. 1976. Biology of Earthworms. Bookworm Publishing Company, Ontario, California.

Fender, W. M. 1985. Earthworms of the western United States. Part I. Lumbricidae. Megadrilogica 4:93-132.

Fender, W.M. 1995. Native earthworms of the Pacific Northwest: An ecological overview. Pages 53-66 *In* P.F. Hendrix (editor), Earthworm Ecology and Biogeography in North America, CRC Press, Boca Raton, Florida.

Fender, W. M. and D. McKey-Fender. 1990. Oligochaeta: Megascolecidae and other earthworms from Western North America. Pages 357-378 *In* D. Dindal (editor), Soil Biology Guide, Wiley, New York.

Franklin, J.F. and C.T. Dyrness. 1973. Natural vegetation of Oregon and Washington. USDA Forest Service General Technical Report PNW-8. Pacific Northwest Forest and Range Experiment Station, Portland, Oregon.

Gates, G. E. 1966. Requiem– for megadrilogica. VII. A contribution toward the understanding of the earthworm fauna of North America. Proceedings Biological Society of Washington 76:239-254.

Gee, G.W. and J.W. Bauder. 1986. Particle size analysis. Pages 383-411 *In* A. Klute (editor), Methods of Soil Analysis, ASA Publication No. 9, Madison, Wisconsin.

Higgins, K.F., J.L. Oldemeyer, K.J. Jenkins, G.K. Clambey, and R.F. Harlow. 1994. Vegetation sampling and measurement. Pages 567-591 *In* T.A. Bookhout (editor), Research and Management Techniques for Wildlife and Habitats, The Wildlife Society, Bethesda, Maryland.

Johnson, D. H. 1999. The insignificance of statistical significance testing. Journal of Wildlife Management 63:763-772.

Kalisz, P.J., and D.B. Dotson. 1989. Land-use history and the occurrence of exotic earthworms in the mountains of Eastern Kentucky. American Midland Naturalist 122:288-297.

Kalisz, P.J., and H.B. Wood. 1995. Native and exotic earthworms in wildland ecosystems. Pages 117-123 *In* P.F. Hendrix (editor), Earthworm Ecology and Biogeography in North America, CRC Press, Boca Raton, Florida.

Piearce, T.G. 1984. Earthworm populations in soils disturbed by trampling. Biological Conservation 29:241-252.

SAS Institute. 1994. SAS/STAT user's guide. Version 6. Fourth Edition. SAS Institute, Cary, North Carolina.

Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology 5:18-32.

Spiers, G.A., D. Gagnon, G.E. Nason, E.C. Packee, and J.D. Lousier. 1986. Effects and importance of indigenous earthworms on decomposition and nutrient cycling in coastal forest ecosystems. Canadian Journal of Forest Resources 16:983-989.

Wood, H. B., and S. W. James. 1993. Native and introduced earthworms from selected chaparral, woodland, and riparian zones in southern California. USDA Forest Service General Technical Report PSW-GTR-142. Pacific Southwest Research Station, Albany, California.

Zicsi, A. 1962. Determination of number and size of sampling unit for estimating Lumbricid populations on arable soils. Pages 68-71 *In* P.W. Murphy (editor), Progress in Soil Biology, Butterworths, London.

Received 17 May 2001
Accepted for publication 10 September 2001