Applied Soil Ecology 96 (2015) 240–250

Contents lists available at ScienceDirect

Applied Soil Ecology

journal homepage: www.elsevier.com/locate/apsoil

Agricultural management and flooding shape habitats for non-native earthworms in southern Quebec, Canada

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ARTICLE INFO

Article history:
Received 8 June 2015
Received in revised form 5 August 2015
Accepted 13 August 2015
Available online xxx

Keywords:
Earthworms
Riparian areas
Flooding
Management intensity
Agricultural landscapes

ABSTRACT

Agricultural intensification leading to the cultivation of unmanaged field margins along rivers and streams is expected to impact soil biodiversity. Earthworm communities are typically smaller with fewer species in agricultural soils, but the effect of agriculture on earthworms could be mitigated by the more favorable soil moisture regime in riparian areas, as well as planting perennial grasses or keeping forest fragments as permanently vegetated buffers. The objective of this study was to compare earthworm community composition under contrasting land use (agricultural vs. riparian forest) ~5 m and ~30 m away from the Pike River in southern Quebec, Canada. Furthermore, we evaluated how earthworm communities were affected by management intensity, flooding, soil and vegetation patterns within these land uses. We established 4 transects at 3 sites along the Pike River representing 4 land uses (agricultural field, agricultural buffer, riparian forest fragment, upland forest fragment). Along each transect, earthworm populations and soil properties were evaluated at 5 discrete points on 4 occasions from fall 2009 to spring 2011. Vegetation cover and plant species richness were measured, and management and flooding intensity were documented through farmer surveys. Earthworm abundance and diversity were highest in a riparian forest transect (460 individuals m^{-2}, 9 species) and agricultural buffer (325 individuals m^{-2}, 10 species), and lowest in the agricultural fields with annual crop rotations and agrochemical inputs, which also had the lowest plant diversity. Redundancy analysis revealed that differences in earthworm species compositions across the study area were linked to site-specific management and flooding, represented by differences in soil moisture, vegetation diversity, and soil nutrient concentrations (dissolved organic carbon in soil solution, mineral nitrogen, extractable phosphorus). Generalized linear mixed modeling also showed that less intensively managed agricultural buffers and forest fragments with regular flooding supported higher earthworm diversity. We recommend further research on soil functions affected by earthworms in riparian areas because these non-native earthworms could affect the conservation value of unmanaged agricultural buffers and forest fragments in southern Quebec, Canada.

1. Introduction

The once forested landscape of southern Quebec, Canada, is now highly fragmented and predominantly under agricultural production. Within this landscape, riparian buffer strips and forest fragments are important since they conserve and protect surface watercourses from agricultural run-off. Such riparian areas have greater biodiversity and an array of habitats compared to adjacent agricultural fields, as well as variable nutrient fluxes due to periodic flooding events (Naiman and Decamps, 2007). Greater plant diversity is expected to support more non-native earthworm species with different feeding habits due to a larger amount and variety of plant-derived substrates in the soil (Lee, 1985). For example, throughout forest sites in an agricultural landscape in Georgia, USA, earthworm abundance was positively correlated ($r = 0.91$) with soil organic carbon and plant residue inputs (Hendrix et al., 1992). Therefore, agricultural intensification that maximizes cultivated areas and minimizes forested riparian strips may reduce earthworm habitat, abundance and diversity.

Intense agricultural practices, like tillage, are often associated with lower earthworm abundance and species richness due to physical injuries (e.g., cutting) causing earthworm mortality (Kladivko, 2001), or indirectly by modifying soil temperature, moisture and surface litter supply (Peigne et al., 2009; Dominguez

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http://dx.doi.org/10.1016/j.apsoil.2015.08.011
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et al., 2010). Large anecic earthworms such as *Lumbricus terrestris* and *Aporrectodea longa* are impacted adversely by tillage because they feed primarily on surface litter and have more permanent burrows than smaller endogeic species such as *Aporrectodea turgida*. Consequently, a shift toward\ conservation tillage systems, for example, led to more anecic species relative to other species (Chan, 2001). Likewise, lumbricid earthworm communities were larger and more diverse in long-term pastures containing a mixture of grasses and legumes than in monocultures of annual grain crops (Fraser et al., 1996). We predict, therefore, that the untilled, permanently vegetated forest fragments comprise habitats that are conducive to different earthworm species than surrounding agricultural fields, and thus increase the β-diversity of non-native earthworm communities across agricultural landscapes.

While soil disturbance and food supply are important for earthworm demographics, their populations and communities are also vulnerable to the interactive effects of land use and soil moisture dynamics. The mechanisms responsible for such interactive effects may depend on certain earthworm species' ability to survive in soil with differing moisture conditions, which in turn may be controlled by vegetation characteristics. Likewise, Zorn et al. (2005) found that in a temperate floodplain, earthworm density was highest in the riparian areas with larger herbaceous vegetation than in areas with short grass vegetation. Larger, herbaceous vegetation might improve the habitat value because of both soil protection and improved food supply. It is thus expected that habitats with abundant vegetation that are more susceptible to flooding and residual high soil moisture will have larger and more diverse earthworm species composition than habitats further away from the river that less susceptible to flooding. Understanding how land use and associated environmental factors affect the spatial distribution and composition of earthworm communities is important to predict the contribution of non-native earthworms to processes such as litter decomposition and nutrient turnover; (Bohlen et al., 2004a,b; Eisenhauer et al., 2007; Lubbers et al., 2013) across diverse habitats. This is particularly true for Quebec, where their range is expected to grow, in part by using streams for dispersal (Costello et al., 2011), and they may therefore significantly influence ecosystem processes in riparian areas (Costello and Lamberti, 2008, 2009).

In this study, we focused on the banks of the Pike River, near the town of Bedford, Quebec (Canada). This 67 km long waterway transports high nutrient loads from the surrounding farmlands into the Missisquoi Bay of Lake Champlain (Smeltzer et al., 2012). This setting thus presents a eutrophic river in a mosaic of agricultural fields, forest fragments and unmanaged riparian buffer strips. Our objectives were to (1) compare earthworm community composition between riparian habitat types in agricultural and forested land use systems, at different distances from the Pike River, and (2) evaluate whether soil or vegetation gradients were determinants of earthworm community composition.

2. Materials and methods

2.1. Site description

Earthworms and their habitats were studied in 3 sites along the Pike River in southern Quebec, Canada (45°08′N, 73°03′W), from fall 2009 to spring 2011. According to the recent 29 year average (1981–2010), the mean daily temperature is 6.4 °C, mean highest temperature is 11.6 °C, lowest mean temperature is 1.2 °C, the mean precipitation is 1132 mm, July is the month with the mean highest temperatures, and January is the month with the mean lowest temperatures (http://climate.weather.gc.ca/climate_normals/results_1981_2010_e.html?stnID=5358&autofwd=1, last accessed on 26.04.2015). Soils at sites 1 and 3 were Suffield clay loam soils (brown podzolic group) with textures ranging from clay loam to silt loam. At site 2, the soil was a Ste. Rosalie clay loam (dark grey Gleysolic group). The topography was gently undulating across sites, such that sites were 0–2 m above the river level.

2.2. Experimental design

Earthworm communities were characterized in 4 habitats at each of the 3 sites. These were (i) uncultivated herbaceous buffer

Table 1
Dominant vegetation (>15% relative abundance of total vegetation) in 3 sites along the Pike River, Quebec, Canada, as affected by land use and distance to the river. The management intensity index (on a scale from 0 to 6 where 0 is the least intensity and 6 is the greatest intensity) is reported for each site.

Habitat	Dominant understory vegetation and trees	Herbicide	Fertilizer	Tillage	Traffic	Total intensity
Site 1						
Ag-5 m	*Bromus inermis, Dactylis glomerata, Echinoclea crusgali, Phalaris arundinacea, Ambrosia artemisefolia, Hydrophyllum virginianum, Physalis heterophylla, Solidago rugosa, Solidago canadensis, Solidago gigantean, Anthicus sylvestris*	0	0	0	0	0
Ag-30 m	*Zea mays* L. and *Glycine max* L. rotation	1	2	1	2	6
For-5 m	*Acer negundo, Ulmus americana, Laportea canadensis, Dactylis glomerata, Eupatorium maculatum, Crataegus* sp., *Pilea pumila, Geum* sp., *Matteuccia struthioptensis, Brassicacaeae* sp.	0	0	0	1	1
For-30 m	*Prunus virginiania, Pinus strobus, Lysimachia nummularia, Bromus inermis, Dirca palustris, Geum* sp., *Acer negundo*	0	0	0	1	1
Site 2						
Ag-5 m	*Bromus inermis, Dactylis glomerata, Echinoclea crusgali, Phalaris arundinacea, Caprifoliaceae* sp., *Cornus sericea, Acer negundo, Prunus virginiana, Lysimachia nummularia, Vitis riparia, Toxirodendron radicoms, Prunus coratona, Quercus rubra, Tilia americana*	0	0	0	0	0
Ag-30 m	Hay forage	0	0	0	2	2
For-5 m	*Tovara virginiana, Lysimachia nummularia, Prunus virginiana, Acer saccharum, Bromus inermis, Dactylis glomerata, Echinoclea crusgali, Phalaris arundinacea, Solidago rugosa, Solidago gigantum, Acer negundo*	0	0	0	1	1
For-30 m	*Impatiens capensis, Tovara virginiana, Lysimachia nummularia, Laportea, Onoclea sensibilus, Prunus serotina, Acer negundo, Fraxinus pensylvanica, Crataegus* sp.	0	0	0	1	1
Site 3						
Ag-5 m	*Phalaris arundinacea, Anemone canadense, Toxirodendron radicoms, Solidago rugosa, Tilia americana, Fraxinus pensylvanica*	0	0	0	0	0
Ag-30 m	*Triticum aestivum* L. and *Glycine max* L. rotation	1	2	0	2	5
For-5 m	*Mattucia strutheopris, Maianthemum canadense, Hemecopalis* sp., *Rubus allegheniensis*	0	0	0	1	1
For-30 m	*Prunus serotina, Acer saccharum, Fagus grandifolia, Abies balsamea, Smilacena trifoliata, Cornus alternifolia*	0	0	0	2	2

strips within 10 m of the river (Ag-5 m), (ii) agricultural fields under cultivation at least 30 m upland from the river (Ag-30 m), (iii) riparian forest strips within 10 m of the river (For-5 m), and (iv) non-riparian forest fragments at least 30 m upland from the river (For-30 m). In each habitat, we established a 3×90 m transect parallel to the river. Each transect was divided into 5 contiguous sampling plots (each 3×18 m, $n = 60$). We randomly sampled each of the 5 plots at each of the 4 sampling dates (fall 2009, spring 2010, fall 2010, spring 2011). Therefore, we had a total of 240 samples over the course of our study. Given that the spatial dependence of forest soil properties is reported to be no more than 5–10 m (Qian and Klinka, 1995), we considered plots within each transect to be replicates, not pseudoreplicates.

2.3. Assessing management intensity

Landowners were surveyed to collect management data of each site. Management intensity was ranked according to 4 variables: herbicide use, fertilizer application, tillage, and traffic. Herbicide and tillage were binary variables such that 1 and 0, respectively, indicated that these management practices did or did not occur. There were 3 possible scores for fertilizer application: 0 = no fertilizer application, 1 = manure application, and 2 = inorganic NPK fertilizer application. Likewise, there were 3 possible scores for traffic: 0 = no traffic, 1 = human pedestrian traffic, and 2 = motorized vehicle traffic. The management intensity index for each plot was calculated by summing the scores from these 6 variables such that low values indicated no or little disturbance from management, whereas high values indicated strong human disturbance (Table 1).

2.4. Earthworm collection and soil analyses

Earthworms were collected during each of the 4 sampling events, in each of the 5 plots, by excavating soil blocks (25×25 cm^2 area $\times$ 15 cm depth) randomly at 4 sampling events within each of the 5 plots. Dilute formalin solution (0.05% v/v) was poured into the bottom of each pit to retrieve deeper dwelling earthworms, which were dominated by anecic species. Soil blocks were taken back to McGill's Macdonald Campus in Ste. Anne-de-Bellevue, Quebec, and earthworms were removed by hand-sorting. All earthworms were immediately stored in formaldehyde 5% (v/v) solution until they could be identified. Earthworms were first separated into fragments, juvenile, pre-clitellate, and adult categories. Adults were then identified to the species level using the key of Reynolds (1977). Each earthworm was weighed for "formaldehyde fresh weight". They were then dried (65 °C for 48 h) and ashed (360 °C for 4 h) to obtain the ash-free dry weight (AFDW). Earthworm abundance (number of individuals) and biomass (g AFDW) were extrapolated to 1 m^2 surface area.

At each sampling event, a subsample of field-moist soil was extracted with 0.5 M K_2SO_4 and analyzed for NH_4^+ and NO_3^- (Maynard et al., 2008), and for dissolved organic C with a Shimadzu TOC-V analyzer (Shimadzu Scientific Instruments, Kyoto, Japan). Microbial biomass C and N were determined by the chloroform fumigation–direct extraction followed by persulfate digestion (Voroney et al., 2008). Another subsample of soil representative of each soil block was dried (65 °C for 48 h) and gravimetric water content was calculated by mass loss. Dried soil was subsequently used to measure pH in 1:2 (soil: distilled water) slurries. Finally, Mehlich III-extractable P was analyzed colorimetrically on a Lachat Quik-Chem AE flow-injection auto-analyzer (Lachat Instruments, Milwaukee, WI, USA), and the Mehlich III-extractable K and Ca concentrations were analyzed on a PerkinElmer 2380 atomic adsorption spectrometer (PerkinElmer, Waltham, MA, USA).

2.5. Vegetation surveys

Vegetation cover, number of plant species and their relative abundance were surveyed in July 2011. In each plot, we set up 15 quadrats, each 1 m^2. We examined all species occurring within that quadrant and listed them (Table 1). We then assigned a relative abundance value to each species based on visually assessment of cover, estimated as the fraction of the total area that was covered by plants when viewed from above. After species-level identification, plants were grouped into functional guilds: forbs, woody vegetation (trees and shrubs), ferns, graminoids, and annual crops.

2.6. Data analysis

2.6.1. Comparing earthworm species composition between habitats

All statistical analyses were performed in the R environment (R Core Team, 2013). We compared earthworm species composition in each of the 4 habitats based on identifiable adult species pooled across the 4 sampling dates, using non-metric multidimensional scaling (NMDS) in the package vegan (Oksanen et al., 2013). Earthworm abundances were Hellinger transformed allowing low weights to be assigned to the rare species and 1000 iterations were run. Differences in earthworm species composition between land uses, distances to river, and the interaction of these 2 factors were analyzed with PERMANOVA (Anderson, 2001; function adonis) using the Bray–Curtis dissimilarity matrix.

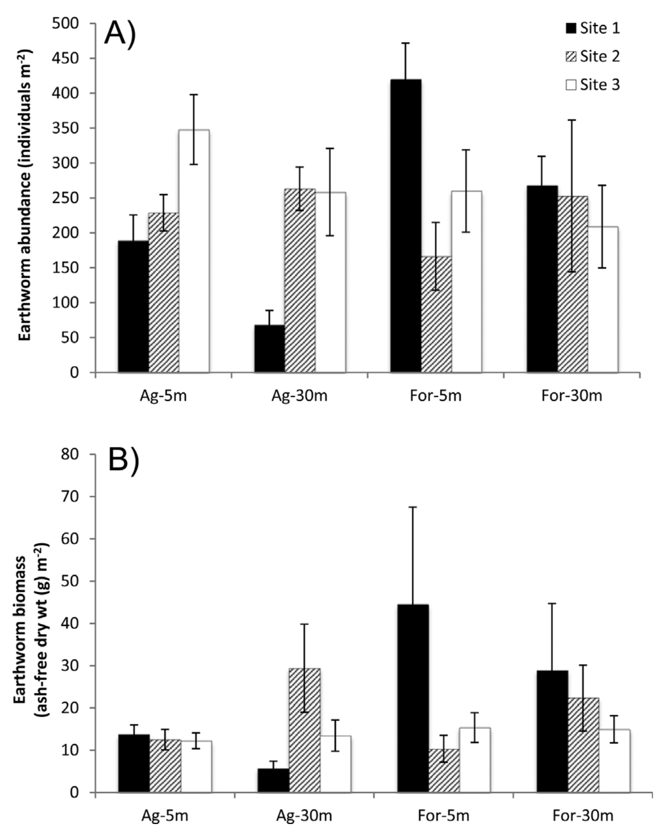

Fig. 1. (A) Mean earthworm abundance (numbers of individuals per meter square) and (B) biomass (ash-free dry weight per meter square) affected by land use (agricultural, forest) and distance from the river (5 m, 30 m) in 5 plots, pooled among 4 sampling dates, at 3 sites along the Pike River, Quebec, Canada. Hatch marks are the standard error of the mean.

Table 2
Total number of identifiable earthworm adults found in each habitat along the Pike River, according to each functional group and species (sum of 4 sampling dates from 5 soil blocks (0.25 m^2 × 0.2 m) for within each of the 12 transects).

	Site 1				Site 2				Site 3			
	Ag-5 m	Ag-30 m	For-5 m	For-30 m	Ag-5 m	Ag-30 m	For-5 m	For-30 m	Ag-5 m	Ag-30 m	For-5 m	For-30 m
Epigeic species												
D. octraedra	1	0	0	1	0	0	1	0	1	0	0	0
L. rubellus	2	0	5	6	1	4	7	2	10	0	3	1
L. castaneus	1	0	0	0	0	0	0	0	0	0	0	0
Anecic species												
L. terrestris	13	3	4	3	4	2	2	4	5	1	6	4
A. longa	0	0	1	1	4	7	1	1	6	1	0	2
Endogeic species												
A. chloratica	3	4	56	11	0	6	0	0	3	0	0	0
A. rosea	11	0	1	3	16	9	7	11	27	10	16	15
O. cyaneum	0	0	5	1	3	4	0	0	0	0	0	0
O. tyrtaeum	20	1	47	31	62	31	17	34	17	0	28	1
A. turgida	13	13	95	50	25	38	4	50	18	39	20	27
A. tuberculata	5	6	8	20	8	8	7	6	10	34	14	15
Species richness	9	5	9	10	9	9	8	8	10	5	6	7

2.6.2. Environmental factors associated with earthworm communities within habitats

Redundancy analysis (RDA) was performed using data from all habitats and sites, as well as separately for each habitat, to determine which soil properties and vegetation groups were most strongly correlated with earthworm species compositions. The environmental matrix had 13 continuous variables including vegetation cover, plant diversity, management intensity, flooding intensity and selected soil properties. Management intensity was considered as equal for each sampling plot within each transect. All of these variables except management intensity were log transformed (log 10 + 1) to standardize the values and units. The earthworm matrix consisted of the identifiable adult earthworm species found in each plot at each sampling event. When no adult earthworm was present, it was considered to be a missing value in the earthworm matrix and the corresponding line in the environmental matrix was deleted. Each matrix had a total of 211 observations, with a maximum of 20 observations within one habitat.

Stepwise model selection, a procedure based on permutations (function ordistep in R), was used to identify the best RDA model for explaining variation in earthworm species compositions for each site, based on the lowest Aikake's Information Criterion (AIC). The fit of the RDAs model was determined by multiplying the proportion of variation explained by eigenvalues with the R^2_{adj}, following the method by Borcard et al. (2011). We used this method to calculate the percent variance explained by the first 2 axes for each RDA ordination. The statistical significance of the model, axes, and each of the terms used in the final RDA was assessed using 1000 permutation tests.

Finally, we also modeled vegetation (species diversity, number of plants within each functional guild, relative cover), earthworm communities (earthworm abundance, biomass (AFDW), species richness per plot), and soil properties (NH_4, NO_3, DOC, MBC, pH, P, K, Ca, and MBC) as a function of the fixed effects land use (agricultural vs. forest), distance from river (5 m or 30 m), management intensity (ranked on a scale from 0 to 6), and flooding, using Generalized Linear Mixed Models (GLMM) applying Residual Maximum Likelihood (Bates et al., 2012), following the method outlined by Zuur et al. (2009). The GLMMs permitted a hierarchy of random effects to be included in the model and therefore allowed for a greater strength of comparison between

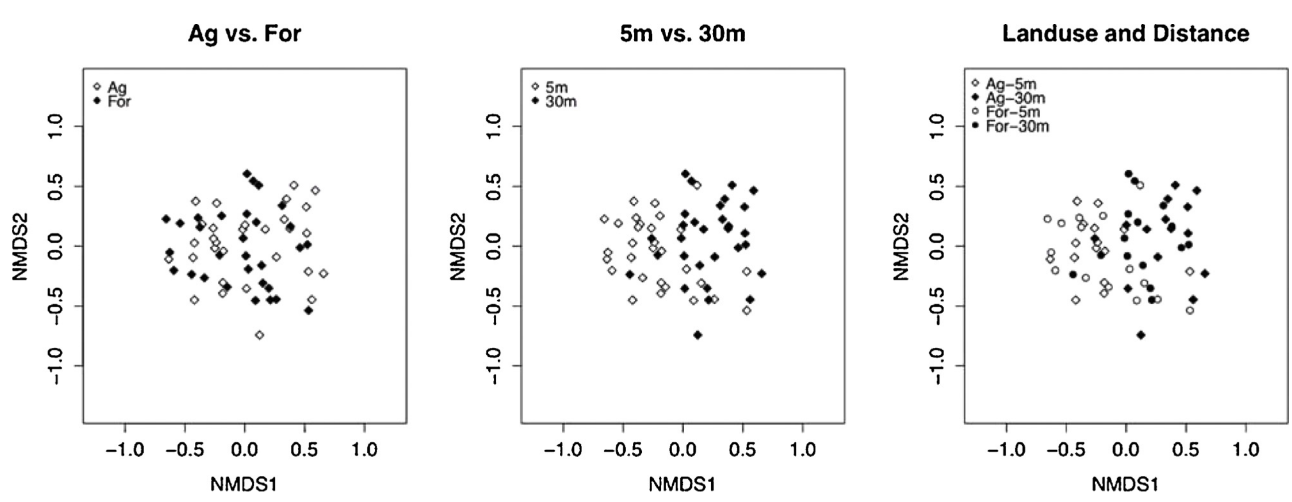

Fig. 2. Non-metric multidimensional scaling of earthworm species composition in different habitats, based on a Bray–Curtis dissimilarity matrix (2 axes; stress = 0.18). Earthworm species composition is depicted in different habitats in agricultural and forested land use, both 5 m and 30 m away from the Pike River. Earthworm community composition did not differ between habitats in agricultural and forested land use ($p = 0.894$), but did differ between habitats either 5 m or 30 m away from the river ($p < 0.001$) and between habitats in different land uses and distances from river ($p < 0.001$).

plots within transects at the 3 sites (where random effects were plot, transect and site). As a proxy for flooding, moisture data was transformed from a continuous to a categorical factor (dry, moderately wet, wet, very wet) with the quantile function. The significance of fixed effects was tested using a likelihood ratio test by comparing a basic model with each fixed factor against the null hypothesis model.

3. Results

We collected 3664 earthworms from 240 sampling points and approximately 67% of these were juvenile earthworms that could not be identified to the species level (Fig. 1,Table 2). Of the 11 adult species identified in this study, the most common were the endogeic species *A. turgida* (398 individuals, 33% of adults), *Octolasion tyrtaeum* (286 individuals, 24% of adults) and *Aporrectodea tuberculata* (173 individuals, 14% of adults).

3.1. Comparing earthworm species composition between habitats

Earthworm species composition was similar in agricultural and forest land use (F = 0.4067, R^2 = 0.0.0069, p = 0.875), although differences in earthworm species composition between agricultural and forest habitats were determined by the distance from river (F = 9.113, R^2 = 0.1357, p = 0.001) and the interaction of land use × distance from river (F = 3.122, R^2 = 0.4171, p = 0.001) in the NMDS ordination and the PERMANOVA (p = 0.001, Fig. 2). The NMDS ordination provided a 2 dimensional solution that minimized stress after 15 attempts to describe earthworm species composition among habitats (final stress = 0.18).

3.2. Environmental factors associated with earthworm species composition within habitats

In the RDA analyses, the first 2 canonical axes together explained 5.5% of the total variation in earthworm community composition. Accumulated constrained eigenvalues of 0.5967 and 0.7961 accounted for 4.1 (p < 0.001) and 1.4% (p < 0.003), of the total variation in earthworm community composition and were constrained by environmental factors. Management and disturbance intensity (p = 0.01), plant diversity (p = 0.01), moisture (p = 0.01), P (p = 0.02), and pH (p = 0.05) were responsible for the variation observed in the earthworm species composition (data not shown). Across the 3 sites, *A. turgida* and *A. tuberculata* were associated with agricultural fields, whereas *A. chlorotica, O. tyrtaeum, L. rubellus*, and *A. rosea* were associated with agricultural buffers and forest fragments.

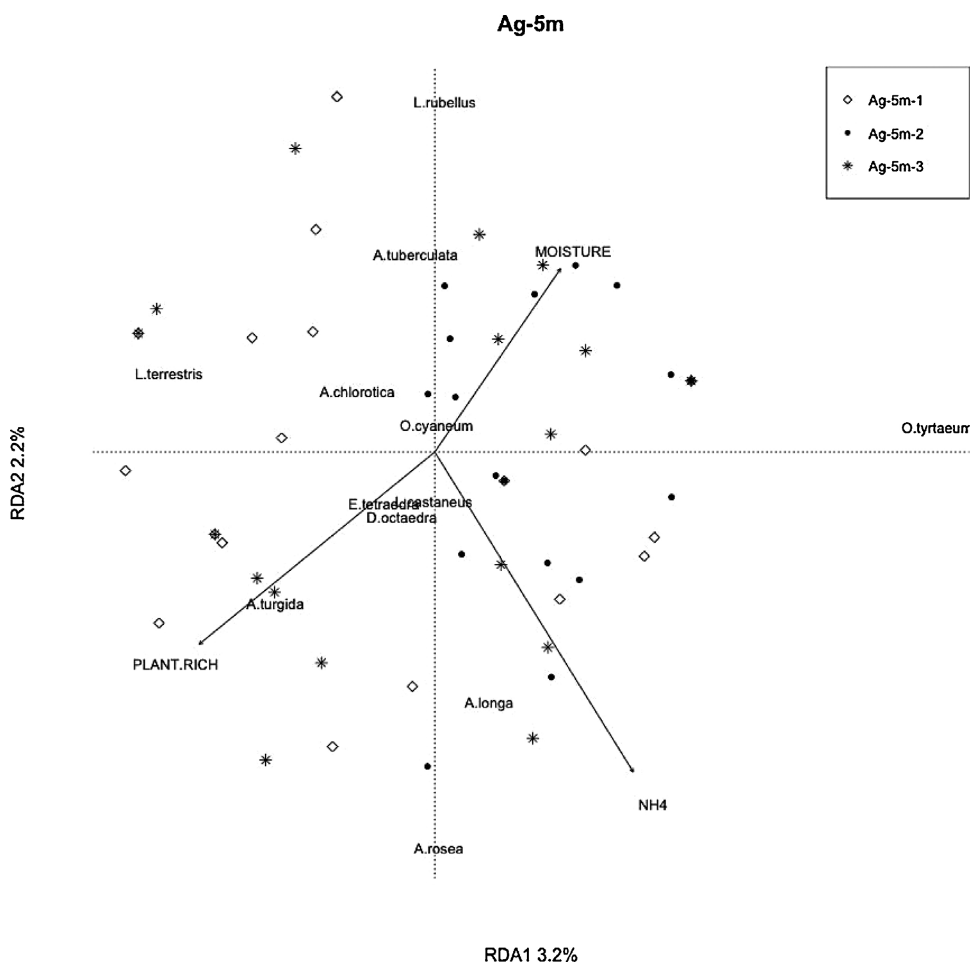

Fig. 3. RDA triplot of adult earthworm communities plots in the Ag-5 m habitat constrained by plant species richness, soil moisture, and NH_4 (p = 0.009) with scaling 2. Points represent the earthworm species composition in each sampling plot in the different transects. The plots that contain more of a particular species have their points scattered around the species label accordingly. The distance between a sampling plot and a species label indicates the abundance of that species in that sampling plot. Earthworm species labels indicate the weighted averages of site scores that are associated with an abundance of the species indicated. Length of constraining arrows for each constraining variable indicates greater variability. Species are labeled accordingly: *A. chloratica*: *Allolobophora chlorotica*; *O. cyaneum*: *Octolasion cyaneum*; *A. turgida*: *Aporrectodea turgida*; *A. tuberculata*: *Aporrectodea tuberculata*; *A. rosea*: *Aporrectodea rosea*; *A. longa*: *Aporrectodea longa*; *L. rubellus*: *Lumbricus rubellus*; *L. terrestris*: *Lumbricus terrestris*; *O. tyrtaeum*: *Octolasion tyrtaeum*; *E. tetraedra*: *Eiseniella tetraedra*; *L. castenous*: *Lumbricus castaneus*; *D. octaedra*: *Dendrobaena octaedra.*

Within habitats, environmental and management factors were associated with earthworm communities and species composition. The most parsimonious model included moisture ($p = 0.32$), plant species richness ($p = 0.0046$), and NH_4 ($p = 0.007$) as the environmental factors separating earthworm species compositions along the first 2 axes (Fig. 3). Within the Ag-5 m habitat, *A. longa* was associated with soil NH_4, and *A. chlorotica, A. tuberculata*, and *L. rubellus* were most closely associated with the soil moisture gradient, particularly in Ag-5 m plots at site 2, which were adjacent to a permanent pasture with legumes.

The strongest RDA explaining variation in earthworm communities in Ag-30 m was significant ($p = 0.017$), with environmental factors explaining 6.6% of the total variation in the first 2 canonical axes ($R^2_{adj} = 0.065$). Soil extractable P concentration ($p = 0.021$) and pH ($p = 0.066$) accounted for the observed variation in the earthworm community along axes 1 and 2 (Fig. 4), with a separation between the Ag-30 m at site 1 (higher extractable P concentration) from the Ag-30 m locations at sites 2 and 3.

In the most parsimonious RDA of For-5 m, the first 2 axes had eigenvalues of 0.0844 and 0.02722 and after adjustment ($R^2_{adj} = 0.15$), they significantly explained 8.3% ($p = 0.001$) and 2.7% ($p = 0.014$) of the variation in earthworm community composition. The model revealed that soil moisture ($p = 0.01$), K ($p = 0.05$), Ca ($p = 0.011$), DOC ($p = 0.16$), and MBC ($p = 0.015$) concentrations were the important explanatory variables of earthworm species composition (Fig. 5).

In the For-30 m site, the most parsimonious model had 2 RDA axes with eigenvalues of 0.05026 and 0.0213 that were significant and accounted for 5.1% ($p = 0.001$), and 2.1% ($p = 0.057$) of the total variation in earthworm community composition ($R^2_{adj} = 0.0849$). Plant species richness ($p = 0.431$), pH ($p = 0.01$), P ($p = 0.047$) and DOC ($p = 0.006$) concentrations explained the variation in earthworm species composition (Fig. 6).

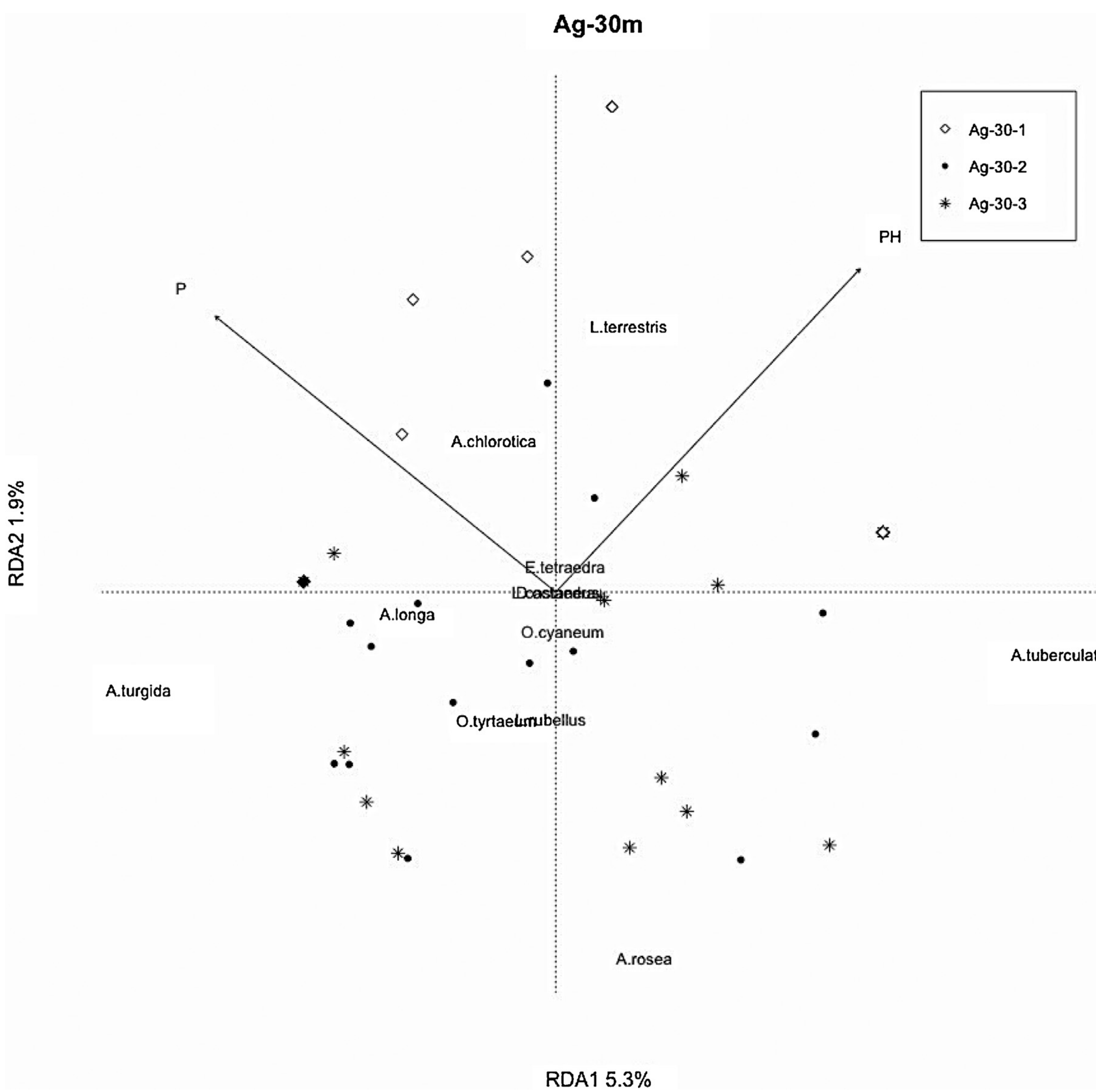

Fig. 4. RDA triplot of adult earthworm communities throughout plots in the Ag-30 m habitats constrained by phosphorus (P), and pH ($p = 0.017$) with scaling 2. Points represent the earthworm species composition in the different sampling plots in the different transects. The sites that contain more of a particular species are scattered around that species label. The distance between a sampling plot and a species label indicates the abundance of that species in that sampling plot. Earthworm species labels indicate the weighted averages of site scores that are associated with an abundance of the species indicated. Length of constraining arrows for each constraining variable indicates greater variability. Species are labeled accordingly: *A. chloratica*: *Allolobophora chlorotica*; *O. cyaneum*: *Otolasion cyaneum*; *A. turgida*: *Aporrectodea turgida*; *A. tuberculata*: *Aporrectodea tuberculata*; *A. rosea*: *Aporrectodea rosea*; *A. longa*: *Aporrectodea longa*; *L. rubellus*: *Lumbricus rubellus*; *L. terrestris*: *Lumbricus terrestris*; *O. tyrtaeum*: *Octolasion tyrtaeum*; *E. tetraedra*: *Eiseniella tetraedra*; *L. castenous*: *Lumbricus castaneus*; *D. octaedra*: *Dendrobaena octaedra*.

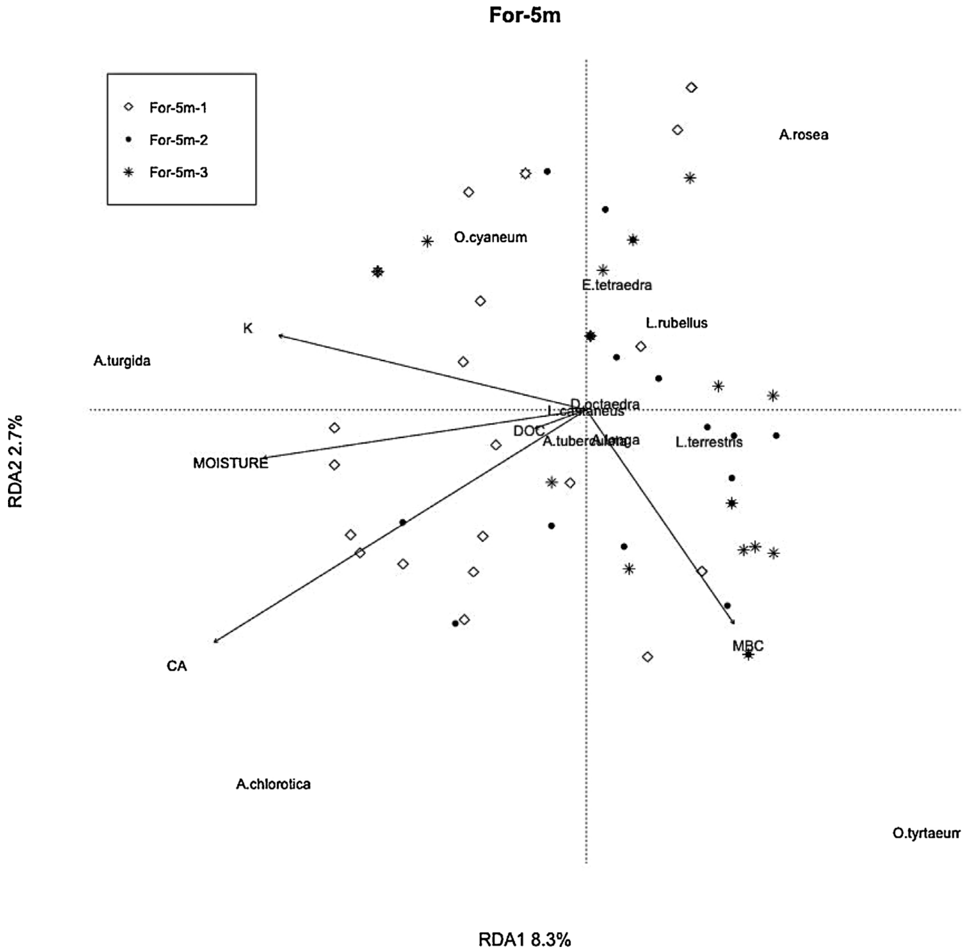

Fig. 5. RDA triplot of adult earthworm communities throughout plots in For-5 m constrained by potassium (K), soil moisture, calcium (CA), and microbial biomass carbon (MBC) ($p = 0.001$) with scaling 2. Points represent the earthworm species composition in the different sampling plots in the different transects. The sites that contain more of a particular species are scattered around that species label. The distance between a sampling plot and a species label indicates the abundance of that species in that sampling plot. Earthworm species labels indicate the weighted averages of site scores that are associated with an abundance of the species indicated. Length of constraining arrows for each constraining variable indicates greater variability. Species are labeled accordingly: *A. chloratica*: *Allolobophora chlorotica*; *O. cyaneum*: *Octolasion cyaneum*; *A. turgida*: *Aporrectodea turgida*; *A. tuberculata*: *Aporrectodea tuberculata*; *A. rosea*: *Aporrectodea rosea*; *A. longa*: *Aporrectodea longa*; *L. rubellus*: *Lumbricus rubellus*; *L. terrestris*: *Lumbricus terrestris*; *O. tyrtaeum*: *Octolasion tyrtaeum*; *E. tetraedra*: *Eiseniella tetraedra*; *L. castenous*: *Lumbricus castaneus*; *D. octaedra*: *Dendrobaena octaedra*.

The GLMM was used to further explain how earthworm diversity, populations and communities were related to land use, distance from river, and management intensity and flooding. Results indicated that plant cover and plant species richness were negatively correlated with high intensity management (Ag-30 m-1), but positively correlated with low management intensity (plots within For-5 m, For-30 m, Ag-5 m habitats). Likewise, earthworm biomass, abundance, and species richness were negatively correlated with higher management intensity. Furthermore, species richness was lower at 30 m than 5 m away from the river, and high soil moisture was positively correlated with earthworm abundance (Table 3).

4. Discussion

4.1. Comparing earthworm species composition between habitats

Throughout the landscape, earthworm communities differed between habitats (Ag-5 m, Ag-30 m, For-5 m, For-30 m) along the Pike River (Figs. 1 and 2), with distinct species composition between 5 m and 30 m habitats, likely due to the high management intensity in the 30 m habitats vs. soil moisture effects in the 5 m habitats. Earthworm species richness, biomass, and abundance differed between habitats in our study sites, with values ranging from 68 earthworms m^{-2} in Ag-30 m at site 1–420 individuals m^{-2} in For-5 m at site 1 (Fig. 1, Table 2). Higher agricultural intensity was negative for earthworms and it was not surprising that annually cropped agricultural fields were not as conducive to earthworm species richness, biomass and abundance as the forests. The smallest earthworm population (68 individuals m^{-2}) was in the agricultural upland field that was conventionally tilled and cultivated with a soybean–corn rotation. In another study comparing earthworm communities between land use systems in southern Quebec, abundance ranged from 124 to 480 individuals m^{-2} in a forest, compared to 13–229 individuals m^{-2} in a tilled corn field (Whalen, 2004), similarly underlining the reduction of habitat quality for earthworms in cultivated agroecosystems. Our findings corroborate with Eriksen-Hamel et al. (2009), who reported 2–9 times fewer earthworms in conventionally tilled than no-till systems in southern Quebec. Still, Bradley et al. (2011) found no consistent differences in earthworm abundance and biomass between cultivated cornfields and mowed agricultural buffers with permanent grass cover at one sampling date in the Pike River watershed, suggesting that agricultural management may not always affect earthworm community composition. This could be a function of the time of year that the earthworms were collected and other soil properties (e.g., soil moisture) that greatly influence earthworm demographics and population size in this region

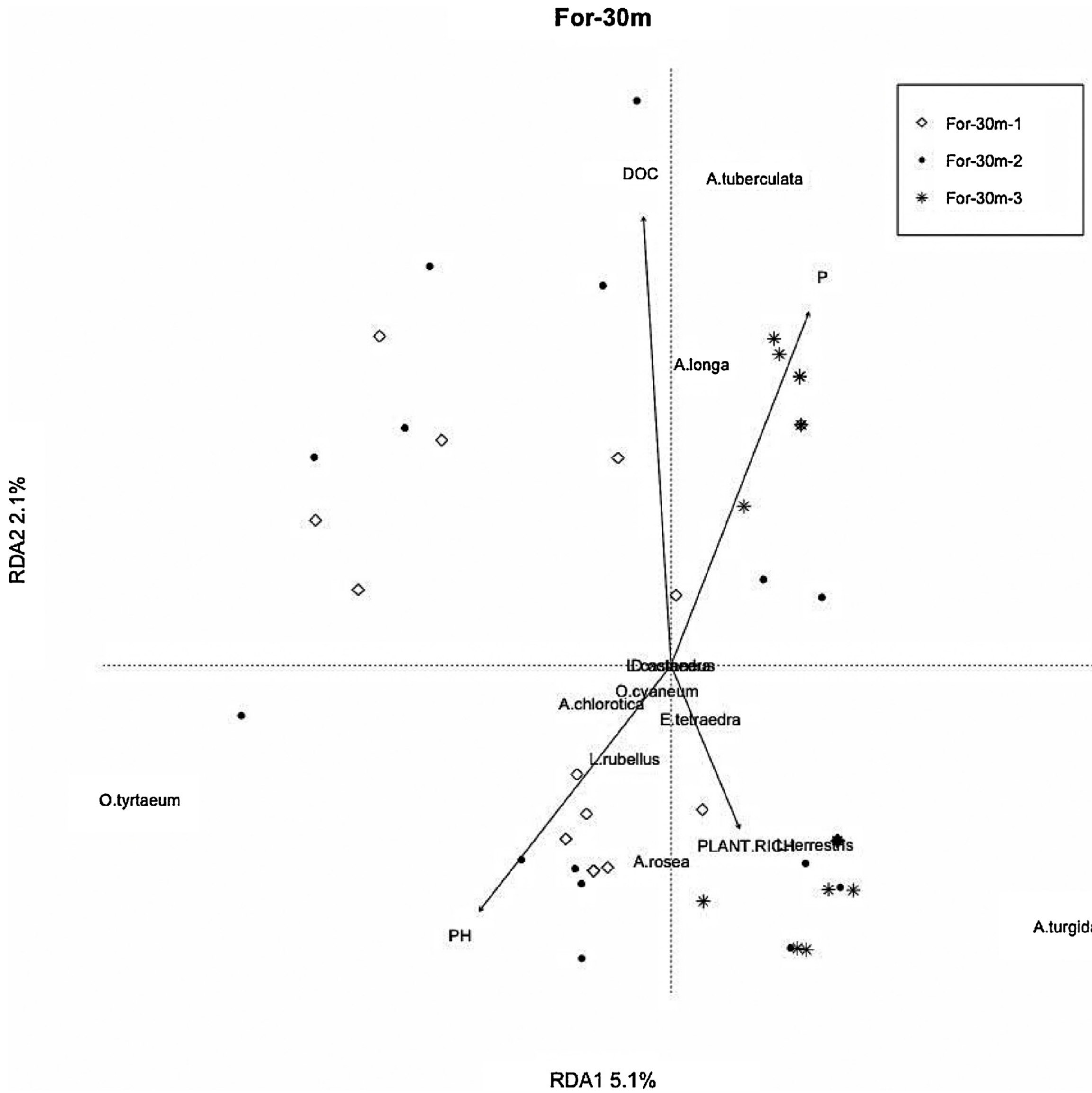

Fig. 6. RDA triplot of adult earthworm communities throughout plots in For-30 m habitats constrained by phosphorous (P), plant species richness, pH, and dissolved organic carbon (DOC) ($p = 0.008$) with scaling 2. Points represent the earthworm species composition in the different sampling plots in the different transects. The sites that contain more of a particular species are scattered around that species label. The distance between a sampling plot and a species label indicates the abundance of that species in that sampling plot. Earthworm species labels indicate the weighted averages of site scores that are associated with an abundance of the species indicated. Length of constraining arrows for each constraining variable indicates greater variability. Species are labeled accordingly: *A. chloratica*: *Allolobophora chlorotica*; *O. cyaneum*: *Octolasion cyaneum*; *A. turgida*: *Aporrectodea turgida*; *A. tuberculata*: *Aporrectodea tuberculata*; *A. rosea*: *Aporrectodea rosea*; *A. longa*: *Aporrectodea longa*; *L. rubellus*: *Lumbricus rubellus*; *L. terrestris*: *Lumbricus terrestris*; *O. tyrtaeum*: *Octolasion tyrtaeum*; *E. tetraedra*: *Eiseniella tetraedra*; *L. castenous*: *Lumbricus castaneus*; *D. octaedra*: *Dendrobaena octaedra*.

(Whalen, 2004). Based on multiple-year sampling, we conclude that earthworm communities and species composition are likely to be larger and more diverse in less intensively managed habitats with higher soil moisture in riparian areas of southern Quebec.

4.2. Environmental gradients associated with earthworm species composition within habitats

Soil moisture and management intensity generated heterogeneity within riparian habitats along the Pike River in southern Quebec and controlled the soil and vegetation factors that were associated with variation in earthworm communities and species composition. Although we assumed that plots located 5 m from the Pike River would be subject to flooding and therefore produce an important soil moisture gradient that affects earthworm communities and species composition, not all plots at 5 m were affected similarly by flooding due to undulating topography (for example, see the variation in moisture of forest plots at sites 1–3, Table S1). Nevertheless, higher soil moisture resulted in earthworm communities that tended to have greater species richness in association with high moisture ($p < 0.06$). Soil moisture in riparian areas is controlled by the water table, antecedent moisture, and flooding. Therefore, we suggest that our study supports the hypothesis that natural disturbances like flooding may increase diversity, and is applicable to riparian areas in highly managed landscapes in southern Quebec. Higher moisture also increased earthworm biomass and abundance throughout all habitats (Table 3). Previous studies have found that flooding dynamics exert a strong influence over earthworm communities, usually reducing earthworm diversity and abundances (Ausden et al., 2001; Ivask et al., 2007; Klok and Thorion, 2007), although in some cases, increasing their numbers (Schutz et al., 2008). Earthworm species vary in

Table 3
Results of Generalized Linear Mixed Model (GLMM) showing effect of land use, distance from river, management intensity, and gradient of soil moisture (proxy for flooding) on number of earthworm species, abundance of earthworms, soil properties, and vegetation parameters. Table displays significance of the fixed effect (probability that $p > X^2$), X^2, and the degrees of freedom (DF).

Response variable	Fixed effect	Significance	X^2	DF
Plant functional diversity	Land use	0.1263	2.337	1
	Distance	0.2191	1.51	1
	Intensity	0.6937	2.2291	4
	Flooding	0.9247	0.4733	3
Plant cover (%)	Land use	0.2013	1.6331	1
	Distance	0.0915	2.8473	1
	Intensity	<0.0001	1248.5	4
	Flooding	<0.0001	176.41	3
Plant species richness	Land use	0.1869	1.7416	1
	Distance	0.1377	2.2032	1
	Intensity	<0.0001	22.287	4
	Flooding	<0.0001	26.654	3
Earthworm species richness	Land use	0.8171	0.0535	1
	Distance	0.04664	3.9584	1
	Intensity	0.0004	20.474	4
	Flooding	0.0604	7.3915	3
Earthworm biomass (AFDW; m^{-2})	Land use	0.0092	6.7708	1
	Distance	0.7417	0.1086	1
	Intensity	<0.0001	589.8	4
	Flooding	<0.0001	460.6	3
Earthworm abundance (individuals m^{-2})	Land use	0.2133	1.5491	1
	Distance	0.07188	3.295	1
	Intensity	<0.0001	3818.2	4
	Flooding	<0.0001	3071.2	3
NO_3	Land use	0.0022	9.3298	1
	Distance	0.716	0.1324	1
	Intensity	<0.0001	75.382	4
	Flooding	<0.0001	146.18	3
NH_4	Land use	0.02355	5.1277	1
	Distance	0.3861	0.7511	1
	Intensity	<0.0001	59.858	4
	Flooding	<0.0001	120.67	3
pH	Land use	0.376	0.7839	1
	Distance	0.3818	0.7651	1
	Intensity	0.708	4.2688	4
	Flooding	0.9543	0.3298	3
P	Land use	0.1486	2.0867	1
	Distance	0.2224	1.4887	1
	Intensity	<0.0001	175.61	4
	Flooding	0.0018	14.926	3
K	Land use	0.7385	0.1115	1
	Distance	0.0014	10.124	1
	Intensity	<0.0001	157.15	4
	Flooding	<0.0001	79.671	3
CA	Land use	0.0405	4.1949	1
	Distance	0.4766	0.5067	1
	Intensity	<0.0001	40247	4
	Flooding	<0.0001	14651	3
DOC	Land use	0.1999	1.6434	1
	Distance	0.1423	2.1534	1
	Intensity	<0.0001	265.99	4
	Flooding	<0.0001	1614	3
MBC	Land use	0.0772	3.1214	1
	Distance	0.434	0.6122	1
	Intensity	<0.0001	329.06	4
	Flooding	<0.0001	1509	3

their optimal soil moisture range and not all species can tolerate inundated soils (Curry, 2004). For example, the earthworm species *Allolobophora chlorotica* (Table 2), an earthworm known for its preference for saturated and moist soils (Roots, 1956), and characteristic of riverine habitats (Reynolds, 1977), was most abundant in the For-5 m plots at site 1, which was the wettest habitat in the study. Whalen and Costa (2003) found that earthworm populations in Quebec forest sites were positively correlated with soil moisture ($r \approx 0.51$), and Suarez et al. (2006) found that poorly drained forest soil in New York had higher earthworm populations than better drained soils. Since riparian soils (5 m) are closer to the water table and consequently tend to be moister than upland soils, we assume that these soils provide habitat for abundant and diverse earthworm communities, with greater numbers of earthworms that prefer high soil moisture.

Management intensity, with corresponding patterns in plant species richness, also played a key role in defining habitat suitability for earthworm communities. More specifically, management intensity was negatively correlated with earthworm diversity, biomass, and abundance, most likely due to soil disturbance. Management intensity was concurrently negatively correlated with plant species richness, which was important for variations in earthworm species composition between Ag-5 m habitats throughout sites. The gradient in plant species richness was related to differences in earthworm species composition in For-30 m in sites 2 and 3 from For-30 m in site 1. Accordingly, Spehn et al. (2000) found that earthworm populations declined with a reduction in plant diversity, which corresponded to a decrease in organic matter inputs via residue. Plant species traits via roots or residue are related to earthworm nutrition (Curry and Schmidt, 2007). Riparian soils are considered a sink for NH_4, because they harbor abundant vegetation, which senesces (Hefting et al., 2005) and provides substrate for earthworms and enhances its mineralization. As such, we found that high soil NH_4 in agricultural buffers (Ag-5 m) was related to dissimilarities in earthworm species composition between Ag-5 m in all sites (Fig. 3). High organic matter inputs in the form of senesced plant residue is also a source of dissolved organic carbon (DOC), and may have shaped the variation in earthworm species composition within For-30 m habitats. Moreover, we found a strong association between earthworm biomass and exchangeable Ca in forest floors, possibly due to earthworm activity (Reich et al., 2005). In the forest floor, the diverse plant and tree species in For-5 m was interrelated to the variation of Ca in soils. Plant species can influence the distribution and cycling of Ca and other nutrients (Vesterdal et al., 2008). Therefore, plant species richness and earthworm species composition may be linked via soil nutrients, given that different plant species will have different degrees of palatability to earthworms. Greater vegetation diversity would provide more diverse substrates for earthworm communities in forests and unmanaged agricultural buffers, therefore promoting their numbers and diversity compared to intensively managed agricultural fields.

Non-native earthworm species composition was somewhat homogenous between and within habitats, which reflects the low percent of variation explained by redundancy analysis. We found a total of 11 species, which is not uncommon for the region. However, the low number of species may lead to lower variation that could be explained with our analyses. Adding other explanatory factors, such as predators, to analyses may further our understanding of how the riparian environment may be conducive to non-native earthworm community sizes and species compositions.

5. Conclusion

Our study showed that earthworm species composition differed between habitats that were 5 m and 30 m away from the Pike River. These results underline the small-scale difference in habitats closer to and further away from rivers, which can result in distinct earthworm communities. Higher management intensity occurring in cultivated fields and flooding that was heaviest in forest fragments were likewise related to the differences in earthworm species composition. Non-native earthworm communities were larger and more diverse closer to the river, particularly in forest fragments, which may reflect more ecosystem complexity and greater overall higher biodiversity. Throughout southern Quebec, forest fragments provide ecosystem services (Mitchell et al., 2014) and help control the detrimental effects of flooding and nutrient losses from agricultural fields, thereby protecting surface watercourses in southern Quebec. Non-native earthworms' role as indicator species for biodiversity within ecotones may be more important than their potential role in compromising ecosystem services in forested and unmanaged riparian areas in southern Quebec. Therefore, monitoring riparian forest fragments throughout Quebec may provide more insight to the way non-native earthworms influence ecosystem function, particularly soil hydrology and nutrient dynamics.

Acknowledgements

We would like to acknowledge Alicia Goodhue, Bethany Templeton, Tahmid Huq Easher, Shamim Gul, Hicham Benslim, Olaf Mayer, and Ricardo Fontoura for assistance in the field. Thank you to Hélène Lalande for analysis of soil characteristics in the lab and to Nadia Cavallin for assisting with the plant survey. Funding was from an Équipe grant (grant number 131894) and the Centre SÈVE's Regroupements stratégiques grant (grant number 144531), both provided by the Fonds de Recherche du Québec Nature et Technologies (FQRNT) program.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.apsoil.2015.08.011.

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