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Indirect and direct effects of exotic earthworms on soil nutrient and carbon pools in North American temperate forests

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ABSTRACT

Earthworm invasions in North American temperate forests cause considerable changes to soil and litter horizons, which can lead to changes in soil biogeochemistry and plant communities. These ecosystem changes have complex causal relationships, and the cascades of indirect effects from earthworm burrowing and feeding may have larger net effects on soil biogeochemistry than direct effects. In this study we partitioned the effects of earthworms on particular soil nutrient and carbon pools into direct and indirect effects. We defined direct effects as consisting of the association between the soil nutrient or carbon pool and earthworm biomass, whilst indirect effects included the impacts earthworms have on these soil pools through changing litter layer depth and soil chemical and biotic factors. We quantified these direct and indirect effects using a path analysis approach applied to data collected from 24 plots across an earthworm gradient in a northern hardwood forest stand in Ontario, Canada. As potential predictors, we measured earthworm functional group biomass, litter depth, microbial biomass, soil pH, texture, and organic matter. We related these predictors to extractable nutrient and carbon concentrations, including nitrate/nitrite, ammonium, orthophosphate, and dissolved organic nitrogen, phosphorus, and carbon. We found few direct effects and primarily indirect effects of earthworms on the soil nutrient and carbon pools we measured. Endogeic earthworms had the strongest indirect effects via changes to pH, microbial biomass carbon, and proportion of soil organic matter. Anecic earthworms only indirectly affected soil and nutrient pools through changes in pH, and epigeic earthworms did not have either direct or indirect effects. Because endogeic earthworms had indirect effects through changing multiple soil factors, for some soil and nutrient pools these indirect effects augmented each other (primarily yielding negative effects), although in some cases indirect positive effects mitigated negative effects. Overall, the net effects of exotic earthworms on soil and nutrient pools were mostly negative. Of particular concern was the potential exacerbation by endogeic earthworms of phosphorus limitation in N-saturated forest systems, as well as carbon loss from mineral soils in addition to losses from the forest floor.

1. Introduction

Invasive ecosystem engineers, such as exotic earthworms, have strong impacts on nutrient, trophic, and physical resources in soils (Crooks, 2002). Non-native earthworms are recognized as an emerging threat to temperate North American forest ecosystems, and are considered one of the most globally important agents of change to biodiversity and associated ecological and evolutionary processes (Sutherland et al., 2011). Earthworms change forest floor systems by rapidly consuming litter and homogenizing the organic and mineral layers of soil, leading to a gradual elimination of the litter layer (Langmaid, 1964; Alban and Berry, 1994). Earthworm invasion in forests has also been associated with changes to soil chemistry (Edwards and Bohlen, 1996), altered microbial communities and processes (Burtelow et al., 1998; Li et al., 2002; Groffman et al., 2004; McLean et al., 2006), shifts in microarthropod communities (McLean and Parkinson, 2000; Migge-Kleian et al., 2006; Straube et al., 2009) and shifts in nutrient and carbon pools and dynamics (Bohlen et al., 2004a; Suárez et al., 2004; Hale et al., 2005; Wironen and Moore, 2006; Costello and Lamberti, 2009). These changes to nutrient availability and the soil environment may contribute to observed changes to the plant community that are correlated with earthworms, including seed banks

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(Hopfensperger et al., 2011), community composition (Hale et al., 2006; Holdsworth et al., 2007) and growth (Larson et al., 2010).

The multiple ecosystem changes observed with earthworm invasion have complex causal relationships. In the conceptual model presented by Bohlen et al. (2004b) earthworms cause three interdependent categories of changes: physical effects (e.g., changed soil and litter structure), geochemical effects (e.g., homogenized soil horizons), and biological effects (e.g., altered nutrient cycling, microbial communities). These changes lead to ecological consequences which include short-term carbon loss and changes to soil N and P availability. In this study we explored a model pathway of the links between edaphic changes due to earthworms and shifts in soil nutrient and carbon pools. We suggest that earthworm burrowing and litter consumption may directly change nutrient and carbon concentrations, and also indirectly affect these pools by altering litter layer depth, and soil pH, organic matter, texture, and microbial biomass (Fig. 1). Although previous studies have quantified the direct relationships between earthworms and soil nutrient and carbon pools (Bohlen et al., 2004b; Addison, 2009), and earthworms and pH, organic matter, and microbial biomass (Haimi and Huhta, 1990; Schrader, 1994; Edwards and Bohlen, 1996), no studies, to our knowledge, have partitioned the effects of earthworms into direct and indirect components.

The specification and testing of models that include direct and indirect effects is particularly valuable for understanding ecosystem consequences of invasive species (Gandhi and Herms, 2010; Weidenhamer and Callaway, 2010). Cascades of indirect effects from invasive species potentially cause larger and more persistent ecosystem changes than direct effects (e.g., Peltzer et al., 2010). Studies that quantify only direct effects (e.g., direct relationship between available nutrients and earthworm biomass) may underestimate the total earthworm effects on a response variable, which may be also affected indirectly via changes to other soil factors. Depending on the magnitude and direction of indirect effects they can either augment or mitigate other direct and indirect impacts of the invasive (Eubanks, 2001; Atwater et al., 2011).

One strategy that can be used to explore indirect and direct effects is path analysis, and this technique has been used to quantify the relative importance of the indirect and direct effects of predictor variables on response variables in many ecosystems (Mitchell, 1992; Wootton, 1994; Bakker et al., 2003; Vogel et al., 2010), including the impacts from invasive species (Eubanks, 2001; Atwater et al., 2011). Path analysis is similar to multiple regression, as it is based on the analysis of correlations, but unlike multiple regression, it allows the partitioning the effects of predictor variables on a response variable into direct and indirect components (Fig. 1). The relative magnitude of these components can be calculated, and the total effect of a predictor on a response variable consists of the sum of direct and indirect effects (Quinn and Keough, 2002). Because path analysis uses correlations to calculate path coefficients, this method can only test how the data fit the proposed causal pathways, and not prove causality.

In this study we focus on the earthworm invasion of a northern temperate hardwood forest with acidic and nutrient-poor soils and quantify the direct and indirect (through changes in litter layer depth, pH, soil organic matter, soil texture, and microbial biomass) effects of earthworms in different functional groups (Edwards and Bohlen, 1996) on soil nutrient and carbon pools.

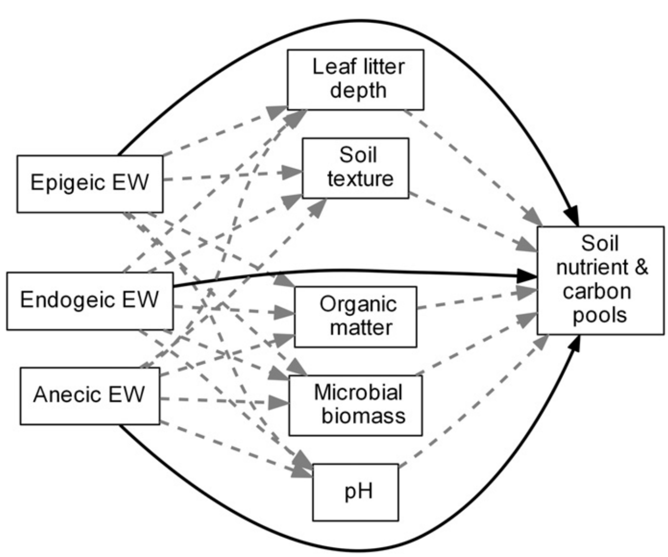

Fig. 1. Direct and indirect pathways by which earthworm functional groups may alter soil nutrient and carbon pools. Black solid arrows indicate direct effects, while gray dashed arrows indicate indirect effects via changes to soil or litter factors.

2. Materials and methods

2.1. Study site and sampling design

The study was conducted in 2010 at Haliburton Forest and Wild Life Reserve (HF), a mixed-use forest in eastern Ontario, Canada (45.29 N, −78.64 W) with no native earthworm species. Haliburton Forest is dominated by sugar maple (*Acer saccharum* Marshall), red maple (*Acer rubrum L.*), eastern hemlock (*Tsuga canadensis (L.) Carrière*), yellow birch (*Betula alleghaniensis* Britton), and American beech (*Fagus grandifolia* Ehrh.). This area receives ~1100 mm of precipitation per year, and has a mean annual temperature of 4.9 °C. Soils, generally in the Dystric Brunisols great group (Soil Classification Working Group, 1998), have low pH (range: 4.2–5.1 (Gradowski and Thomas, 2006)) and base saturation and a sandy to sandy-loam texture overlaying granite bedrock. Although we do not know the exact dates of earthworm introduction at this site, earthworms were widespread across this rural county in the 1970s (Reynolds, 1972), and our site is within the main settlement area of Haliburton Forest which has been in constant use since its initial settlement as a farm in the 1870s, with subsequent use as a base for logging and recreation. We therefore suspect that earthworms have been invading this forest stand for decades. The study was conducted in a forest stand adjacent to two horse pastures near to the original settlement. The stand was primarily maple (80% by basal area) interspersed with hemlock and beech (each 9% basal area), and isolated black cherry (*Prunus serotina* Ehrh.) and yellow and white birch (*Betula papyrifera* Marsh.). This site was selected because there was a visible gradient of earthworm invasion in the forest from the sides closest to the pastures and continuing into the forest, providing us with an earthworm abundance gradient from high to low (zero) densities. In the forest, beginning 100 m and 15 m from the pastures (a distance beyond the transitional zone between pasture and forest), we set up 7 transects, 50 m apart, which ran perpendicular to the nearest pasture. Along each transect we sampled every 50 m until earthworms were not present at 2 consecutive sampling points, at which point we stopped extending the transect. To delineate the spread front more accurately we added an additional sample point on the transect 25 m beyond the final sample where earthworms were found. In total we sampled 26 points. A map of the site is provided in Appendix 1.

2.2. Earthworm sampling, identification, and mapping

We chose to sample earthworms in August (Haliburton, ON, August climate data 1971–2000: mean daily temperature: 17.8 °C, daily minimum–daily maximum 1971–2000: 12.2–23.4 °C, mean