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Modelling interacting effects of invasive earthworms and wildfire on forest floor carbon storage in the boreal forest

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ABSTRACT

In forest ecosystems, earthworms and wildfire are two ecological agents that cause carbon (C) stored in the forest floor to be transferred to the atmosphere as greenhouse gases, either through heterotrophic respiration (earthworms) or through periodical combustion (wildfire). For centuries, wildfire has been an important ecological driver in the boreal forests of Canada where most fire emissions to the atmosphere originate from the forest floor. In contrast, earthworms are recent invaders, having been introduced to the Canadian boreal during the 20th century. Their spread is mainly associated with anthropogenic activities. We examined stand-level effects of earthworms and wildfire on forest floor C by adapting an earthworm-C simulation model for the boreal and using it in combination with a forest C accounting model. Because the overall impact of an invasive species depends on its areal extent, we used a spatial model of earthworm spread to calculate the total predicted change in C storage at the landscape-level following earthworm invasions in northeastern Alberta. Depending on the ecological groups of earthworms modelled in stand-level simulations, the forest floor C stock was reduced by 49.7–94.3% after 125 years, although the majority of this reduction occurred 35–40 years after initiation of the invasion. Because earthworm activities reduced the amount of forest floor C available for burning, emissions from wildfire were lower in the presence of earthworms. Spatial modelling of earthworm effects within the 5,905,400 ha Alberta–Pacific Forestry Management Area projected that forest floor C stocks in the invaded stands decreased 50,875 Mg C by 2006, and 2,706,354 Mg C by 2056, compared with the same area if earthworms were not present. Loss of forest floor C averaged over the 50 year simulation was 10 g m^2 yr^{-1}; similar in magnitude to estimates for C loss in the Canadian boreal due to wildfire or harvesting. These results indicate effects of non-native earthworms on the forest floor should be included in predictions of forest ecosystem C budgets to ensure accurate attribution of emissions to heterotrophic respiration versus combustion.

1. Introduction

Both abiotic and biotic disturbances influence forest carbon (C) dynamics, but our understanding of how they interact to influence C storage is limited (Hicke et al., 2012). Wildfire is often the primary abiotic disturbance altering the C balance in boreal and temperate forests (Bond-Lamberty et al., 2007), whereas insect outbreaks and invasive species can exert similarly strong effects (Peltzer et al., 2010; Hicke et al., 2012). Outbreaks of insects such as bark beetles and spruce budworm (*Choristoneura fumiferana* Clem.) modify the quantity and quality of fuels available, leading to changes in the timing or intensity of fires (Fleming et al., 2002; Jenkins et al., 2008). Fires can also influence insect outbreaks by causing changes in tree species composition and stand structure (Parker et al., 2006; Hicke et al., 2012). In contrast, little is known about the potential interacting effects of wildfire and animals that live belowground on forest floor C.

The forest floor is important to the C balance of forest ecosystems because it can store substantial amounts of C (Kurz et al., 2013). It is a source of greenhouse gas emissions, primarily in the form of carbon dioxide (CO_2) from annual processes (e.g.,

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decomposition), and it is sensitive to losses from episodic natural and anthropogenic disturbances (e.g., harvesting and wildfire). Here we use the term forest floor to describe the combined soil organic horizons L, F and H as defined in the Canadian system of soil classification (SCWG, 1998). Our definition is consistent with the litter pool as defined by the Intergovernmental Panel on Climate Change – guidance documents (Penman et al., 2003; Eggleston et al., 2006; Tanabe et al., 2013) for reporting on forest C stocks and stock changes (see Kurz et al., 2009). In Canadian forests, mean forest floor mass ranges from 45 ± 34 (SD) to 206 ± 103 (SD) Mg ha^{-1} for stands dominated by different tree species (Letang and de Groot, 2012). Approximately half of this mass is C. In the managed forest area of the Canadian boreal zone, the average C density of the litter pool (approximately 46.0 Mg C ha^{-1}) is slightly larger than the aboveground biomass pool (approximately 39.6 Mg C ha^{-1}) (Kurz et al., 2013). Carbon is transferred from the forest to the atmosphere as greenhouse gases largely through heterotrophic respiration (R_h) (391 Tg C yr^{-1}) resulting from the decomposition of the litter pool as well as the deadwood and mineral soil C pools. Combustion, primarily of the forest floor component (Letang and de Groot, 2012) of the litter pool (15 Tg C yr^{-1}; Kurz et al., 2013), is also important. The annual processes of photosynthesis and R_h tend to balance one another out and thus periodic fire disturbances are a major determinant of the net C balance in the Canadian boreal zone (Kurz et al., 2013).

Currently, no forest C budget estimates for Canadian forests include the effects of earthworms on the forest floor. North American boreal forests have developed in the absence of earthworms which are believed to have been extirpated approximately 10,000 years ago during the Pleistocene glaciations and have only recently moved into boreal forest systems (Gates, 1982). Invasions of European earthworms in northern Canadian forests appear to have occurred primarily within the last 30–60 years (Scheu and Parkinson, 1994; Cameron and Bayne, 2009). In the boreal forest of northern Alberta, six species of non-native earthworms have been detected (Cameron et al., 2007) and have been projected to invade 49% of suitable habitat in northeastern Alberta over the next 50 years (Cameron and Bayne, 2009).

Earthworm invasions are occurring worldwide, resulting in extensive above- and belowground changes in forest ecosystems (Bohlen et al., 2004a; Hendrix et al., 2008). Earthworms alter the C cycle directly by consuming and redistributing leaf litter and organic matter (Bohlen et al., 2004a; Hale et al., 2005). They also affect soil C storage indirectly via changes in microbial and invertebrate communities (Frelich et al., 2006). Decreases in soil C following earthworm invasions are hypothesized to result from increased mineralization rates, which are caused by earthworm respiration and stimulation of microbial activity in earthworm guts and casts (Bohlen et al., 2004b). However, a recent analysis illustrated that the increase in mineralization rates due to earthworms can also be associated with high rates of C stabilization in the mineral soil (Zhang et al., 2013). Thus, the nature and magnitude of impacts of invasive earthworm species are related to three ecological functional groups: epigeic (litter-dwelling), endogeic (mineral soil-dwelling) and anecic (deep-burrowing but feeding on litter) (Bouché, 1977). Invasions of deep-burrowing earthworm species may increase C storage due to redistribution of organic matter deeper into soil layers (Wironen and Moore, 2006) while also resulting in enhanced stabilization of C in the mineral soil (Shaw and Pawluk, 1986; Zhang et al., 2013). Epigeic species feed on litter at the soil surface and thus may be likely to lead to reductions in C storage (Alban and Berry, 1994). Endogeic species have a less direct effect on litter decomposition in the forest floor as they feed primarily on organic matter within the mineral soil (Huang et al., 2010). Earthworms have been estimated to increase CO_2 loss from soil by an average of 33% globally (Lubbers et al., 2013). However, no information is available on their effects in the boreal forest specifically (Addison, 2009) despite the region's importance as a global C sink (Stinson et al., 2011).

Though currently a net C sink (Pan et al., 2011), the boreal forest may become a C source over the next century as a result of climate change (Zhuang et al., 2006). In part due to climate warming, the frequency and intensity of wildfires is expected to increase in the future (Stocks et al., 2002; Flannigan et al., 2005; Bond-Lamberty et al., 2007). A 74–118% increase in the total area burnt annually in Canada is predicted over the next 100 years (Flannigan et al., 2005) with significant implications for Canada's forest carbon balance (Metsaranta et al., 2010). Furthermore, increases in fire frequency in the last half of the twentieth century have already led to increased C loss in central Canadian boreal forests (Bond-Lamberty et al., 2007). Thus, in the Canadian boreal, it is expected that wildfire will reduce forest floor C stocks in response to a future change in climate. If earthworm invasion and spread continues, it is expected that invasive earthworms will concurrently reduce forest floor C stocks. Interactions between the effects of these two different ecological agents on the C budget are also expected because reduction of the forest floor by earthworms can reduce the amount of forest floor available for combustion in a wildfire. Conversely, reduction of the forest floor by wildfire decreases the amount of substrate available to sustain earthworm populations.

As little to no long-term data are currently available on the effects of earthworm invasions in the boreal, simulation modelling is needed to examine the potential future impacts of non-native earthworms on the fate of forest floor C. We used a set of simulation models to investigate the effects of non-native earthworms and their interactions with fire frequency on forest floor C storage in the boreal forest of northeastern Alberta, Canada. Our main objectives were to adapt an earthworm-C model for the boreal, evaluate stand-level effects of earthworms and wildfire on the forest floor, and use the stand-level results to evaluate the effect of earthworms on forest floor C at the landscape-level. Simulations were designed for stands where trembling aspen (*Populus tremuloides* Michx.) is dominant on Orthic Gray Luvisolic soils (SCWG, 1998), a typical forest type in northeastern Alberta where the landscape-level analysis was located (Fig. 1a). Invasive earthworms are expected to be most abundant within upland deciduous/mixedwood forests in northern Alberta (Cameron et al., 2007; Cameron and Bayne, 2009).

2. Materials & methods

We used three different simulation models to examine the effect of earthworms on forest floor C. A simulation model for earthworm effects on soil C created by Huang et al. (2010) was adapted for boreal conditions to examine the effect of ecologically distinct earthworm groups on R_h and the forest floor. Our goal was to make this model compatible with the pool structure of the Carbon Budget Model of the Canadian Forest Sector (CBM–CFS3) (Kurz et al., 2009; Kull et al., 2011) so that if this study found significant effects of earthworms, the modified earthworm-C model would have the potential to be developed as a module for the CBM–CFS3. We also used the CBM–CFS3 to provide a time series of dead tree biomass inputs to the earthworm-C model and to simulate the effects of fire frequency on forest floor C stocks. In its original form, the earthworm-C model only allowed for inputs from foliar litter but not fine and coarse woody material. The boreal earthworm-C model and the CBM–CFS3 were used in combination for the stand-level analyses. Results from the stand-level analyses were then combined with an earthworm spread model to calculate the total predicted change in C storage at the landscape-level following

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