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Long-term effects of pest-induced tree species change on carbon and nitrogen cycling in northeastern U.S. forests: A modeling analysis

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ABSTRACT

Invasive insects and pathogens can cause long-term changes in forest ecosystems by altering tree species composition, which can radically alter forest biogeochemistry. To examine how tree species change may alter long-term carbon (C) and nitrogen (N) cycling in northeastern U.S. forests, we developed a new forest ecosystem model, called Spe-CN, that allows species composition to shift over time. We simulated the effects of species change due to three invaders—beech bark disease (BBD), hemlock woolly adelgid (HWA), and sudden oak death (SOD)—on forest productivity, C storage, and N retention and loss over a 300-year period. The model predicted changes in C and N cycling rates and distribution between vegetation and soils after stands were invaded, with the magnitude, direction, and timing dependent on tree species identity. For a stand in which sugar maple (*Acer saccharum* Marsh.) replaced American beech (*Fagus grandifolia* Ehrh.) due to BBD, the model predicted a change from net C loss (−13% after 100 years) to net C storage (+10% after 300 years), as plant C gain (+36%) overtook C loss from soils (−11%) and downed wood (−24%). Following replacement of eastern hemlock (*Tsuga canadensis* (L.) Carr.) by yellow birch (*Betula alleghaniensis* Britt.) due to HWA, early loss of forest floor C (−28% after 100 years) was exceeded by gain of plant and downed wood C after 145 years; by 300 years, total C differed little between invaded and un-invaded stands. Where red maple (*Acer rubrum* L.) replaced red oak (*Quercus rubra* L.) due to SOD, loss of plant and soil C generated net C loss (−29%) after 100 years that continued thereafter. In contrast to C, for which patterns of storage and loss differed considerably among invasion scenarios, total N was ultimately lower following invasion across all three scenarios. Predicted nitrate leaching was also correspondingly higher in invaded vs. un-invaded stands (+0.3 g m^{-2} $year^{-1}$ of N from nitrate), but the leaching increase lagged by nearly 100 years following HWA invasion. Together, these results demonstrate that the effects of pest-induced tree species change on forest C and N cycling vary in magnitude, direction of effect, and timing of response following invasion, depending on the identity of the declining and replacing species, and that species-specific modeling can help elucidate this variation. Future predictions will need to account for tree species change to generate meaningful estimates of C and N storage and loss.

1. Introduction

Forests of the U.S. have been subject to repeated invasions by destructive insects and diseases imported from other continents, with particular severity in the Northeast (Aukema et al., 2010; Liebhold et al., 2013). As with other disturbances, these pests can produce short-term ecosystem effects due to tree mortality, including reductions in productivity and shifts in nutrient cycling (Loo, 2009; Lovett et al., 2006; Peltzer et al., 2010). Unlike other types of disturbance, however, invasive insects and diseases often target individual tree species, which can change the species composition of the forest. Such shifts in species composition can have long-term implications for forest ecosystems (e.g., Ellison et al., 2005; Lovett et al., 2006).

Replacing one tree species with another can considerably alter key forest ecosystem functions (e.g., Binkley and Menyailo, 2005). Differences among species in growth rate, tissue nitrogen (N) concentrations, allocation to wood, foliage, and roots, litter chemistry, and mycorrhizal associations cause differences in net primary productivity (NPP), decomposition, soil carbon (C) storage, and N cycling (Finzi et al., 1998; Hobbie, 1992; Lovett et al., 2004).

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Different tree species grown in the same climate and soil conditions can vary in foliar and wood productivity by over 100% (Gower et al., 1993; Reich et al., 2005). Likewise, stands dominated by different species can vary more than 600% in the rate of nitrate (NO_3^-) leaching to surface waters (Lovett et al., 2002), and species-driven differences in net nitrification rates can reach 1000% (Lovett et al., 2004). Carbon and N pools and C:N ratios vary widely in soils under different tree species (e.g., Cools et al., 2014; Ross et al., 2011; Vesterdal et al., 2008), and tree species-specific effects on surface soils extend to soil microbial communities (Scheibe et al., 2015; Urbanova et al., 2015). Loss of a dominant tree species due to an invasive insect or pathogen therefore can have considerable consequences for forest ecosystem functions such as C storage or N retention.

In the northeastern U.S., invasive insects and pathogens are causing, or predicted to cause, declines in several dominant tree species. For example, beech bark disease (BBD) has affected American beech (*Fagus grandifolia* Ehrh.) trees across the northeastern U.S. via the interaction of a scale insect (*Cryptococcus fagisuga*) and fungi of the genus *Neonectria*, beginning in the 1890s (Houston, 1994). Across the region, beech mortality rates have increased and growth rates have declined with time since invasion, despite frequently prolific sprout or seedling regeneration (Morin and Liebhold, 2015). In the Catskill Mountains of southeastern New York, the focal area for our study, decline in beech due to BBD has resulted in a shift toward increasing sugar maple (*Acer saccharum* Marsh.) (Lovett et al., 2010). Sugar maple and beech differ in several plant traits, including lower foliar N and lignin concentrations and more decomposable litter in sugar maple than in beech (Lovett et al., 2013a, 2010, 2004), that strongly influence nutrient cycling processes.

Hemlock woolly adelgid (HWA) is a more recent, insect invader of northeastern U.S. forests that has spread rapidly since the 1950s through the range of eastern hemlock (*Tsuga canadensis* (L.) Carr.), halted in its northward movement by current climatic limits (Trotter and Shields, 2009). In hemlock-dominated stands, hemlock can generate a stable ecosystem with slow decomposition and low rates of N cycling (Ellison et al., 2005; Jenkins et al., 1999). During invasion by HWA, black birch (*Betula lenta* L.) often replaces hemlock in southern New England (Orwig et al., 2002; Stadler et al., 2005), but this pattern is not consistent at the regional scale (Morin and Liebhold, 2015), and yellow birch (*Betula alleghaniensis* Britt.) is a more common associate of hemlock in the Catskills (Lovett et al., 2013b). As with beech and sugar maple, hemlock and birch differ in influential traits such as tissue N concentrations and litter decomposability, which influence C and N cycling in underlying soils (Cobb, 2010; Lovett et al., 2004).

In addition to ongoing invasions, new insects and diseases continue to enter U.S. forests, with new insect arrivals estimated at approximately 2.6 per year (Aukema et al., 2010). Sudden oak death (SOD), a disease caused by the pathogen *Phytophthora ramorum*, has resulted in extensive oak (*Quercus* spp.) mortality in California (Cobb et al., 2012; Rizzo et al., 2005) but has not yet reached the northeastern U.S. Simulation modeling suggests that the invasion is in its early stages and the pathogen is climatically suited to a large area worldwide, including areas of the eastern U.S. where oak species frequently dominate (Ireland et al., 2013). In California, tree species differ in their susceptibility to SOD; thus, in a study of ecosystem effects of SOD, the largest effects on ecosystem processes occurred via changes in species composition, which in turn altered litterfall chemistry, litterfall mass, and soil NO_3^- availability (Cobb et al., 2013). Oak species are frequent dominants in eastern U.S. forests, and habitat suitability for the oak-hickory forest type is predicted to increase in the Northeast as the climate warms (Iverson et al., 2008). If SOD reaches the eastern U.S., it may drive replacement of abundant red oak (*Quercus rubra* L.) by species such as red maple (*Acer rubrum* L.), a common associate of red oak in the Catskill Mountains of New York (Lovett et al., 2013b) but with lower foliar N and lignin concentrations and more decomposable litter.

Given observed variation in species-specific traits and distinctive effects of individual tree species on ecosystem processes, species transitions following disease or insect invasion are likely to have long-term effects on forest C and N cycling. Long tree life spans limit tests of such predictions, however. In the Catskill Mountains, a chronosequence study of stands with increasing BBD invasion demonstrated effects of decreasing beech and increasing sugar maple abundance on C and N cycling over a time scale of approximately 50 years (Lovett et al., 2010). Similarly, studies in central and southern New England have examined impacts of HWA along gradients of increasing hemlock mortality (Jenkins et al., 1999) and increasing successional age following infestation (Finzi et al., 2014; Raymer et al., 2013).

Another approach to the problem of predicting long-term impacts of species change is to use simulation models in which differences in key traits of dominant tree species drive differences in forest C and N cycling over long time scales. Along these lines, Albani et al. (2010) used the Ecosystem Demography (ED) model to simulate HWA effects on C dynamics across the eastern U.S., modifying a late-successional conifer functional type to better represent eastern hemlock; however, ED does not specifically simulate individual species or changing composition within a functional type. Other ecosystem models used extensively in the region (e.g., PnET-CN (Aber et al., 1997; Ollinger et al., 2008) and CENTURY (Parton et al., 1987)) also do not allow species composition to change over time.

Here we present a new forest ecosystem model, Spe-CN, that simulates C and N cycling in single- and mixed-species stands as tree species composition changes, and use the model to predict effects of invasive insects and pathogens on forest ecosystem processes over a period of 300 years. Specifically, we use Spe-CN to simulate changing tree species composition associated with BBD, HWA, and SOD in hypothetical forest stands in the Catskill Mountains of New York, and examine short- and long-term predictions of the effects of these tree species transitions on forest productivity, C storage, and N retention and loss.

2. Materials and methods

2.1. Study area

We developed the Spe-CN model for application to species change scenarios in northeastern U.S. forests. We used field data from across the region to develop and parameterize the model, both to make the model regionally applicable and to improve parameter estimates. To achieve sufficient testing of single-species effects, we tested the model using field data from three sub-regions (Table 1): the Catskill Mountains of New York (Lovett et al., 2013a, 2002, 2004; Templer et al., 2005); the White Mountain National Forest (WMNF) in New Hampshire (Goodale and Aber, 2001; Ollinger et al., 2002); and the Great Mountain Forest (GMF) in Connecticut (Finzi et al., 1998). Tests against field data used versions of the model parameterized with temperature records, N deposition estimates, and foliar N concentrations specific to each sub-region.

To run simulations of species transitions due to BBD, HWA, and SOD, we used the version of the model parameterized for the Catskill Mountains, an area severely affected by invasive forest pests (Liebhold et al., 2013; Lovett et al., 2013b). We ran invasion scenarios for a single focal area to emphasize responses to tree species change, rather than factors such as temperature or N deposition