

Effects of nitrogen deposition on nitrate leaching from forests of the northeastern United States will change with tree species composition

Katherine F. Crowley and Gary M. Lovett

Abstract: As tree species composition in forests of the northeastern United States changes due to invasive forest pests, climate change, or other stressors, the extent to which forests will retain or release N from atmospheric deposition remains uncertain. We used a species-specific, dynamic forest ecosystem model (Spe-CN) to investigate how nitrate (NO_3^-) leaching may vary among stands dominated by different species, receiving varied atmospheric N inputs, or undergoing species change due to an invasive forest pest (emerald ash borer; EAB). In model simulations, NO_3^- leaching varied widely among stands dominated by 12 northeastern North American tree species. Nitrate leaching increased with N deposition or forest age, generally with greater magnitude for deciduous (except red oak) than coniferous species. Species with lowest baseline leaching rates (e.g., red spruce, eastern hemlock, red oak) showed threshold responses to N deposition. EAB effects on leaching depended on the species replacing white ash: after 100 years, predicted leaching increased 73% if sugar maple replaced ash but decreased 55% if red oak replaced ash. This analysis suggests that the effects of tree species change on NO_3^- leaching over time may be large and variable and should be incorporated into predictions of effects of N deposition on leaching from forested landscapes.

Key words: nitrogen deposition, tree species, forest ecosystem model, nitrate leaching, critical load.

Resume : A mesure que la composition en espèces d'arbres change dans les forêts du nord-est des Etats-Unis à cause des ravageurs forestiers envahissants, du changement climatique ou d'autres sources de stress, on ne sait pas dans quelle mesure les forêts vont retenir ou libérer l'azote (N) provenant des dépôts atmosphériques. Nous avons utilisé un modèle de la dynamique de l'écosystème forestier propre à chaque espèce (Spe-CN) pour étudier de quelle façon le lessivage du nitrate (NO_3^-) peut varier parmi des peuplements dominés par différentes espèces et qui reçoivent différentes quantités de N atmosphérique, ou qui subissent un changement d'espèce causé par un ravageur forestier envahissant (agile du frêne; AF). Dans les simulations du modèle, le lessivage du NO_3^- variait beaucoup parmi les peuplements dominés par 12 espèces d'arbres du nord-est de l'Amérique du Nord. Le lessivage du NO_3^- augmentait en fonction des dépôts de N ou de l'âge de la forêt, généralement avec plus d'amplitude dans les cas des feuillus (sauf le chêne rouge) que des conifères. Les espèces dont le taux de lessivage de référence est le plus faible (p. ex., l'épinette rouge, la pruche du Canada et le chêne rouge) avaient des réactions à seuils aux dépôts de N. Les effets de l'AF sur le lessivage dépendaient de l'espèce qui prenait la place du frêne blanc. Après 100 ans, le modèle prévoyait une augmentation du lessivage de 73% si l'érable à sucre remplait le frêne mais une diminution de 55% si c'était le chêne rouge. Cette analyse indique qu'avec le temps les effets du changement d'espèce d'arbres sur le lessivage du NO_3^- peuvent être importants et variables et qu'ils devraient être intégrés aux prédictions des effets des dépôts de N sur le lessivage dans les paysages forestiers. (Traduit par la Redaction)

Mots-clés : dépôt d'azote, espèce d'arbre, modèle d'écosystème forestier, lessivage du nitrate, charge critique.

Introduction

Elevated atmospheric nitrogen (N) deposition from fossil fuel combustion or agricultural activities may cause N saturation in forest ecosystems, ultimately resulting in greater leaching of nitrate (NO_3^-) from forests to surface waters (Aber et al. 1998; Agren and Bosatta 1988; Lovett and Goodale 2011). High amounts of NO_3^- entering aquatic systems can result in acidification of streams and lakes and eutrophication of estuaries and coastal waters (e.g., Driscoll et al. 2003). Limiting N deposition to levels that prevent ecosystem harm from this added NO_3^- requires determining to what extent elevated levels of N deposition will increase NO_3^- leaching loss from forests and over what time scale.

Forests are key regulators of N pollution, denitrifying or retaining in vegetation and soils about 75% of N deposited in major

watersheds of the northeastern United States (US) (van Breemen et al. 2002). Leaching of NO_3^- from forests varies considerably, however, because of factors such as land use history (Goodale and Aber 2001; Goodale et al. 2000) and dominance by different tree species (Lovett et al. 2004). For example, forest stands dominated by different species can vary more than 600% in NO_3^- export to surface waters (Lovett et al. 2002). In the Catskill Mountains of southeastern New York State, sugar maple (*Acer saccharum* Marsh.) stands exhibited high measures of nitrification and extractable NO_3^- in soil relative to other tree species, suggesting higher leaching (Lovett et al. 2004, 2013a). In contrast, low rates of nitrification and NO_3^- leaching have been observed in stands dominated by red oak (*Quercus rubra* L.) (Lovett et al. 2004, 2013a). A number of studies have found similar relationships between tree species composition and variables associated with NO_3^- production and loss

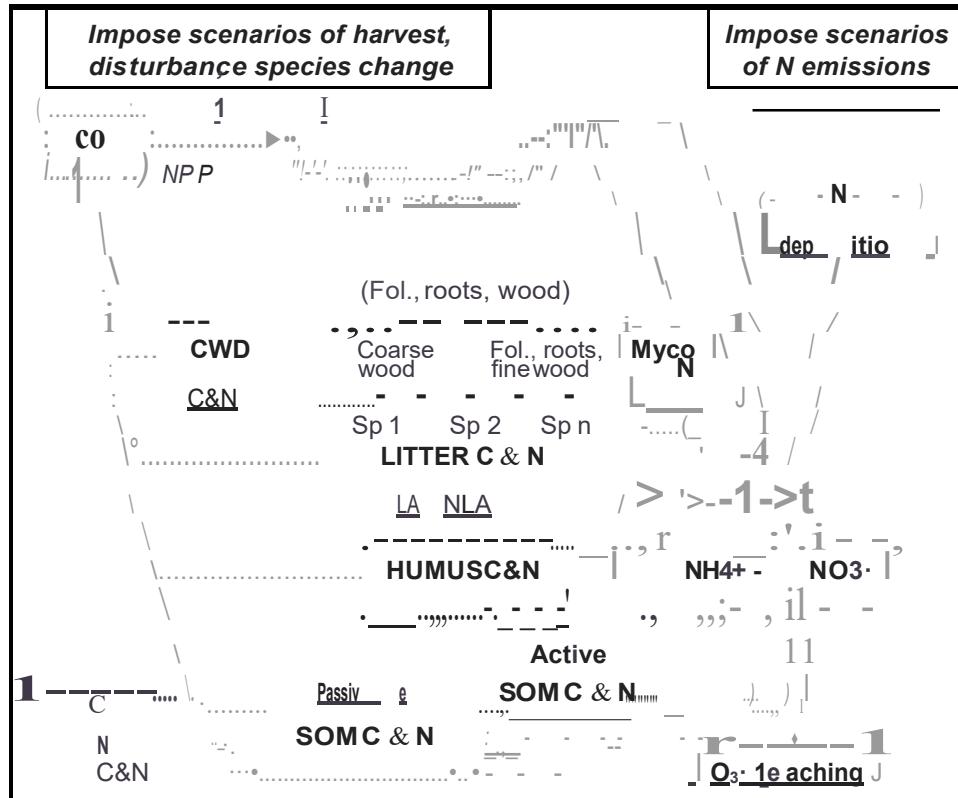
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Fig. 1. Structure of the Spe-CN forest ecosystem model. Dotted, dashed, and solid lines show movement of C, N, or both C and N, respectively. Carbon and N move among pools in the atmosphere, vegetation (species-specific foliage, root, finewood, and coarse wood pools), coarse woody debris (CWD), forest floor (litter and humus), and upper mineral soil (active and passive SOM). A fraction of mineralized N also moves into a mycorrhizal N pool (MycoN). Mineralized N released as NH_4^+ may be used by plants, immobilized in soil, or nitrified; NO_3^- leaches out of the system if not taken up by vegetation. Changes in tree species composition, harvest, other disturbance, or N deposition are imposed by the user. Sp, species; IA, lignin-associated; NIA, non-lignin-associated. Further detail is provided in Crowley et al. (2016).



(Finzi et al. 1998; Lewis and Likens 2000; Lovett et al. 2002, 2004, 2013a; Ollinger et al. 2002; Ross et al. 2009). Given this species-driven variation among stands experiencing the same N deposition regime, levels of N deposition that elevate NO_3^- leaching from forests may also vary across forests dominated by different tree species.

Because movement of NO_3^- varies with tree species, tree species change due to stressors such as invasive pests could substantially alter N cycling and ultimately N loss from forests to adjacent waterways (e.g., Lovett et al. 2006). In field studies, replacement of one tree species with another due to invasive insects or disease has been associated with increases in extractable soil NO_3^- , NO_3^- in soil solution, or nitrification rates (Cobb et al. 2013; Jenkins et al. 1999; Lovett et al. 2010), suggesting increased leaching from these invaded forests. Our prior modeling simulations of pest-induced tree species transitions caused by three distinct invasive forest pests also predicted increased NO_3^- leaching after invasion, with the timing and duration of the leaching peak dependent on species identity (Crowley et al. 2016). Tree species composition is changing due to invasive pest activity, as well as other factors, particularly in the northeastern US (Aukema et al. 2010; Liebhold et al. 2013), and the effects of species changes on loss of NO_3^- from forests are potentially large.

We used a recently introduced, species-specific, dynamic forest ecosystem model called Spe-CN (Crowley et al. 2016) to run new simulations investigating the extent to which NO_3^- leaching below the rooting zone might vary in long forest stands dominated by different tree species and receiving a range of N deposition inputs. We also examined changes in leaching attributable to different tree species replacements caused by the same invasive

forest pest, under a consistent N deposition regime. Ultimately, our goal was to investigate the extent to which tree species change might influence NO_3^- leaching from forests. Relationships among species, forest age, N deposition, and leaching then provide a framework for identifying N deposition levels at which NO_3^- leaching from forests could exceed defined leaching thresholds due to changing species composition across northeastern US forests.

Materials and methods

Mode 1 description

Spe-CN is a dynamic forest ecosystem model that simulates C and N cycling in single- and mixed-species forest stands as tree species composition changes (Crowley et al. 2016). We developed Spe-CN for application in the northeastern US, using available field data and field-based empirical relationships wherever possible. We also adapted relevant algorithms from ecosystem models such as PnEf-CN (Aber and Federer 1992; Aber et al. 1997) and CENTURY (Parton et al. 1987, 1988) for use in a species-specific context. As with other forest C and N cycling models, Spe-CN incorporates the processes of net primary productivity (NPP), tree N uptake, litter production, decomposition, and soil organic matter (SOM) formation (Fig. 1; Crowley et al. 2016). The Spe-CN model differs from other models primarily by including individual tree species such that the user can simulate forest stands that change in tree species composition over time. Spe-CN simulates pools of C and N in plant structures (foliage, finewood, coarse wood, roots) for individual species and plays out the long-term consequences

of user-specified trends in species composition for C and N cycling in the forest.

In the Spe-CN model, many of the processes transpiring C and N among vegetation and soil pools are governed by species-specific traits. Key parameters include minimum and range of N concentrations in foliage, fine wood, coarse wood, and roots; foliar turnover; allocation to foliage vs. wood; fraction of N resorbed from foliage before litterfall; tissue lignin and cellulose concentrations; the slope of the relationship between litter N concentration and mass loss (NML; Aber et al. 1990); and maximum biomass attainable in pure stands (Appendix A, Tables A1 and A2; Crowley et al. 2016). These plant traits differentially influence productivity, nutrient uptake, turnover, and decomposition such that changing species composition will gradually alter C and N cycling on the site. Because these parameter values represent averages across available data for the northeastern U.S., the model simulates a mean condition associated with each tree species, averaged across variability in site-specific characteristics such as soil texture, hydrology, or unknown aspects of site history. A detailed description of how these species-specific traits govern process rates and movement of C and N between pools, detailed testing of model output, a sensitivity analysis for model parameters, and a discussion of uncertainties in model development are included in Crowley et al. (2016).

In the mode 1, total NO_3 leaching reflects cumulative species-specific effects on C and N cycling processes. Productivity, nutrient uptake, and decomposition processes interact to determine the amount of NO_3 that is leached rather than retained in vegetation, downedwood, or soils. Nitrogen mineralized from organic or mineral soil pools or CWD has several possible fates: it may be nitrified, as a function of soil C:N (for species other than red oak; Lovett et al. 2004) and plant demand for N (Aber et al. 1997); immobilized in soil; moved into a mycorrhizal N pool to contribute to plant N uptake; or moved into inorganic soil ammonium (NH_4^+) pools available for direct plant uptake (Fig. 1). Soil NO_3 is also available for plant uptake, and any remaining NO_3 leaches from the system. The Spe-CN model simulates NO_3 leaching from beneath the soil rooting zone for an individual stand. Leaching estimates thus do not necessarily represent surface water values, due to additional N processing that may occur as water moves from the rooting zone to the stream. Henceforth, we refer to loss of NO_3 from beneath the soil rooting zone in a forest stand as NO_3 leaching and NO_3 loss from a watershed via the stream as stream NO_3 export. In the current version of the model, the only N loss from the system is NO_3 leaching; dissolved organic N (DON) leaching and denitrification are not simulated. Leaching of DON is a minor N loss mechanism for most watersheds in our focal study area of the Catskill Mountains (Lovett et al. 2000). Although denitrification may be important in some locations (e.g., Morse et al. 2015), including seeps, toeslopes, and stream edges in the Catskills (Ashby et al. 1998), we assume that denitrification is unlikely to be an important flux in our study area's aerobic, well-drained soils (Crowley et al. 2016). The model may overestimate NO_3 leaching below the rooting zone somewhat, however, due to the lack of gaseous N losses.

For the analyses presented here, we updated four parameters that influence nitrification or leaching rates, relative to previous work (Crowley et al. 2016). First, we updated the NO_3 fraction of total ($\text{NO}_3 + \text{NH}_4^+$) N deposition ($\text{NDepNO3frac} = 0.6$) to better correspond to recent measured values, although simulated leaching showed low sensitivity to changes in this value, so it is held constant throughout each model run (Crowley et al. 2016). The NO_3 fraction of total N deposition is calculated as the mean 2010 value (for 2007–2013) from National Atmospheric Deposition Program National Trends Network (NADP NTN: NY68, NH02, ABT147) and Clean Air Status and Trends Network (CASTNET: CAT175, ABT147, WST109; <http://java.epa.gov/castnet/clearsession.do>) data from three model testing subregions: the Catskill Mountains in

New York, the White Mountain National Forest in New Hampshire (WMNF), and the Great Mountain Forest in Connecticut (GMF). Formerly, this value was derived from the ClimCalc model (Ollinger et al. 1993). Second, we updated the fractions of NO_3^- -N and NH_4^+ -N from deposition that move into soil pools ($\text{NdepNO3Soi!Frac} = 0.5$; $\text{NdepNH4Soi!Frac} = 0.75$, respectively) to better reflect rapid soil immobilization of NO_3 and NH_4^+ (Bernston and Aber 2000; Lewis et al. 2014; Templer et al. 2005). Finally, for red oak, we modified the nitrification fraction (Nitfrac) to equal the ratio of nitrification to N mineralization measured in oak-dominated plots in the Catskills (Lovett et al. 2004). For other tree species, we were able to use a linear relationship with soil C:N to predict Nitfrac (Crowley et al. 2016). In contrast, for red oak, Nitfrac remained low (near zero) regardless of C:N, suggesting that nitrification may be inhibited in red oak stands (Lovett et al. 2002, 2004). Further work is needed to investigate how nitrification might be inhibited in stands dominated by red oak.

Study area

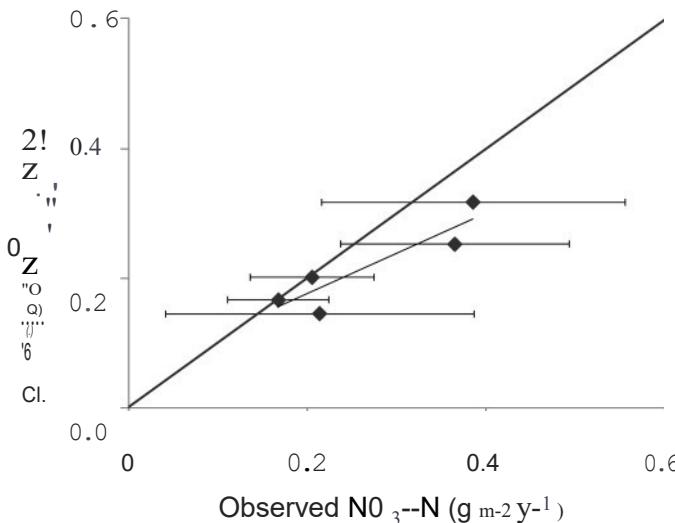
While the model is applicable in the northeastern US and potentially in areas of adjacent Canada with similar forest types, we focused this study on the Catskill Mountains in southeastern New York. We chose this area because Catskill forests receive N deposition levels among the highest in the northeastern US (Ollinger et al. 1993) and are threatened by multiple invasive forest pests that are changing forest composition (Liebhold et al. 2013; Lovett et al. 2013b), and extensive data were available for model parameterization and testing (Lovett et al. 2002, 2004, 2013a; Templer et al. 2005). We ran model scenarios for a single focal area to emphasize responses to tree species change, rather than factors such as climate that vary across the larger region. Model runs were parameterized with Catskill temperature records, foliar N concentrations, and N deposition estimates (Crowley et al. 2016). Simulated tree species included American beech (*Fagus grandifolia* Ehrh.), balsam fir (*Abies balsamea* (L.) Mill.), black birch (*Betula lenta* L.), eastern hemlock (*Tsuga canadensis* (L.) Carr.), paper birch (*Betula papyrifera* Marsh.), red maple (*Acer rubrum* L.), red oak, red spruce (*Picea rubens* Sarg.), sugar maple, white ash (*Fraxinus americana* L.), white pine (*Pinus strobus* L.), and yellow birch (*Betula alleghaniensis* Britt.), which occur frequently in Catskill forests and across the region.

Model testing

In Crowley et al. (2016), Spe-CN model simulations were tested against available field data including C and N pools and C:N ratios for the Oe + Oa (henceforth referred to as OeOa) horizons in the forest floor, wood C, foliar N, nitrification fraction in the OeOa, and aboveground NPP. Field testing data were from species-dominant plots in the Catskills (Lovett et al. 2002, 2004, 2013a; Templer et al. 2005), the WMNF (Goodale and Aber 2001; Ollinger et al. 2002), and the GMF (Finzi et al. 1998). With the modifications to the model described above, we re-tested model simulations against these field data; the updated tests differed little from those presented in Crowley et al. (2016) (data not shown).

For the present analysis, we further tested the ability of the Spe-CN model to simulate NO_3 leaching from forest stands dominated by different tree species using independent field data (not used to parameterize the model) from species-dominant plots in the Catskills (Lovett et al. 2013a). Spe-CN model estimates of NO_3 leaching corresponded linearly to NO_3 flux estimates from tension lysimeters installed in field plots dominated by sugar maple, American beech, red oak, yellow birch, or eastern hemlock (Fig. 2). The Spe-CN model slightly (but not significantly) underestimated the observed NO_3 leaching flux, particularly at high levels of NO_3 leaching, suggesting that model estimates of NO_3 leaching may be conservative.

Fig. 2. Relationship between mean NO_3^- flux estimates from species-dominant Catskill plots and Spe-CN model estimates of NO_3^- leaching. Each point represents the mean tension lysimeter flux in the B horizon ($n = 4$) across plots dominated by a single species (sugar maple, American beech, yellow birch, eastern hemlock, or red oak); error bars are $\pm \text{SE}$. Predicted NO_3^- -N = $(0.6267 \times \text{observed } \text{NO}_3^-$ -N) + 0.0499. The relationship is linear ($F_{1,13} = 13.57, p = 0.03, r^2 = 0.82$) with a slope not significantly different from 1 ($F_{1,13} = 4.81, p = 0.12$).



We were unable to test Spe-CN leaching estimates directly against field data for all tree species abundant in the Catskill study area because of the paucity of data for NO_3^- leaching below the rooting zone for single-species stands. We therefore considered model simulations of alternative variables that corresponded empirically to NO_3^- leaching and for which more field data were available. In the Catskills, stream NO_3^- concentrations have been shown to decrease as the OeOa C:N increased across 13 watersheds (Lovett et al. 2002). Similarly but at the stand scale, across Catskill plots dominated by single tree species, NO_3^- flux below the rooting zone also decreased as OeOa C:N increased (Fig. 3; data from Lovett et al. 2013a). Soil C:N ratios have been shown to vary in relation to the identity of dominant tree species in forested stands of the northeastern US (Finzi et al. 1998; Lovett et al. 2004; Ollinger et al. 2002; Ross et al. 2011), and the Spe-CN model was able to simulate this variation for species typical of the region (Crowley et al. 2016). Predicted OeOa C:N had a nearly 1:1 relationship with observed C:N across species-dominant stands from the Catskills, the WMNF, and the GMF (Fig. 4). Because the model was able to predict OeOa C:N (Fig. 4), which is correlated with NO_3^- leaching both in the model and in the field data (Fig. 3), we would expect Spe-CN predictions of differences in NO_3^- leaching among tree species to be reasonable for the broader set of tree species modeled in this paper. Measured NO_3^- fluxes were highly variable (Fig. 2), and individual model predictions also have uncertainty associated with them due to variation in model parameters (Crowley et al. 2016). Additionally, model predictions for the subset of species with regional parameterization but without regional testing data (balsam fir, white pine, black birch) should be interpreted with caution. However, our testing results suggest that we can use the Spe-CN model to predict broad patterns in NO_3^- leaching among tree species and to obtain conservative estimates of NO_3^- leaching from stands dominated by species typical of the Catskill Mountains.

Tests of simulated NO_3^- leaching employed data from Catskill single-species plots approximately 90 years in age (Lovett et al. 2004). We are unaware of data sets appropriate for testing simulated changes in leaching below the rooting zone for stands in

Fig. 3. Relationship between OeOa C:N and NO_3^- flux for Catskill plots dominated by single tree species. Each point represents the mean tension lysimeter flux in the B horizon ($n = 4$) and mean OeOa C:N ($n = 5$) across plots dominated by a single species (sugar maple, American beech, yellow birch, eastern hemlock, or red oak); error bars are $\pm \text{SE}$. NO_3^- -N flux = $-0.0318 \times \text{OeOa C:N} + 0.9269$ ($F_{1,31} = 7.74, p = 0.07, r^2 = 0.72$).

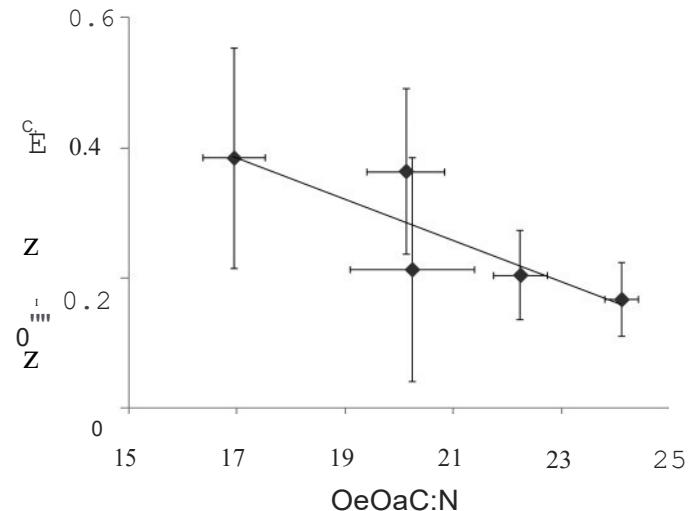
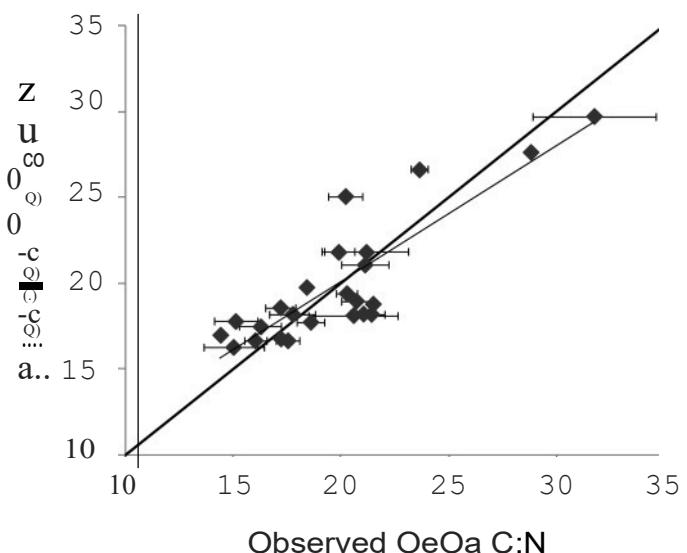


Fig. 4. Relationship between Spe-CN model predictions and mean OeOa C:N across plots dominated by nine tree species occurring in the Catskills, the WMNF, or the GMF. Minimum relative basal area for the dominant species in each plot was 70%. Each point represents the mean OeOa C:N for a given species within a given subregion and forest age (second growth or old growth, simulated at 90 or 300 years after disturbance, respectively); error bars are $\pm \text{SE}$. Predicted OeOa C:N = $(0.7920 \times \text{observed OeOa C:N}) + 4.2685$. The relationship is strongly linear ($F_{1,22} = 62.47, p < 0.0001, r^2 = 0.74$), with a slope slightly less than 1 ($F_{1,22} = 4.31, p = 0.05$).



which tree species composition has changed over time. In a chronosequence of plots with increasing impact by beech bark disease (BBD), Lovett et al. (2010) found greater NO_3^- concentrations in soil solution as BBD impact (and, correspondingly, sugar maple abundance) increased, but measured NO_3^- fluxes are not available for testing model predictions of changes in leaching over time. Direct comparisons between long-term stream NO_3^- data sets and simulated leaching below the rooting zone are not appropriate because additional NO_3^- processing occurs between the rooting zone and

the stream. This may include soil adsorption, assimilation, or transformation in the stream, which may result in very different NO_3^- flux estimates at the stand level vs. the stream level. Additionally, Spe-CN does not yet include the water dynamics required to simulate seasonal or annual variation in stream NO_3^- fluxes. Rather, the Spe-CN model simulates mean effects over multiyear, decadal time scales, which are primarily controlled by factors such as species change, land use, climate, or N deposition. Model testing of C and N cycling processes for second-growth vs. old-growth stands across the northeastern US gives us confidence in broad predicted patterns for stands of different species composition and age (Crowley et al. 2016).

Model Scenarios

To investigate how NO_3^- leaching might vary with tree species, we used the Spe-CN model to simulate (i) single-species stands in which tree species differed in long stands but remained constant over time and (ii) tree species replacements in which one dominant species was replaced by another due to invasive pest activity. Following a model spin-up period starting in year 0, each model simulation included a forest harvest in 1910 (80% harvest, 90% removal of aboveground biomass, 10% forest floor loss). This approximates the disturbance history of the Catskill region, where

many forests were harvested in the early 1900s (Kudish 2000), and establishes an appropriate starting condition for the stand, including factors such as forest age, plant C and N pools, and soil C and N pools. Model simulations that changed tree species or N deposition were then imposed on the re-growing forest. The baseline N deposition was set to Catskill levels, increasing from a low level through 1940 (0.2 g N m⁻² year⁻¹, wet plus dry deposition) to a peak in 1990 (1.11 g N m⁻² year⁻¹), and then declining to a mean 2010 level (0.67 g N m⁻² year⁻¹) and held constant thereafter. The N deposition regime was based on data from NADP and CASTNET and is further described in Crowley et al. (2016). To emphasize the effects of tree species and N deposition on leaching, we held climate to 30-year averages of mean monthly temperature for the Catskill Mountains, using data from the National Oceanic and Atmospheric Administration National Climatic Data Center's Climate Data Online (<http://www.ncdc.noaa.gov/cdo-web/>; see Crowley et al. (2016) for more detail). Within this framework, we ran simulations to evaluate the following questions.

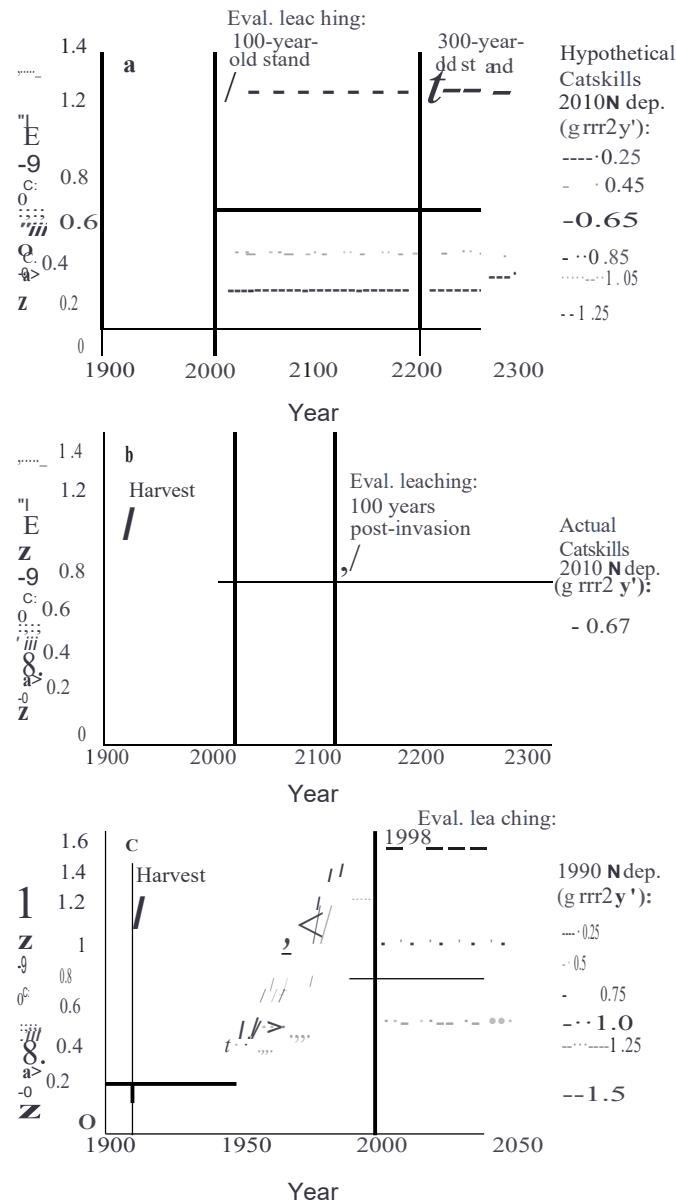
How does N deposition affect NO_3^- leaching from stands of various tree species?

We simulated forest stands dominated by each of 12 frequently occurring tree species in the Catskill Mountains and across the region, with composition held constant throughout each run. Nitrogen deposition followed the Catskill N deposition regime described above, but total N deposition stabilized at a range of six hypothetical 2010 levels from 0.25 to 1.25 g N m⁻² year⁻¹ (Fig. 5a). We then evaluated NO_3^- leaching for each tree species and level of final N deposition for a 100- or 300-year-old stand (i.e., years 2010 or 2210). By holding tree species constant in each run and varying the final level of N deposition, we could use the model both to assess variability in leaching among tree species at a specific deposition level and to identify how differences in N deposition trajectory affected leaching from stands dominated by different tree species and at different stand ages.

How does NO_3^- leaching respond to changing tree species composition under a consistent N deposition regime?

In addition to simulating single-species stands that remained constant in composition over time, we also simulated forest stands that changed in species composition over time due to invasive insect activity but for which the N deposition trajectory remained constant during the species change (following the Catskill N deposition trajectory described above; Fig. 5b). We used as an example the loss of white ash due to the invasive insect pest

Fig. 5. Simulated N deposition trajectories: (a) for Catskill Mountains simulations of 12 frequently occurring tree species, baseline N deposition increased from 0.2 g m⁻² year⁻¹ through 1940 to 1.11 g m⁻² year⁻¹ in 1990 and then transitioned to each of six hypothetical mean 2010 levels; (b) for Catskill simulations of tree species change due to EAB, N deposition stabilized at the measured mean Catskill 2010 N deposition level of 0.67 g m⁻² year⁻¹; and (c) for simulations of the northeastern US N deposition gradient, baseline N deposition increased from 0.2 g m⁻² year⁻¹ through 1940 to each of six 1990 deposition levels corresponding to the gradient assessed in Aber et al. (2003).



emerald ash borer (EAB; *Agrilus planipennis* Fairmaire). Since its introduction in the Detroit, Michigan, area in the early 1990s, EAB has spread throughout the northeastern, central, and Rocky Mountain states of the US and the provinces of Ontario and Quebec in Canada, where it causes the rapid death of ash trees and their replacement by neighboring species (Lovett et al. 2016; Poland and McCullough 2006). White ash can be abundant in the Catskills, and Lovett et al. (2013b) identified the three most common co-dominants in Catskill white ash stands to be sugar maple, red oak, and American beech. To explore the effects of tree species

change on NO_3 leaching, we simulated the invasion of a hypothetical 110-year-old white ash forest (80% ash, 20% replacing species) by EAB such that white ash was replaced over a 20-year period (2020–2040) by sugar maple, red oak, or American beech. We then evaluated NO_3 leaching for each replacement scenario 100 years following invasion (i.e., year 2120). By holding N deposition constant while varying final tree species composition, we could use the model to investigate how these alternative scenarios of tree species replacement might influence NO_3 leaching.

How do patterns of NO_3 leaching from stands of different tree species vary across a regional N deposition gradient?

Aber et al. (2003) reported a pattern of greater NO_3 export in streamwater with increasing N deposition across a spatial gradient spanning the northeastern US: sites below about $0.7\text{--}0.8 \text{ g m}^{-2} \text{ year}^{-1}$ of N from deposition had little NO_3 export, whereas sites above that threshold had elevated export in some cases but not in others. We asked if the Spe-CN model could simulate this observed threshold and how much of the observed variation in stream NO_3 export at higher N deposition levels could potentially be caused by variation in tree species composition among sites. To do this, we simulated second-growth forests (harvested in 1910, as above) dominated by a set of tree species abundant in the northeastern US. For each simulation, we increased total N deposition (from a baseline of $0.2 \text{ g N m}^{-2} \text{ year}^{-1}$, as above) to a range of N deposition levels consistent with the northeastern US N deposition gradient (Aber et al. 2003; Ollinger et al. 1993). These target deposition levels, ranging from 0.25 to $1.5 \text{ g N m}^{-2} \text{ year}^{-1}$, were achieved in 1990 and then held constant (Fig. 5c). Simulated NO_3 leaching below the rooting zone was evaluated in 1998, consistent with the period of most of the data in the Aber et al. (2003) analysis (mid- to late-1990s). While stand-level NO_3 leaching and stream NO_3 export are not directly comparable due to NO_3 processing between the stand and the stream, this comparison between simulated and observed values indicates the potential magnitude of the contribution of tree species to the variability in stream NO_3 export observed across the region.

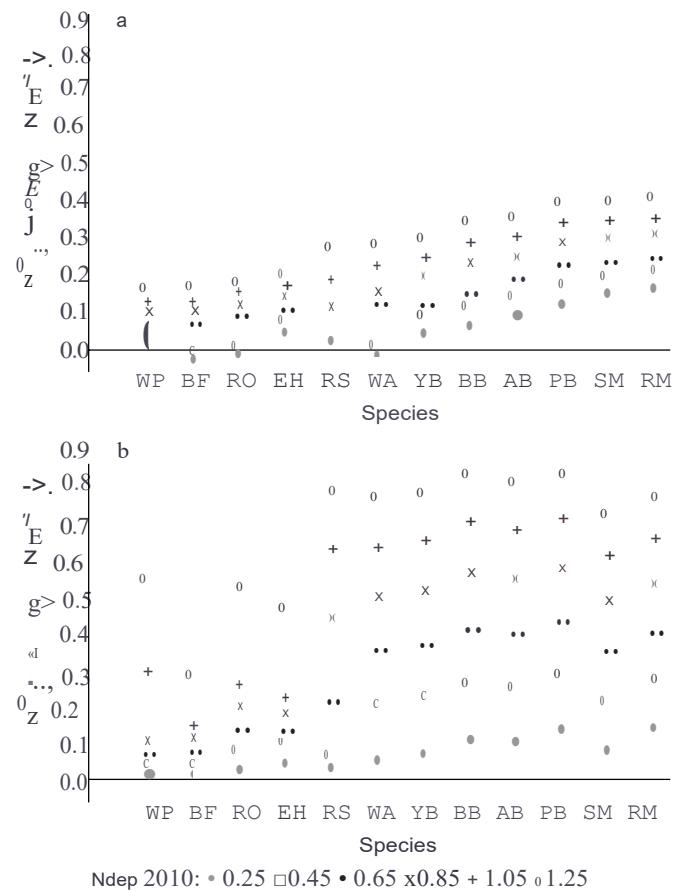
Results

How does N deposition affect NO_3 leaching from stands of different tree species?

For a given level of N deposition, simulated NO_3 leaching for the Catskill Mountains varied widely among 12 tree species abundant in forests of the northeastern US and adjacent Canada (Fig. 6). Nitrate leaching was generally predicted to increase with increasing N deposition or forest age, but the magnitude of increase in leaching varied by species (Fig. 6). For instance, for a 100-year-old forest, simulated leaching was consistently higher (at any given level of N deposition) for species such as sugar maple or red maple than for species such as red spruce or red oak (Fig. 6a). As N deposition or forest age increased, corresponding increases in leaching were considerably greater for most deciduous species than for coniferous species or red oak (Fig. 6). Furthermore, the range in leaching across species also increased with increasing N deposition or forest age: for a 300-year-old forest, the leaching difference between species with the highest leaching rates and those with the lowest leaching rates was 4.5 times greater ($0.55 \text{ vs. } 0.12 \text{ g N m}^{-2} \text{ year}^{-1}$) when the 2010 N deposition level was set to $1.25 \text{ vs. } 0.25 \text{ g m}^{-2} \text{ year}^{-1}$ (Fig. 6b).

In Spe-CN model simulations, species with the lowest baseline leaching rates showed a threshold response to increased N deposition: i.e., beyond a threshold deposition level, leaching increases were abruptly larger in magnitude. For example, for a 100-year-old red spruce stand, increases in leaching with increasing N deposition were larger once N deposition exceeded $0.85 \text{ g m}^{-2} \text{ year}^{-1}$ (Fig. 6a). Additional species reached such leaching thresholds in a

Fig. 6. Nitrate leaching predicted by the Spe-CN model from forest stands dominated by each of 12 tree species at (a) 100 years and (b) 300 years of age. For each model run, N deposition was held constant at $0.2 \text{ g m}^{-2} \text{ year}^{-1}$ of N through 1940, increased to $1.11 \text{ g m}^{-2} \text{ year}^{-1}$ by 1990, and stabilized at a final level ranging from 0.25 to $1.25 \text{ g m}^{-2} \text{ year}^{-1}$ of N in 2010 and thereafter (Fig. 5a). Each symbol on the graph represents a single 2010 N deposition level across all species considered. Stabilization at $0.65 \text{ g m}^{-2} \text{ year}^{-1}$ represents the approximate N deposition trajectory for the Catskill Mountains (actual mean 2010 Catskill N deposition was $0.67 \text{ g m}^{-2} \text{ year}^{-1}$). WP, white pine; BF, balsam fir; RO, red oak; EH, eastern hemlock; RS, red spruce; WA, white ash; YB, yellow birch; BB, black birch; AB, American beech; PB, paper birch; SM, sugar maple; RM, red maple.

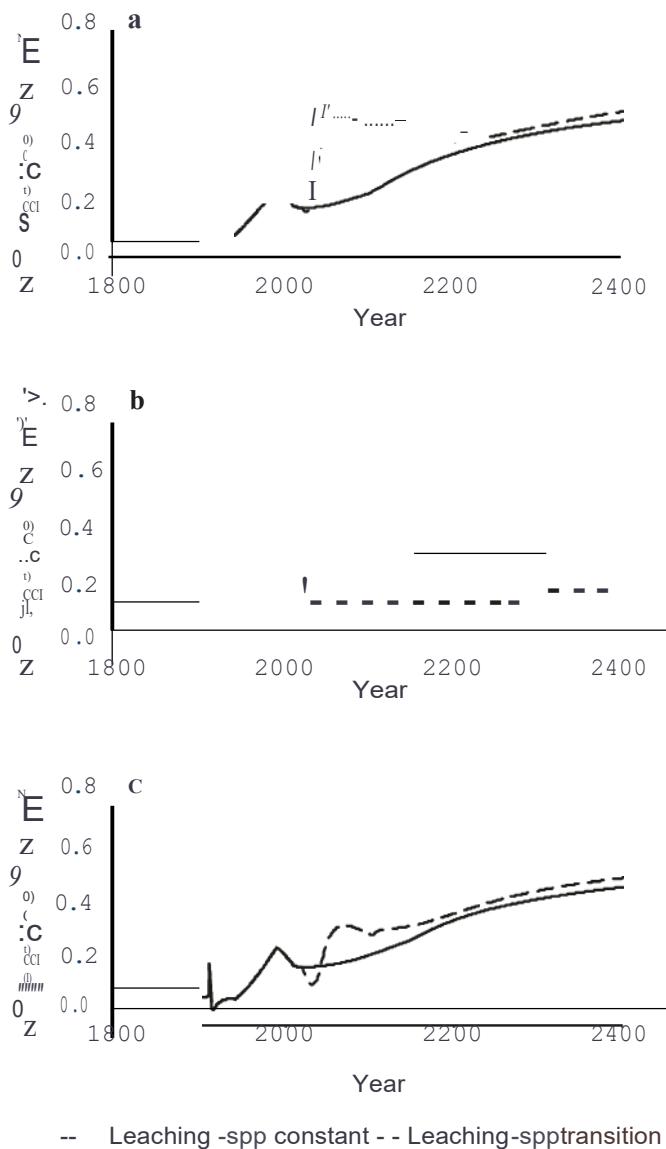


300-year-old stand relative to a 100-year-old stand (e.g., white pine, balsam fir, eastern hemlock, red oak; Fig. 6b).

How does NO_3 leaching respond to changing tree species composition under a consistent N deposition regime?

Spe-CN model simulations indicated that changes in tree species composition due to invasive pest activity could alter rates of NO_3 leaching, even when N deposition was held constant during the invasion. In simulations in which white ash was replaced by sugar maple, red oak, or American beech due to EAB, the magnitude and direction of effect (increased or decreased leaching) depended on the identity of the species replacing ash. Replacement of white ash with sugar maple caused an immediate increase in predicted nitrate leaching relative to an uninvaded ash-maple stand (155% increase 49 years after invasion began (peak leaching); 73% increase 100 years following invasion; Fig. 7a). In contrast, replacement of white ash with red oak caused predicted leaching to fall below that of a corresponding uninvaded ash-oak stand

Fig. 7. Comparison of Spe-CN model predictions of NO_3^- leaching between an uninvaded stand dominated by white ash and a stand in which FAB causes death of ash trees, with replacement by (a) sugar maple, (b) red oak, or (c) American beech. Initial stand composition is 80% ash, 20% replacing species. Changes over time are in response to an 80% harvest in 1910; an increase in N deposition from 0.2 to $1.11 \text{ g m}^{-2} \text{ year}^{-1}$ of N from 1940 to 1990, followed by a decrease to $0.67 \text{ g m}^{-2} \text{ year}^{-1}$ of N by 2010 (Fig. 5b); and a transition from ash to sugar maple, red oak, or beech from 2020 to 2040.

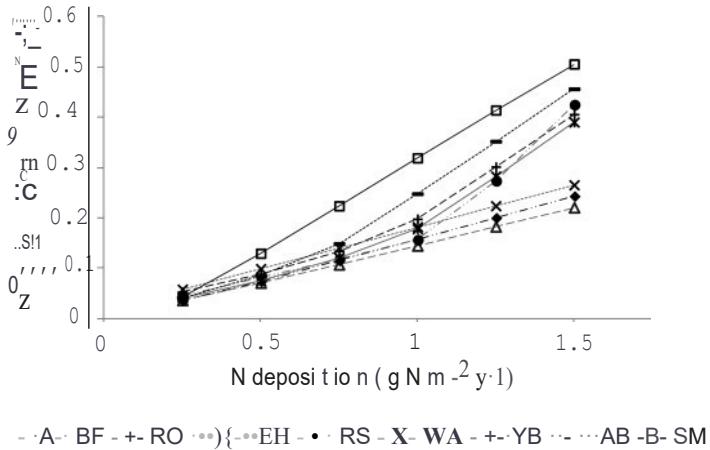


(55% decrease 100 years following invasion; Fig. 7b). As a result, 100 years following invasion, predicted leaching was 3.7 times higher when white ash was replaced by sugar maple rather than red oak. If white ash was instead replaced by American beech, however, leaching was predicted to differ much less between an invaded and corresponding uninvaded stand (Fig. 7c). Nitrogen deposition was consistent across the three invasion-stand response scenarios.

How do patterns of NO_3^- leaching from stands of different tree species vary across a regional N deposition gradient?

Varying tree species composition only, the Spe-CN model was able to reproduce much of the variability in measured stream

Fig. 8. Simulated NO_3^- leaching for eight tree species abundant in forests spanning the northeastern US N deposition gradient. Each symbol-line represents simulated leaching for a single tree species across the deposition gradient. Each point represents 1998 leaching from a single model run in which N deposition increased from a baseline level through 1940 ($0.2 \text{ g m}^{-2} \text{ year}^{-1}$) to one of six 1990 N deposition levels (from 0.25 to $1.5 \text{ g m}^{-2} \text{ year}^{-1}$ of N), consistent with the gradient in Aber et al. (2003), and was held constant thereafter (Fig. 5c). BF, balsam fir; RO, red oak; EH, eastern hemlock; RS, red spruce; WA, white ash; YB, yellow birch; AB, American beech; SM, sugar maple.



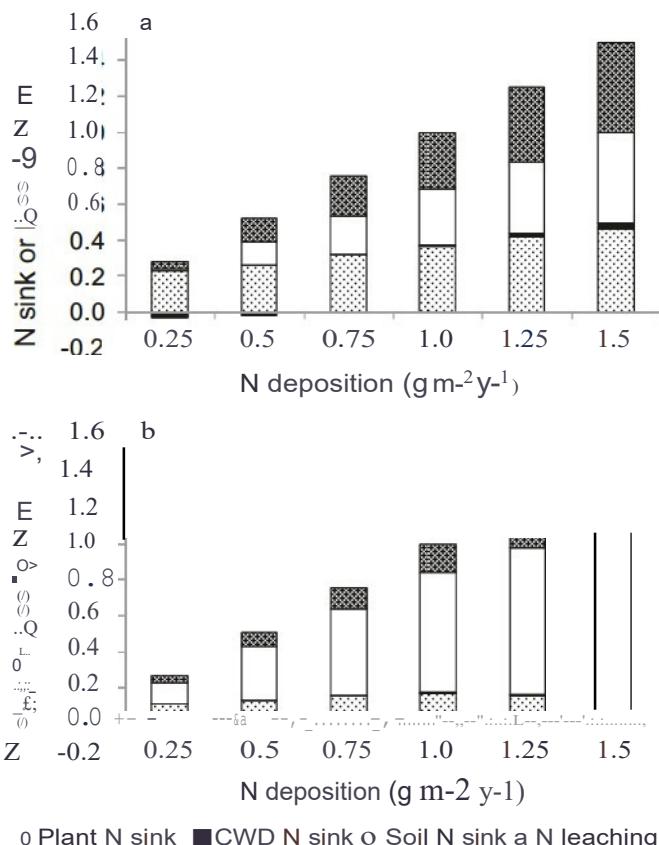
NO_3^- export observed at higher levels of N deposition across the northeastern US deposition gradient. At N deposition of $0.75 \text{ g m}^{-2} \text{ year}^{-1}$, the simulated range in NO_3^- leaching below the rooting zone across tree species was 0.10 – $0.24 \text{ g m}^{-2} \text{ year}^{-1}$ of NO_3^- -N (Fig. 8) compared with a range in measured stream NO_3^- export of approximately 0.03 – $0.2 \text{ g m}^{-2} \text{ year}^{-1}$ of NO_3^- -N (Aber et al. 2003). For a deposition level of $1.25 \text{ g m}^{-2} \text{ year}^{-1}$, the simulated range in NO_3^- leaching across tree species was 0.18 – $0.42 \text{ g m}^{-2} \text{ year}^{-1}$ of NO_3^- -N as opposed to 0.05 – $0.55 \text{ g m}^{-2} \text{ year}^{-1}$ of NO_3^- -N in measured stream export. Thus, the simulated range in NO_3^- leaching across species was approximately 50%–75% of the observed range in stream NO_3^- export.

While the Spe-CN model simulated much of the field variability observed at higher levels of N deposition, it was not able to capture the negligible stream NO_3^- export measured at N deposition below $0.7 \text{ g m}^{-2} \text{ year}^{-1}$ (Aber et al. 2003). Below this threshold, the model simulated a range in NO_3^- leaching across tree species from 0.04 to $0.14 \text{ g m}^{-2} \text{ year}^{-1}$ of NO_3^- -N (Fig. 8). Additionally, when N deposition exceeded $0.7 \text{ g m}^{-2} \text{ year}^{-1}$, the model did not capture the lowest (near-zero) levels of measured stream NO_3^- export; minimum predicted NO_3^- leaching was $0.10 \text{ g m}^{-2} \text{ year}^{-1}$ of NO_3^- -N. This baseline leaching level simulated by Spe-CN represented loss of a fraction of atmospherically deposited N during wintertime.

Discussion

The model simulations presented here suggest that tree species changes caused by factors such as invasive forest pests have the potential to alter NO_3^- leaching from forests to downstream waterways. The magnitude and direction of change in NO_3^- leaching will vary with the identity of the declining and replacing tree species, the age of the forest following disturbance, and the amount of atmospheric N deposited over time. Effects of tree species change may be large but unpredictable based on characteristics of the declining tree species and the neighboring species that replace them. Because different tree species affect NO_3^- leaching very differently, the effects of N deposition on leaching from forests can be expected to change as tree species composi-

Fig. 9. Nitrogen sinks and losses simulated by the Spe-CN model for forest stands dominated by (a) sugar maple and (b) red spruce. Nitrogen deposition followed the scenarios outlined in Fig. 5c, representing the N deposition gradient spanning the northeastern US, and N sinks and losses were evaluated for 1998.



tion changes across the landscape over time. Dynamic ecosystem models should therefore incorporate shifts in tree species composition in projecting the effects of N deposition or changes in other environmental factors on leaching from forest stands.

Mechanisms of species response

In Spe-CN model simulations, stands dominated by different tree species varied in NO_3 leaching due to species-specific traits governing storage of N relative to leaching losses. The main sinks for N entering a forest include vegetation, downed wood, and soil pools; losses are gaseous or hydraulic (i.e., NO_3 leaching) (e.g., Lovett and Goodale 2011). For this analysis, we have assumed negligible gaseous N loss from the generally aerobic, well-drained soils of the Catskill Mountains, although gaseous losses could be important in some locations (Ashby et al. 1998; Fitzhugh et al. 2003; Morse et al. 2015).

In Spe-CN simulations, stands dominated by individual tree species varied in N sink strengths, which drove variation in N leaching losses in response to different N deposition levels (Figs. 8–9). For example, for the N deposition gradient spanning the northeastern US, the model simulated high N leaching losses for sugar maple relative to other species. A sugar maple stand showed consistent increases in all N sink and loss terms (again, not considering gaseous losses) with increasing N deposition across the gradient (Fig. 9a). Where N deposition was low, the plant N sink was greater than either the soil N sink or N leaching losses; with increasing N deposition, the soil N sink and N leaching rate increased to ultimately match the vegetation N sink. This demonstrated that a sugar maple stand receiving high N deposition was

in a state of kinetic N saturation (continuing to store N but with N input greater than N sinks; Lovett and Goodale 2011) with N inputs approximately evenly distributed among tree vegetation N sink, the soil N sink, and N leaching losses (Fig. 9a) (the contribution to CWD was minimal relative to other fates of N). These patterns reflected traits characteristic of sugar maple, including (i) low tissue N concentrations and slow growth rates relative to other deciduous species, which caused the plant N sink to increase slowly with added N, (ii) high maximum biomass such that the plant N sink was ultimately large, (iii) low lignin concentrations in litter, resulting in fast soil turnover and therefore limiting the soil N sink, and (iv) low soil C:N ratios, which were associated with high nitrification rates and therefore high leaching (Appendix A, Tables A1 and A2; Crowley et al. 2016).

In contrast, red spruce was among the species with the lowest simulated leaching levels at low levels of N deposition, but in the regional simulations, leaching losses increased abruptly when N deposition inputs exceeded $1.0 \text{ g N m}^{-2} \text{ year}^{-1}$ (Figs. 8, 9b). The abrupt leaching increase reflected a stabilization and then slight decline of the plant N sink as the red spruce stand approached both maximum growth rate and maximum tissue N concentrations (Fig. 9b). A red spruce stand was also in a state of kinetic saturation overall, with most N storage in the soil. At N inputs greater than $1.0 \text{ g N m}^{-2} \text{ year}^{-1}$, the plant N pool began to approach its maximum N storage rate, and higher N inputs caused a jump in NO_3 leaching (Fig. 9b). These patterns reflected traits characteristic of red spruce, including (i) very low tissue N concentrations, slow growth rate, and lower maximum biomass relative to sugar maple, which limited the plant N sink, (ii) high lignin concentrations in litter resulting in slow decomposition and a strong soil N sink, and (iii) high C:N ratios, which were associated with low nitrification rates and low leaching until sinks were exceeded by inputs (Appendix A, Tables A1 and A2). In general, other species were similar to or intermediate between sugar maple and red spruce in the allocation of N inputs to sinks vs. losses.

Whether or not the model simulates an accurate leaching threshold for a 100-year-old red spruce stand is difficult to evaluate. In a study of spruce-fir stands across an N deposition gradient in the northeastern US, potential net nitrification (measured in lab incubations) increased abruptly once forest floor N concentration exceeded 1.5%, which occurred at total N deposition of approximately $0.85 \text{ g N m}^{-2} \text{ year}^{-1}$ (McNulty et al. 1991; Boggs et al. 2007). Because these studies did not measure NO_3 leaching, we cannot compare their data directly with model output, but the observed nitrification threshold approached the simulated leaching threshold at $1.0 \text{ g N m}^{-2} \text{ year}^{-1}$ of deposition. We would therefore hypothesize that a decline in the plant N sink, as simulated by the model, could be one cause of greater leaching from spruce stands subject to increasing N inputs.

Species-specific patterns

Driven by the species-specific mechanisms described above, modeled variation in leaching among second- and old-growth stands dominated by different tree species generally corresponded to patterns in field data. Simulated leaching NO_3 fluxes from second-growth, single-species stands, using Catskill N deposition levels (see Fig. 6a; 2010 N deposition = $0.65 \text{ g N m}^{-2} \text{ year}^{-1}$), declined in the order sugar maple > (beech, yellow birch) > (hemlock, red oak). This order was consistent with expectations based on NO_3 fluxes from Catskill plots dominated by these species (Lovett et al. 2013a). Prior model simulations captured a generally similar relationship among species based on the ratio of nitrification to N mineralization (nitrification fraction) in the OeOa (Crowley et al. 2016; Lovett et al. 2002, 2004, 2010; Finzi et al. 1998; Ollinger et al. 2002), which correlates with NO_3 leaching. Ross et al. (2009) also found greater nitrification rates from deciduous plots than from coniferous plots across the northeastern US, although at the species level, sugar maple and yellow birch

together were stronger predictors of high nitrification than maple alone. For older forests, higher simulated leaching from 300-year-old stands than from 100-year-old stands was consistent with higher nitrification rates and greater measured NO_3 export from old-growth stands than from second-growth (burned or logged) stands and watersheds in the WMNF (Goodale and Aber 2001; Goodale et al. 2000; Ollinger et al. 2002).

Simulated NO_3 leaching from ash-dominated stands was lower than expected based on field estimates of nitrification (Finzi et al. 1998; note that no NO_3 flux data were available from ash stands). Simulated ash stands have high N demand because of their high tissue N concentrations and high growth rates. The model suggests that high nitrification rates in the soil of ash stands do not necessarily lead to high leaching rates because of tree N uptake; unfortunately, we do not know of any data to test this hypothesis. Differences between simulated and measured values (for ash or other species) also may derive in part from very high variability in field measurements of nitrification or leaching, both within and among stands and overtime.

Simulated NO_3 leaching from beech-dominated stands was also lower than expected based on Catskill NO_3 flux data (Lovett et al. 2013a), although it corresponded well to beech's lower nitrification rates relative to species such as maple (Finzi et al. 1998; Lovett et al. 2013a). Beech litter is higher in lignin than that of ash or sugar maple, resulting in lower simulated rates of litter decomposition, and forest floor C:N is higher, resulting in lower simulated rates of nitrification and therefore leaching. In Catskill field plots, however, NO_3 fluxes from beech-dominated plots were nearly as high as those from sugar maple plots, possibly due to beech bark disease and the subsequent death of beech trees (Lovett et al. 2010, 2013a).

Responses to pest invasion

Model simulations of the replacement of white ash by sugar maple, red oak, or American beech due to EAB suggest that long-term effects of invasive forest pests on NO_3 loss from forests will be large and highly dependent on the identity of the declining and replacing tree species. We are unaware of studies specifically assessing the impacts of EAB on forest N cycling via loss of ash or replacement with other tree species. For other invasive pests currently affecting the northeastern US such as beech bark disease or hemlock woolly adelgid, loss of a host tree species or replacement with a neighboring species has been shown to increase variables such as extractable soil NO_3 , NO_3 in soil solution, nitrification rates, or NO_3 fluxes, particularly over the short term, suggesting increased leaching from these invaded forests (Oenkins et al. 1999; Lovett et al. 2010; Orwig et al. 2008; Yorks et al. 2003). Our prior modeling simulations of these species transitions also predicted greater leaching from invaded relative to uninvasd stands, with the timing and duration of leaching dependent on species identity (Crowley et al. 2016). The EAB simulations presented here extend these field observations and predictions of invasive pest impacts to include a broader range of possible long-term leaching responses - with a difference in leaching of greater than 3.5 times due to the early invader, 100 years following invasion - associated specifically with tree species characteristics that determine long-term responses. These characteristics include the ability of the forest to take up and store N in biomass and to create soil organic matter with the capacity to immobilize N. This suggests that management efforts to reduce NO_3 entering waterways will need to incorporate the net effects of tree species change across forested landscapes.

Tree species as a source of variability in stream NO_3 export

In simulating the northeastern US N deposition gradient, we asked to what extent variation in tree species composition might contribute to variability in measured stream NO_3 export (Aber et al. 2003). In model simulations in which the only source of

variation in NO_3 leaching at a given level of N deposition was variation in tree species composition, the Spe-CN model was able to reproduce 50%-75% of the range in measured stream NO_3 export, above a threshold N deposition level of $0.7 \text{ g m}^{-2} \text{ year}^{-1}$. Thus, these simulations aligned with Aber et al.'s (2003) conclusion that a portion of the large variability in NO_3 export at a given N deposition level could be driven by differences in species composition. Note that for our simulations, we chose a set of species that are common in the watersheds used in the Aber et al. (2003) study, but we do not know the actual species composition of these watersheds. Additionally, the Spe-CN model simulated NO_3 leaching below the rooting zone rather than stream NO_3 export and therefore may overestimate the Aber et al. (2003) values. Other factors that probably contributed to variation in NO_3 export in the field data include forest disturbance history, stand age, hydrologic flow paths, climate parameters, and the physical character of the catchments (Aber et al. 2003; Goodale and Aber 2001; Goodale et al. 2000; Watmough et al. 2004). Thus, our conclusion is not that tree species explain all of the variation observed in the data reported by Aber et al. (2003) but rather that differences in tree species could explain a portion of it, and the variation is predictable based on properties of the species.

The largest discrepancy between simulated NO_3 leaching and measured stream NO_3 export was the model's inability to simulate near-zero leaching at the low N deposition levels reported by Aber et al. (2003). A portion of this discrepancy may result from the additional processing of NO_3 between a forest stand and the stream. Additionally, the model predicts little retention of deposited N in the dormant season, even at low N deposition because of a lack of dormant-season sinks in the system. This could indicate a need to better simulate either a rapid-uptake soil pool that would retain incoming N deposition (Berntson and Aber 2000; Colman et al. 2008; Fitzhugh et al. 2003; Lewis et al. 2014) or wintertime microbial activity that would retain N when N is limiting (Groffman et al. 2009). If denitrification or other processes are a meaningful component of N loss in Catskill watersheds (Ashby et al. 1998; Fitzhugh et al. 2003; Morse et al. 2015), then incorporation of gaseous N losses could reduce model estimates of NO_3 leaching. Addition of water dynamics to Spe-CN could result in greater forest N retention during dry or cold periods when NO_3 would be less mobile, therefore reducing leaching in some instances. More exact knowledge of past land use history (e.g., multiple harvests, other disturbances) might also lower minimum simulated leaching values to correspond more closely to measured NO_3 export.

Implications

If changes in tree species composition alter the response to N deposition of NO_3 leaching from northeastern US forests as model simulations suggest, this will have several implications for protecting waterways from added NO_3 . One approach to protection is to determine the critical load of N deposition that will increase leaching above an ecologically important threshold and use this value to inform air pollution policy and standards, an approach that is currently used in Europe and Canada and is gaining ground in the US (Ahern and Posch 2013; Burns et al. 2008; Lovett et al. 2009; Pardo et al. 2011; Porter et al. 2005). A critical load is "the quantitative exposure to one or more pollutants below which significant harmful effects on sensitive elements of the environment do not occur, according to present knowledge" (Nilsson and Grennfelt 1988). For the northeastern US, Pardo et al. (2011) suggested an empirical critical load (i.e., determined from observations of harmful responses to known N inputs) of $0.8 \text{ g m}^{-2} \text{ year}^{-1}$ of atmospherically deposited N based on the threshold in stream NO_3 export reported by Aber et al. (2003). Critical loads can also be set or evaluated for exceedance using steady-state mass balance modeling approaches, which assume no changes in forest N fluxes over time, or dynamic models,

which incorporate time-dependent changes in N pools and fluxes (e.g., Quin et al. 2006; Whitfield et al. 2007; Wu and Driscoll 2010; Zhou et al. 2015). For sugar maple - beech - yellow birch forests in the northeastern US, simulations using the dynamic ForSAFE-Veg model showed that NO_3 leaching could only approach historical values when N and S deposition were reduced to preindustrial levels (Phelan et al. 2016). The Spe-CN model simulations presented here suggest that in addition to such direct effects of deposition, changes in tree species composition may also alter the amount of N from deposition that would elevate NO_3 leaching. Thus, managers may need to reevaluate previously established empirical critical loads when species composition changes markedly over time across a broad spatial scale. Only extensive species compositional changes could be expected to affect the regional empirical critical load estimate, which already incorporates current variability in tree species composition across the region. For example, regional species compositional shifts are predicted to occur as a result of climate change. If an oak-dominated forest replaces a maple- beech-birch forest in the northeastern U.S. (Iverson et al. 2008), Spe-CN would predict a corresponding increase in the N deposition level that would elevate leaching relative to the current threshold (Fig. 8) due to the loss of the forest type that contributes most to elevated leaching at lower N deposition levels. Furthermore, dynamic models used to project when nitrate leaching might change markedly for a given location should take tree species change into account.

Together, the analyses presented here suggest that changes in tree species composition across the landscape over time may interact with changing levels of N deposition to increase or decrease NO_3 leaching from forests. These interactions will be mediated by the very different ways in which individual tree species take up and process added N, in turn influencing movement of N into plant, downed wood, or soil pools or NO_3 leaching losses. Thus, as tree species composition changes due to invasive insects and disease, climate change, or other environmental stressors, the amount of N deposition that will cause elevated leaching from an area will also change. Inversely, larger reductions in N deposition may be needed to reduce NO_3 leaching from stands dominated by some tree species than by others: for example, from stands dominated by maple or beech vs. conifer species or red oak. Emerald ash borer simulations indicated that even at a constant level of N deposition, changes in tree species composition could elevate or reduce leaching substantially. Dynamic ecosystem models should therefore incorporate tree species change in projecting the effects of N deposition or other environmental stressors on leaching from forested landscapes.

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Appendix A. Species-specific parameters used in the Spe-CN model

In the Spe-CN model, many of the processes transferring C and N among vegetation and soil pools are governed by species-specific traits. Key parameters include minimum and range of N concentrations in foliage, fine wood, coarse wood, and roots; foliar turnover; allocation to foliage vs. wood; fraction of N resorbed from foliage before litterfall; tissue lignin and cellulose concentrations; the slope of the relationship between litter N concentration and mass loss (N mass loss or NML; Aber et al. 1990); and maximum biomass attainable in pure stands (Tables A1, A2; Crowley et al. 2016). These plant traits differentially influence productivity, nutrient uptake, turnover, and decomposition processes such that changing species composition will gradually alter C and N cycling on the site. A detailed description of how these species-specific traits govern process rates and movement of C and N between pools is included in Crowley et al. (2016).

Table A1. Descriptions and sources for species-specific parameters for black birch, balsam fir, paper birch, red spruce, white ash, and white pine.

Parameter	Description	References
MinFolNCon	Minimum foliar N(%) = 10th percentile (P10) in NERC foliar chemistry database	Northeastern Ecosystem Research Cooperative (NERC) 2010
FolNConRange	Fractional range in foliar N(%) from 10th to 90th percentile ((P90-P10)/P10)	NERC 2010
MinRootNCon	Minimum root N (%) = 80% of mean value	Aber et al. 1990; Fahey et al. 1988; McClaugherty et al. 1982, 1984; Templer et al. 2005
MinFineWoodNCon	Minimum finewood N (%) = 80% of mean value	Pare et al. 2013
MinCoarseWoodNCon	Minimum coarsewood N (%) = 80% of mean value	Alban and Pastor 1993; Fahey et al. 1988; Foster and Lang 1982; Lambert et al. 1980; Templer et al. 2005
NomMaxWoodC	Maximum wood C (g·m ⁻²) (mean of highest three available values for each species)	Baskerville 1965; Goodale and Aber 2001; Magill et al. 2004; Park et al. 2008; Sprugel 1984; USFS 2013
FolTumover	Foliar turnover (year ⁻¹)	Aber et al. 1995
CoarseWoodk	Decomposition constant for coarse woody debris (CWD) (year ⁻¹)	Fahey et al. 1988; Foster and Lang 1982; Lambert et al. 1980; Smith et al. 2007
FolLigCon	Mean foliar liner lignin concentration (%)	Aber et al. 1990; Downs et al. 1996; Magill and Aber 1998; Melillo et al. 1982
RootLigCon	Mean root lignin concentration (%)	Aber et al. 1990; Fahey et al. 1988; McClaugherty et al. 1982, 1984
FineWoodLigCon	Mean finewood lignin concentration (%)	Alban and Pastor 1993; Macmillan 1988
CoarseWoodLigCon	Mean coarse wood lignin concentration (%)	Alban and Pastor 1993; Macmillan 1988
FolLigCell	Foliar lignin to cellulose ratio	NERC 2010
FolNML	Slope of the relationship between liner N (%) and mass loss (%) for foliar liner	Aber et al. 1990; Bockheim et al. 1991; Cobb 2010; Demers et al. 2007; Loven et al. 2016; Magill and Aber 1998; Melillo et al. 1982; Parsons et al. 2008; Rustad 1994; Strukelj et al. 2012
RootNML	Slope of the relationship between liner N (%) and mass loss (%) for fine roots	Aber et al. 1990; McClaugherty et al. 1984
FineWoodNML	Slope of the relationship between liner N (%) and mass loss (%) for fine wood	Foster and Lang 1982
CoarseWoodNML	Slope of the relationship between liner N (%) and mass loss (%) for coarse wood	Foster and Lang 1982
Resorp	Ratio between mean foliar liner N(%) and foliar N(%)	Aber et al. 1990; Bockheim et al. 1991; Cobb 2010; Downs et al. 1996; Gower and Son 1992; Magill and Aber 1998; Melillo et al. 1982; NERC 2010; Parsons et al. 2008; Rustad 1994; Templer et al. 2005
HumusSpk	Decomposition constant for humus (year ⁻¹)	Estimated based on Parton et al. (1988), Olsson et al. (2012), and Tonino et al. (2014)
HumusNGR	Ratio of net to gross N mineralization in humus	Estimated to reproduce range of soil C:N under Catskill tree species
MycoNFrac	Fraction of N mineralized from humus that moves into the mycorrhizal N pool	Estimated value

Note: Parameter values for these species are provided in Table A2. Units are given within the parameter descriptions, except where parameters are dimensionless. Sources for parameters for American beech, eastern hemlock, red oak, red maple, sugar maple, and yellow birch are included in Crowley et al. (2016).

Table A2. Species-specific parameter estimates for balsam fir, black birch, paper birch, red spruce, white ash, and white pine.

Parameter (units)	Balsam fir	Black birch	Paper birch	Redspruce	White ash	White pine
NE US MinFolNCon (%)	1.25	2.14	1.83	0.85	2.01	1.10
Catskills MinFolNCon (%)	1.27	2.34	2.08	0.898	2.17	1.25
WMNF MinFolNCon (%)	1.28	2.14	1.91	0.86	1.975	1.1
NE US FolNConRange	0.43	0.32	0.50	0.50	0.32	0.38
Catskills FolNConRange	0.38	0.25	0.26	0.50	0.32	0.32
WMNF FolNConRange	0.41	0.32	0.48	0.42	0.33	0.38
MinRootNCon (%)	0.78	1.38	1.38	0.78	1.36	0.74
MinFineWoodNCon (%)	0.30	0.35	0.32	0.22	0.27	0.33
MinCoarseWoodNCon (%)	0.10	0.20	0.20	0.09	0.19	0.10
NomMaxWoodC (g C·m ⁻²)	6590	6549	10000	12160	14086	13366
FolTumover (year ⁻¹)	0.25	1	1	0.25	1	0.44
CoarseWoodk (year ⁻¹)	0.025	0.06	0.06	0.025	0.06	0.025
FolLigCon (%)	29.9	21.2	17.6	29.9	12.2	22.5
RootLigCon (%)	23.8	26.8	26.8	23.8	26.8	23.8
FineWoodLigCon (%)	28.8	16.2	16.2	28.8	16.2	28.8
CoarseWoodLigCon (%)	28.8	16.2	16.2	28.8	16.2	28.8
FolLigCell	0.77	0.52	0.59	0.61	0.31	0.68
FolNML	0.0168	0.0271	0.0249	0.0168	0.0291	0.0165
RootNML	0.02	0.019	0.019	0.02	0.019	0.02
FineWoodNML	0.005	0.005	0.005	0.005	0.005	0.005
CoarseWoodNML	0.005	0.005	0.005	0.005	0.005	0.005
Resorp	0.53	0.41	0.45	0.61	0.38	0.42
HumusSpk (year ⁻¹)	0.015	0.045	0.045	0.015	0.045	0.015
HumusNGR	0.8	0.8	0.8	0.8	0.7	0.8
MycoNFrac	0.75	0.75	0.75	0.75	0.25	0.75

Note: For parameter descriptions and sources for these species, see Table A1. Parameters without units are dimensionless. Parameters for American beech, eastern hemlock, red oak, red maple, sugar maple, and yellow birch are included in Crowley et al. (2016).

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