Development and evaluation of a nutrient cycling extension for the LANDIS-II landscape simulation model

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ABSTRACT

Long-term nutrient cycling dynamics are the result of interactions between forest succession, disturbance, nutrient cycling, and other forest processes. We developed NuCycling-Succession, a simple nutrient cycling and succession extension for the LANDIS-II landscape model of forest dynamics, to examine the interactions between these forest processes in order to develop more realistic predictions of forest response to management practices and global change. NuCycling-Succession models carbon, nitrogen, and phosphorus nutrient fluxes and masses associated with the living biomass, dead biomass, soil organic matter, soil mineral N and P, charcoal, and bedrock nutrient pools. It includes direct effects of disturbance events on nutrient cycling as well as indirect effects mediated through changes in forest composition and structure. NuCycling-Succession represents the continuum of decomposition and associated changes in chemistry using annual cohorts of leaf and fine root litter. This formulation includes the interaction of decomposition dynamics with disturbances that affect the forest floor, such as fire. Evaluation of model results relative to field data and results reported in the literature indicate the model adequately represents nutrient pools and fluxes. We present a case study of the effects of changing fire and biomass harvesting regimes on nutrient cycling in the Lake Tahoe Basin. Model results suggest that fire exclusion has resulted in substantially increased mass of nutrient pools. The NuCycling-Succession extension provides a useful simulation framework for exploring how global change factors (climate change, altered disturbance regimes) may influence nutrient cycling processes and nutrient budgets in forested ecosystems.

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1. Introduction

Interactions between forest dynamics, disturbance, and nutrient cycling occur across a range of spatial and temporal scales, leading to complex relationships between them that cannot easily be quantified using empirical studies, which necessarily occur at limited spatial and temporal scales (Oreskes et al., 1994). Alternatively, spatially-explicit simulation modeling of these interactions can be used to understand how succession, disturbance, and nutrient cycling interact. Due to nonlinearities in many forest processes across both time and space, the relationships between forest processes at fine and coarse scales may differ substantially, limiting the ability of model formulations to accurately translate across scales (Rastetter et al., 1992). At small spatial scales (i.e., within a forest stand), individual-tree based gap models simulate establishment, growth, competition, and mortality of individual trees

and their interactions with environmental conditions, particularly resource availability, within the stand (Bugmann, 2001). These models can have great mechanistic detail for physiological processes, but have limited spatial extent (generally less than 1 km^2), exclude interactions between patches, and frequently lack spatial locations for individual trees, limiting their ability to include disturbances and other large-scale spatial processes (Bugmann, 2001). Although these models can include detailed, mechanistic plant–soil interactions (Bugmann, 2001), they have limited ability to simulate interactions between disturbance and both forest structure and nutrient cycling.

At large spatial scales, forest simulation models focusing on stand production and growth are frequently used to explore the effects of disturbances and forest management actions on forest productivity and carbon sequestration (e.g., Peng and Apps, 1999; Keane et al., 1996; Scheller et al., 2011). Forests are modeled as stands rather than individual trees in the majority of biogeochemical models derived from CENTURY (Parton et al., 1987, 1988) and Biome-BGC (Running and Hunt, 1993), which facilitates the scaling up of results within a forest type (Rastetter et al., 1992). If stands are modeled as forest types, the effects of differences in species composition and age between stands can be obscured

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(Ollinger et al., 2002). For example, differences in species' responses to soil nutrient status may result in a significant effect of disturbance on the nutrient status of some species in that forest type, but not others. However, the relationship between disturbance and nutrient status may be undetectable at the stand level due to successional changes in species composition and the associated changes in plant–soil interactions (Ollinger et al., 2002). Alternatively, forest stands can be modeled using individual species and age classes as in the LANDIS-II landscape model of forest dynamics (He and Mladenoff, 1999; Scheller et al., 2007). This model structure allows interactions of species and age composition with other forest processes, including disturbance and nutrient cycling.

LANDIS-II represents forest stands as collections of age cohorts for each species, reducing computational complexity relative to individual tree models while retaining potential interactions of forest composition and structure with other forest processes (He and Mladenoff, 1999; Scheller et al., 2007). Ecological processes in LANDIS-II are represented in separate extensions that interact with the main model core, allowing the inclusion of ecological processes relevant to the ecosystem and question of interest, including succession, disturbance, and nutrient cycling (Scheller et al., 2007). The model structure allows for interactions and feedbacks between these ecological processes, leading to forest dynamics not anticipated by gap models, which lack spatial interactions and disturbance, and by stand-level models, which lack species-level details. A modified version of CENTURY has been incorporated into LANDIS-II and used to examine the effects of wind, harvesting, and species composition on forest carbon (Scheller et al., 2011). However, the generality of the interactions between disturbance and nutrient cycling, importance of processes related to weather and a monthly native time step, and relatively complex parameterization of this model are not suited for all ecosystems or research questions. As an alternative, we developed NuCycling-Succession, a computationally efficient and parsimonious nutrient cycling extension of carbon, nitrogen, and phosphorus for LANDIS-II that includes a more complete representation of the effects of disturbance on nutrient cycling and reduces both the complexity of parameterization and processes to those necessary for an annual time step. NuCycling-Succession explicitly incorporates interactions between forest succession, fire and harvesting disturbances, and nutrient cycling, allowing for differences between species and age cohorts in their response to nutrient availability and forest disturbances.

Our primary objective is to describe the structure of NuCycling-Succession and demonstrate its utility through an application in the Lake Tahoe Basin, where forest structure and fire regime have been substantially altered since Euro-American settlement. Our modeling scenario examines the effects of changing disturbance regimes, particularly fire exclusion and biomass harvesting for forest management, on nutrient pools at the landscape scale. We evaluate the extension by comparing model results to field data and previous empirical studies and present a sensitivity analysis of model results to key parameters.

2. Model design

We developed NuCycling-Succession to simulate key processes of nutrient cycling and their interactions with forest succession, environmental conditions, and fire and biomass harvesting regimes. The extension interacts with the LANDIS-II Core, base fire (He and Mladenoff, 1999), and biomass harvesting (Gustafson et al., 2000) extensions and uses the general framework of the biomass extension (Scheller and Mladenoff, 2004).

2.1. LANDIS-II forest landscape model

LANDIS-II is a landscape model of forest dynamics, including succession, dispersal, disturbance, and forest management processes (He and Mladenoff, 1999; Scheller et al., 2007). Landscapes are represented as a raster map of individual cells linked through seed dispersal and disturbance. These cells are user-classified into "ecoregions" of homogenous environmental conditions according to their soil characteristics, topography, climate, and other site conditions. Maximum annual production, standing biomass, and establishment probabilities for all species differ between ecoregions. Similarly, the landscape is classified into fire regions of characteristic fire frequency, size, and severity distributions. Within each cell, cohorts of different ages and species establish, grow, compete for resources, and die due to senescence, growth, and disturbance, leading to nondeterministic successional dynamics of species in accordance with their life history traits and the frequency and severity of disturbances. Details of LANDIS-II (He and Mladenoff, 1999; Scheller et al., 2007) and the independent extensions for fire (He and Mladenoff, 1999) and harvest (Gustafson et al., 2000) are available elsewhere.

2.2. NuCycling-Succession extension

The NuCycling-Succession extension simulates key processes of nutrient cycling in relation to landscape-level dynamics of fire, biomass harvesting, and vegetation succession, and calculates associated C, N, and P fluxes between nutrient pools (Fig. 1; see Table 1 for acronym and abbreviation definitions). Modeled structures of nutrient pools at a site vary in complexity: living biomass is modeled by tissue compartments (leaves, wood, fine roots, and coarse roots) for each species-age cohort, dead leaves and fine roots are modeled separately by annual cohorts, and dead wood and coarse roots, soil organic matter (SOM), soil mineral N and P, bedrock, and charcoal are modeled as single pools (Fig. 1). The greater complexity of the living and dead biomass pools represents the greater spatial and temporal heterogeneity in these pools and provides more realistic interactions with disturbance processes. Processes associated with each nutrient pool are described in the sections below. The extension operates on an annual time step, and nutrient cycling processes occur in this order: (1) fire and biomass harvesting events change forest structure, ecosystem nutrients, and nutrient availability and form charcoal; (2) generation of the available nutrient pool through decomposition and other mineralization processes; (3) humification of dead biomass into SOM; (4) resource competition and production of biomass; (5) litterfall and mortality; (6) leaching of mineral N.

2.2.1. Living biomass dynamics

Fluxes of living biomass (B) are a function of establishment (E), annual net primary productivity ($ANPP$), turnover of leaves and fine roots (T), age- and growth-related mortality (M), fire-related mortality (FM), and biomass harvesting-related mortality (HM) for each species i and cohort j:

$$\frac{dB}{dt} = \sum_j \sum_i \left(E_{ij} + ANPP_{ij} - T_{ij} - M_{ij} - FM_{ij} - HM_{ij} \right) \qquad (1)$$

E_{ij}, $ANPP_{ij}$, T_{ij}, and M_{ij} are modeled as in Scheller and Mladenoff (2004) with modifications to E_{ij} and $ANPP_{ij}$ resulting from the explicit modeling of nutrient cycling. Nutrient uptake is prioritized by cohort age in decreasing order to emulate asymmetric competition associated with deeper rooting depth and greater fine root mass of older cohorts. Use of translocated nutrients ensures $ANPP_{ij} > 0$, even for young cohorts without access to mineral N and P in the soil. This limits E_{ij} of new species-age cohorts to time steps