OIKOS 107: 273–282, 2004

Interactions of ecosystem processes with spatial heterogeneity in the puzzle of nitrogen limitation

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Jenerette, G. D. and Wu, J. 2004. Interactions of ecosystem processes with spatial heterogeneity in the puzzle of nitrogen limitation. – Oikos 107: 273–282.

We examined the potential effects of spatial heterogeneity and its development on the distribution, abundance, and functioning of nitrogen fixing and non-fixing components of a model ecosystem. CAECO, a spatially explicit individual based model approach, simulated the interactions between nitrogen fluxes and plant species community dynamics. Self-organized spatial patterns of nitrogen concentrations and plant occupancy were observed as the system approached an apparently meta-stable state. Nitrogen limitation was tested using chronic and gradient nitrogen amendments to the landscape. The dynamic arrangement of ecosystem components was sufficient to maintain indefinite nitrogen limitation at a local scale. However, landscape scale productivity was not similarly increased with nitrogen amendments. Landscape productivity was independent of nitrogen additions while fixers were present in the ecosystem. The probability of fixer loss from the system responded non-linearly to increasing nitrogen addition. The results of these model experiments suggest local and landscape constraints of primary productivity may be fundamentally distinct.

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Much of the world's terrestrial ecosystem productivity is nitrogen limited; an increase in productivity results from an increase in nitrogen supply (Shaver and Chapin 1980, Agren 1983, Huenneke et al. 1990). Yet, most ecosystems contain species that obtain nitrogen directly from the atmosphere (fixers hereafter), and why sustained nitrogen limitation occurs remains enigmatic (Vitousek and Howarth 1991, Vitousek and Field 1999, Rastetter et al. 2001). Several hypotheses have been advanced to explain the factors preventing fixers from alleviating nitrogen limitation, and whether these factors can maintain nitrogen limitation indefinitely. Potential mechanisms for sustained nitrogen limitation include energetic costs associated with nitrogen fixation, alternate elemental limitation of nitrogen fixation such as molybdenum, and ecological interactions such as inferior competitive abilities of nitrogen fixers and increased herbivore affinities for nitrogen fixers (Vitousek and Howarth 1991, Vitousek and Field 1999, Rastetter et al. 2001, Vitousek et al. 2002).

To examine this problem, a variety of models have been developed to explore how sustained nitrogen limitation occurs in terrestrial ecosystems (Pastor and Binkley 1998, Vitousek and Field 1999, Rastetter et al. 2001). These models have shown a decided progression in mechanistic sophistication. Pastor and Binkley (1998) examined the equilibrium states of monocultures obtaining nitrogen through fixation in a mass balance approach. Vitousek and Field (1999) simulated the interactions between fixers and non-fixers and the linkages between carbon and nitrogen acquisition. They found non-fixers could exclude fixers and maintain indefinite nitrogen limitation if some nitrogen was lost and non-fixers could dominate fixers through mechanisms such as shading. Rastetter et al. (2001) used the multiple element limitation model (MEL) to simulate

Accepted 31 March 2004

ISSN 0030-1299

the detailed mechanisms of resource acquisition between different vegetation functional types. They suggested that the cost associated with uptake or fixation explains the patterns of persistent nitrogen limitation and the failure of fixation to supply a sufficient quantity of nitrogen. All of these models assumed that ecological interactions were occurring in a spatially homogeneous environment.

However, nitrogen fixer and non-fixer distributions in many ecosystems exhibit extensive spatial heterogeneity (Cain et al. 1995, Bowman et al. 1996, Schwinning and Parsons 1996, Grimm and Petrone 1997). Empirical studies have shown nitrogen fixers often form clumps migrating through the landscape (Cain et al. 1995). Schwinning and Parsons (1996) used a spatially explicit model of community interactions between fixers and non-fixers to replicate and understand the dynamic spatial relationships between these two functional groups. As has been shown for a variety of population and community models, spatial heterogeneity can have unexpected effects on ecological interactions. Could spatial heterogeneity be important in understanding the relationships between nitrogen fixers and non-fixers and the cycle of nitrogen in terrestrial ecosystems?

Spatial heterogeneity can have a variety of consequences on ecological processes; in some cases a spatially non-explicit understanding is sufficient while in many cases incorporating spatial relationships can have a profound effect on ecological processes (Durrett and Levin 1994, Wu and Levin 1994, With and Crist 1995). The accuracy of a spatially non-explicit approach will depend on the importance of patch configuration and interactions between patches on patch functioning (Strayer et al. 2003). Several of the proposed mechanisms for maintaining nitrogen limitation, including competitive and consumer interactions, are influenced by both of the characteristics of spatial heterogeneity (Tilman 1994, Ruxton and Doebeli 1996).

Many biogeochemical processes are influenced by and generate spatial heterogeneity. Nitrogen transformation and transport, either accumulation or loss, are often linked to local plant species characteristics (Hungate et al. 1996, Schlesinger et al. 1996). Patches of differential cycling rates generate sink and source areas for materials in the ecosystem. Transport between source and sink patches can have significant effects on overall ecosystem functioning that could not be predicted from a spatially non-explicit analysis. Plants often will selectively concentrate materials, such as limiting nutrients, under the canopy while allowing other materials to be transported (Gross et al. 1995, Cross and Schlesinger 1999). Rates of decomposition and nutrient mineralization are also affected by locally available microbial species distributions, which are spatially variable (DeBoer et al. 1996). Both above ground and below ground processes can lead to spatial heterogeneity in biogeochemical pools (Hook et al. 1991, Jackson and Caldwell 1993, Smith et al. 1994). The effects of spatial heterogeneity on biogeochemical concentrations can affect community level interactions, notably competition between different plant species (Fransen et al. 2001). Therefore, nitrogen transformation and transportation rates can be sensitive to the spatial arrangement of ecosystem components including plant species composition; reciprocally, this heterogeneity can affect plant species distributions. Thus, models linking the processes generating spatial heterogeneity in community distributions and biogeochemical pools are needed.

The generation of spatial heterogeneity by endogenous processes has been observed in a variety of systems. Self-organized spatial patterns are both non-random and insensitive to the spatial patterns of external drivers. Theoretical investigations have shown that simple spatial models can often generate a variety of spatial structures through self-organization (Wolfram 1984, Langton 1986). These findings have been similarly corroborated in investigations of physical, chemical, and geological systems (Nicolis and Prigogine 1977, Bak et al. 1988, Stolum 1996). Recently, ecological systems have been viewed as potentially possessing self-organizing characteristics (Bascompte and Sole 1995, Levin 1999, Zhang and Wu 2002, Bolliger et al. 2003). However, the function of spatial self-organization for an ecosystem is not well understood.

Evaluating the role of self-organizing spatial patterns derived from linked biogeochemical and vegetation community processes has been hampered by a lack of appropriate ecosystem models. Models are needed that incorporate the effect of vegetation patterns on biogeochemical processes and feedbacks to vegetation processes from biogeochemical patterns. Conceptual ecosystem models have addressed the genesis of spatial heterogeneity as important in creating a meta-stable, or shifting mosaic, state (Watts 1947, Whittaker et al. 1975, Bormann 1979, Turner et al. 1993, Wu and Loucks 1995). However, only a few spatially interactive ecological models have been developed to analyze the effects of spatial heterogeneity and spatial interactions on biogeochemical dynamics (Pastor et al. 1999). Most biogeochemical models do not incorporate spatial heterogeneity, those that do are often constructed as non-interactive, iterated point models (IPMs; Schimel et al. 1997). The IPM approach incorporates spatial heterogeneity in the model input parameters, and the spatial units often are not linked through exchanges. In the few ecosystem models that have included spatial interactions, the effect of these interactions has been substantial (Costanza et al. 1990, Pastor et al. 1999).

Thus, the purpose of this paper is to develop a spatially interactive model of plant–nitrogen interactions. We use this model to examine the spatially mediated mechanisms of nitrogen limitation and the potential for self-organizing behavior in a linked biogeochemistry–community dynamic model. In particular, this model includes descriptions of fixer and non-fixer plant functional types, their interactions, and effects of these interactions on ecosystem functioning. We use this model to further explore the factors preventing nitrogen fixers from alleviating sustained nitrogen limitation in terrestrial ecosystems.

Model description

We have developed a simple model, CAECO (cellular automata ecosystem), to simulate interactions between nitrogen-fixing and non-fixing vegetation functional types with biogeochemical fluxes. CAECO was used to investigate ecosystem processes of nitrogen cycling and net primary productivity (NPP) in conjunction with community processes of competition, dispersal, and extirpation at both local and landscape scales.

The cellular automata (CA) framework is a common method for representing space in a variety of models (Hogeweg 1988, Balzter et al. 1998, Sarkar 2000). The traditional CA represents space as a set of discrete, homogeneous cells arrayed in a grid; each cell in the grid changes as a function of its current state and that of its neighbors. Often, only the four cardinal neighbors to a cell are considered in the neighborhood, although any sized neighborhood can be modeled. Boundary conditions of CA models are commonly modeled as absorbent, potential colonists moving beyond the boundary are removed from the system, or a torus, left-right and top-bottom edges are connected, thereby removing boundaries.

CAs have been developed for spatial modeling applications in environmental hazards (Turcotte 1999), land use change (Verburg et al. 1999, Jenerette and Wu 2001), and ecological community interactions (Hogeweg 1988, Balzter et al. 1998). For ecological systems these models have been especially useful in identifying characteristics of spatial self-organization (Rohani et al. 1997, Milne 1998). Ecological implementations of cellular automata have included a variety of changes to the original CA formulation. A common change to the model allows continuous set of states for each cell rather than a set number of discrete states. Further modifications have incorporated a dynamic process model within each of the cells instead of a specific rule set. These modifications have also been used in other applications of CA models (Sarkar 2000).

CAECO was developed as a CA modified to better approximate linked biogeochemical and community processes. CAECO was composed of three spatially referenced grid-layers: (1) vegetation type, 3 discrete states (fixers, non-fixers, and empty); (2) nitrogen content, a continuous variable representing nitrogen concentration in both vegetation and soil pools; and (3) NPP, a continuous variable computed as a function of both the vegetation and nitrogen patterns (Fig. 1). The vegetation layer functions similar to a traditional CA in that cell states are discrete and the transition probabilities between cell states are a function of the states of the focal and neighboring cells. All model equations (Table 1) and initial parameter values (Table 2) are provided.

The model was developed to approximate Vitousek and Field's (1999) non-spatial model of nitrogen fixer/non-fixer interactions. However, the conversion of a systems theoretic model describing the flow of material between distinct pools into a probabilistic based cellular automaton was not exact. Similar to their model, CAECO describes a theoretical ecosystem where the dimensions and absolute quantities to variables are not assigned. Vitousek and Field's (1999) model and CAECO share several simplifying assumptions. Nitrogen is modeled as the sole resource relevant to ecosystem functioning. Fixer processes are modeled independently of nitrogen; whereas, all functions (colonization and production) of non-fixers are constrained by nitrogen. While many ecosystems are solely limited by nitrogen, this assumption is an oversimplification for some ecosystems where other nutrients, water availability, or other factors can limit productivity. Fixers may be limited by alternative nutrients such as phosphorus or molybdenum (Vitousek et al. 2002). We also assumed that there is no response of fixers to available nitrogen. In many cases this is appropriate, however, some fixers can utilize available nitrogen to supplement nitrogen derived from fixation. These assumptions are consistent with previous studies of the interactions between fixers and non-fixers and provide a useful framework for analyzing the potential effects of spatial heterogeneity on ecosystem functioning.

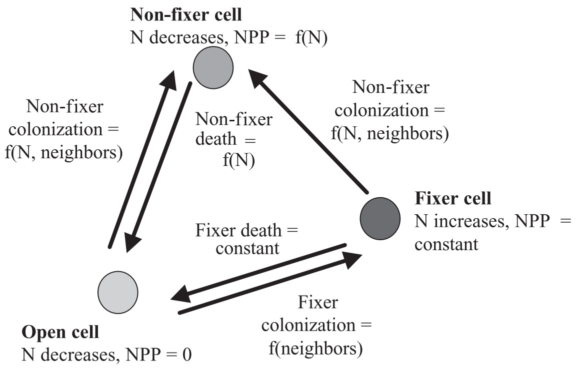

Fig. 1. Patch specific biogeochemical and patch dynamics processes. Transformations of patch types involving non-fixers are a function of nitrogen. Colonization by fixers and non-fixers are also influenced by the neighborhood composition. Nitrogen is lost from non-fixer and open cells; a net nitrogen accumulation occurs in fixer cells.

Table 1. Model equations for CAECO.

Vegetation patch dynamics

Probability of change from open to fixer cell with vegetated neighbors:
P = fixer_colonization_paramater × fixer neighbors
Probability of change from open to fixer cell without vegetated neighbors:
P = distance_fixer_colonization_probability
Probability of change from open to non-fixer with vegetated neighbors:
P = non-fixer_open_colonization_parameter × local nitrogen × non-fixer neighbors
Probability of change from open to non-fixer without vegetated neighbors:
P = distance_non-fixer_colonization_probability
Probability of change from fixer to non-fixer
P = non-fixer_fixer_colonization_parameter × local nitrogen × non-fixer neighbors
Probability of change from fixer to open
P = fixer_death_probability
Probability of change from non-fixer to open
P = non-fixer_death_parameter × local nitrogen

After computing the probabilities for each allowed cell change, the probabilities were normalized.

Nitrogen dynamics

Nitrogen content = current nitrogen + deposition − (current nitrogen × {veg specific}nitrogen_loss_coefficient) + (fixer_nitrogen_coefficient × fixer_biomass).

Net primary productivity

Fixers:
NPP = fixer_NPP
Non-fixer:
NPP = non-fixer_critical_nitrogen × non-fixer_uptake × (1 − non-fixer_cost)
Non-fixer_cost = non-fixer_uptake/local nitrogen) × 0.1 + 0.1
Non-fixer_uptake = minimum {local nitrogen, max_uptake}

Biomass

Biomass = previous biomass + NPP; if colonized this time then previous biomass set to 0.

For all simulations a 250 × 250 cell landscape was constructed. The edges of the landscape were connected to generate a torus for the simulations without deposition and spatially uniform deposition scenarios. In the gradient simulation the edges in the direction of the gradients were absorbing, which prevented interactions between the high and low deposition ends of the gradient. For all simulations the four nearest neighbors in the cardinal directions were considered as the neighborhood. Five replicates of each simulation using different initial spatial patterns were conducted; the results shown are averages of all replicates.

In contrast to traditional CAs, transition probabilities are linked to the dynamic nitrogen concentrations in the nitrogen layer. Colonization of an open cell by a non-fixer is dependent upon the number of non-fixer neighbors as well as the local nitrogen concentration. Non-fixers can also invade fixer cells with a probability dependent upon the number of fixer neighbors and local nitrogen concentrations. Local extirpation, simulated as a transition from vegetated state to an open state, is constant for the fixer and inversely related to the local nitrogen concentration for the non-fixer. The increased competitive success of non-fixers with high nitrogen availability is incorporated as a potential displacement of fixers by non-fixers, whereas the converse is prohibited.

Table 2. Standard parameter set used for implementing CAECO.

Fixer_colonization_parameter (Pfc) = 0.6
Distance_fixer_colonization_probability (dcf) = 0.00001
Non-fixer_open_colonization_parameter (Pnco) = 0.005
Distance_non-fixer_colonization_probability (dcnf) = 0.00001
Non-fixer_fixer_colonization_paratemer (Pncf) = 0.0005
Fixer_death_probability (Pfd) = 0.05
Non-fixer_death_paramater (Pnd) = 10
Fixer_nitrogen_coefficient (Nfx) = 0.001
Fixer_nitrogen_loss_coefficient (Nf) = 0.1
Non-fixer_nitrogen_loss_coefficient (Nn) = 0.02
Open_nitrogen_loss_coefficient (No) = 0.1
Fixer_NPP = 2000
Non-fixer_critical_nitrogen = 50
Max_uptake = 100

Nitrogen dynamics included loss, atmospheric deposition, and fixation at cells occupied by fixers. Local nitrogen loss, representing hydrologic export and denitrification, was modeled as first order loss equation whose loss coefficient was determined by the vegetation present at the cell. Increased rates of loss of nitrogen from sites with fixers compared to those without fixers can occur because soil uptake by non-fixers increases retention relative to those sites with nitrogen fixers. To account for this we simulated loss from fixer cells to be an order of magnitude greater than the non-fixer cells. At the same time fixers increase the nitrogen content in the cells they occupy; the increase is approximated as a function of fixer biomass.

NPP was modeled as a non-linear saturating function of nitrogen in non-fixer cells, and was set to a constant in fixer cells. These assumptions have been incorporated into previous models of nitrogen fixer/non-fixer interactions and are supported by empirical evidence (Bowman et al. 1996, Schwinning and Parsons 1996, Hart et al. 1997, Vitousek and Field 1999). While only a single limiting nutrient is explicitly modeled, the saturating function implicitly incorporates limitation by other factors. Vegetation biomass is modeled as the summed NPP beginning when a cell is first colonized by either a fixer or non-fixer.

For all simulations we initiated the model with a low proportion of cells occupied by either fixer or non-fixer states. We examined the change in spatial patterns of all three layers and whole system averages of cell occupancy, nitrogen content, and NPP through time. To test for persistence of both functional types we ran the model for 100,000 iterations. Initial examinations of model behavior revealed two phases of dynamics, a transitory phase followed by a cyclic phase. To test the sensitivity of the model behavior on parameter settings we ran the model with modifications of each parameter up to ±20% of the original value. When comparing different parameterizations of the model we examined the average model output between iterations 1300–1500; this time period was chosen because it was beyond the initial transitory dynamics and encompassed the full cycle of periodic behavior we had observed in previous model runs. Five independent runs were generated for each scenario to account for stochastic differences in the model. Comparisons were made between the averaged five model runs.

We conducted two experiments with the model to determine the nitrogen limitation status of the ecosystem. Our first experiment was to provide a spatially uniform amendment of nitrogen to the landscape continuously. Simulations were ran that included nitrogen deposition between 0–2.5 units/cell/iteration at 0.5 intervals. Similar to our methods for conducting the sensitivity analysis we averaged the model output between iterations 1300–1500 for three independent model runs. To examine the sensitivity of the model behavior to the parameter settings we also modified each parameter by 5%, 10%, and 20% with nitrogen depositions of 1.2 units/cell/iteration and 2.2 units/cell/iteration.

In our second experiment we added nitrogen to the landscape as a linear gradient. Nitrogen increased from 0–2.5 units across the landscape at a 0.01 unit/cell increase. As before, nitrogen was added at each iteration simulating chronic deposition.

Results

The model ecosystem went through a transition period of approximately 500 time steps, and then reached a quasi-cyclical temporal pattern in which non-fixers are dominant (Fig. 2). The temporal dynamics of the model suggested a strong relationship between NPP and nitrogen content for the entire system; regression analysis between nitrogen and NPP for iterations 1000–1500 results in an $r^2 = 0.77$. The ecosystem and community dynamics generated a landscape where non-random heterogeneities in both the distributions of vegetation types and nitrogen concentrations are endogenously created (Fig. 3). Localized nitrogen limitation mediated by spatial interactions occurred in the model when losses of nitrogen within a cluster of non-fixer cells reduce the amount of NPP and eventually culminates in the death of the non-fixers. These cells are prevented from being colonized by fixers because still extant non-fixers form a temporary dispersal barrier. The spatial pattern of fixers, non-fixers, and empty cells was characterized by the distribution of vegetation patches at multiple locations and of various sizes on the landscape.

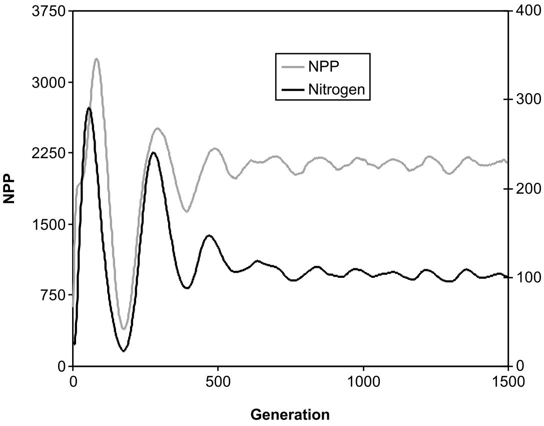

Fig. 2. Temporal dynamics of CAECO without nitrogen deposition. The average nitrogen content and NPP are shown. Proportional occupancy by each patch type has a similar oscillatory pattern. Following the initial transitory dynamics, the system reaches a quasi-cyclical attractor. Temporal fluctuations are primarily due to the temporal scale difference between ecosystem processes (nitrogen accumulation and release) and community dynamics (dispersal and local extirpation).

At the attractor (beyond approximately 500 time steps), the patterns of vegetation distributions formed traveling waves and coherent amorphous patches similar to those described in previous spatially-explicit models of community dynamics showing self-organization (Bascompte and Sole 1995, Ruxton and Doebeli 1996, Rohani et al. 1997, Milne 1998). The spatial patterns of CAECO exemplified the dynamics of a shifting mosaic. Fixers colonized open cells with low nitrogen. The fixers increased the nitrogen content of the cells, and then was displaced by the fixer. Nitrogen was slowly lost from the cell and eventually the non-fixer was replaced by an open cell type. Fixers again colonized the open site and the cycle repeated. The spatial pattern of the ecosystem showed traveling waves from non-fixers to open cells to fixers; nitrogen was at its lowest concentrations at the front edge of fixer patches and highest at the trailing edge of fixer patches.

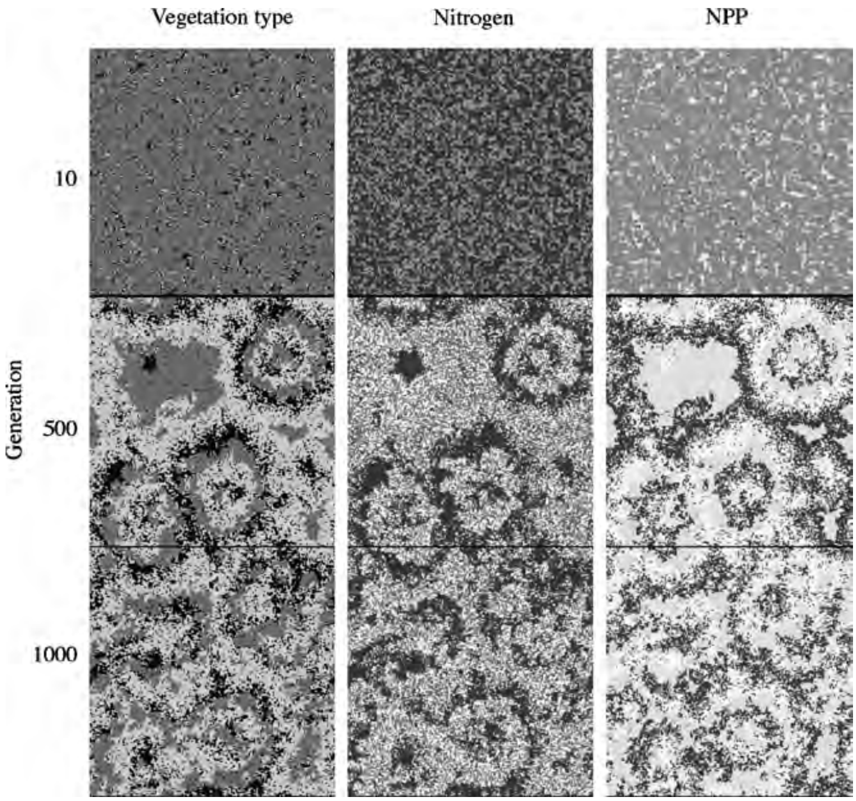

Fig. 3. Maps of the spatial patterns generated by CAECO. Three generations: 10, 500, 1000 are shown for vegetation patches (left images – white is non-fixer, grey is fixer and black is open), nitrogen (middle – increasing from light to dark), and NPP (right – increasing from light to dark). Self-organized spatial patterns are evident, and these patterns lead to localized areas of nitrogen-limited NPP.

While these model results were dependent upon the parameter set originally chosen, our sensitivity analysis showed that modifications of each parameter individually up to 20% generally resulted in disproportionately smaller changes in model output (Table 3). The patch occupancy variables were consistently more sensitive to parameter changes than the biogeochemical variables. Pfc was the most important parameter influencing patch occupancy, while both Pncf and Fixnpp (Table 2 for variable definitions) affected the biogeochemical variables.

The results of the nutrient amendment experiments were unexpected. The spatially uniform nitrogen amendments did not result in an increase in NPP up to nitrogen amendments of 2.0 units N/cell/iteration (Fig. 4a). Entire system nitrogen content in fact decreased following these levels of nitrogen amendments. Once nitrogen amendments increased beyond 2.0 units N/cell/iteration both NPP and nitrogen content increased in correspondence with increases in nitrogen deposition. This non-linear change in model behavior is similarly shown in the changes in vegetation occupancy of the landscape; non-fixers replace fixers until fixers are reduced to near extinction. The near removal of the fixers occured near a deposition rate of 2.0 units N/cell/generation (Fig. 4b). Similarly, creating a gradient of nitrogen deposition did not result in an NPP increase for a large portion of the gradient (Fig. 5). The gradient of nitrogen deposition resulted in three distinct spatial phases in the response of the model to nutrient additions. At low additions, whole

Table 3. Results of sensitivity analysis. The mean relative change from independent modification of all parameters relative to the original parameter set is shown. Model variables are grouped into patch type occupancy variables, proportion of fixers, non-fixers, and open, and two biogeochemical variables, nitrogen content and NPP. The parameter that has the greatest affect for occupancy and biogeochemical variables, the variable it most affects, and the proportional change in that variable are identified.

Parameter change	△ Fixer	△ Non-fixer	△ Open	△ Nitrogen	△ NPP	Key parameter occupancy	Variable, △	Key parameter BGC	Variable, △
5%	1.9%	0.7%	2.0%	1.5%	0.6%	Pfc	Open, 6.3%	Pncf	N, 3.4%
10%	3.6%	1.2%	3.8%	2.1%	1.0%	Pfc	Open, 14.0%	Pncf	N, 5.2%
20%	7.8%	2.5%	6.6%	3.5%	2.0%	Pfc	Open, 32.3%	FixNPP	N, 9.5%

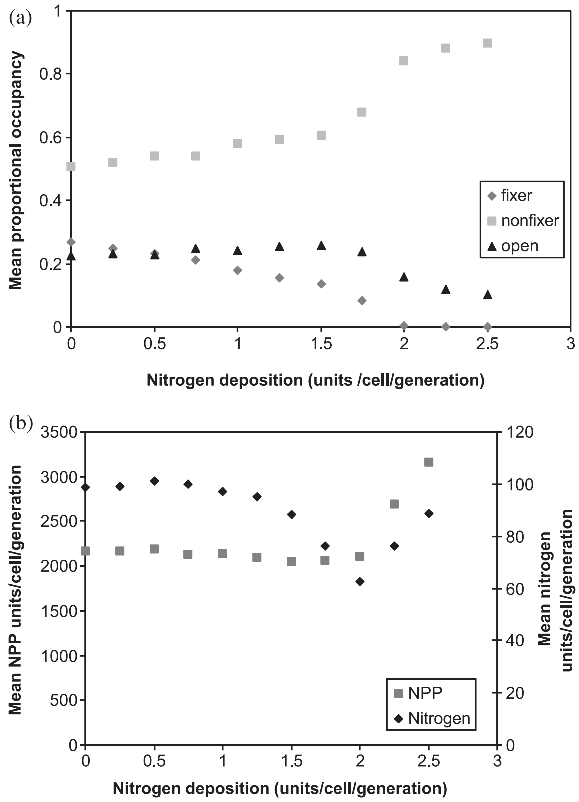

Fig. 4. Comparisons of landscape NPP for uniform environment simulations. The mean occupancy from three simulations of vegetation types (a), nitrogen and NPP (b) is plotted. While fixers and non-fixers and present, nitrogen additions do not result in an increase in NPP. When nitrogen additions cross the 2.0 threshold, the system fundamentally changes with the virtual loss of fixers; beyond this threshold additions of nitrogen result in increased NPP.

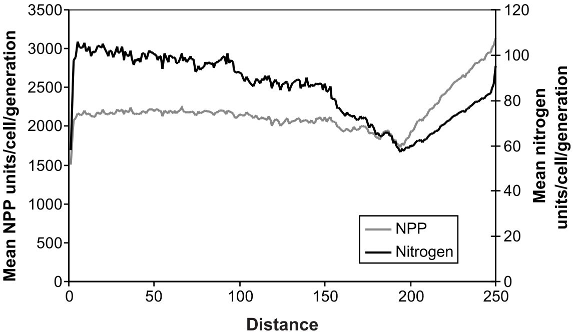

Fig. 5. Average between generations 1000–1500 of NPP and nitrogen values across a gradient of nitrogen deposition increasing linearly with distance. For the majority of the gradient, the system does not respond with increases in NPP and system nitrogen actually decreases. At about a deposition rate of 2.0, both nitrogen and NPP being increasing. This increase co-occurs where the probability of locating a fixer approaches 0.0 – the system has fundamentally changed with a reduction of functional diversity.

system nitrogen and NPP were not affected. At mid-level additions, both the average nitrogen and NPP of the system decreased. At high levels, average nitrogen and NPP increased linearly with increases in nitrogen addition. The transition to a linear response of productivity and nitrogen to high levels of deposition was coupled with a corresponding fundamental change in the system-nitrogen fixers have been removed from the landscape.

The results of nitrogen addition experiments were robust to changes in model parameters from 5–20% (Table 4). Following a deposition rate of 1.2 units N, all the examined model parameter sets resulted in both a depressed NPP rate and nitrogen content. At a deposition rate of 2.2 units nitrogen, all model parameter sets resulted in an increased rate of NPP while nitrogen content was still reduced. These behaviors are consistent with both the spatially uniform and gradient deposition experiments.

Discussion and conclusion

By developing CAECO we linked biogeochemical and community processes in a spatially explicit modeling framework. This modeling framework addresses two limitations in ecological theory, the need for integrations of community and ecosystem processes (Loreau 2000) and the need for spatial explicitness in understanding biogeochemical processes (McClain et al. 2003). As had been shown in a variety of spatially explicit population and community models, CAECO generated self-organized spatial patterns from an initial random distribution of vegetation functional types. These patterns are consistent with the patterns observed by Schwinning and Parsons (1996) in their model of nitrogen fixer and non-fixer interactions. The dynamic spatial patterns of migrating fixers and non-fixers are consistent with the idea of a stable shifting mosaic of spatially organized vegetation distributions. The temporal oscillations are

Table 4. The relative change of model output following nitrogen additions at rates of 1.2 and 2.2 units is shown. The average relative difference between no nitrogen additions and nitrogen additions was obtained from model runs where all parameters were independently changed by 5%, 10%, and 20%.

	1.2 N addition/cell/generation		2.2 N addition/cell/generation	
Parameter change	△ NPP	△ Nitrogen	△ NPP	△ Nitrogen
5%	−3.7%	−4.7%	19.0%	−26.3%
10%	−3.7%	−3.6%	19.0%	−26.2%
20%	−3.5%	−3.4%	12.3%	−29.7%

due to the inherent time scale differences between community and ecosystem processes; nitrogen inputs and losses generate localized historical legacies for the more rapid community dynamics. Similarly in the spatial dimensions, the historical legacies produced by the biogeochemical processes facilitated ecosystem self-organization. Our observed temporal and spatial patterns are consistent with theories of ecosystem stability at large spatial scales that incorporate a dynamic pattern of spatial heterogeneity (Whittaker et al. 1975, Bormann 1979, Turner et al. 1993, Wu and Loucks 1995), although in this case processes are endogenous to the system and not mediated by external disturbance.

In comparison to spatially non-explicit models, CAECO exhibited characteristics both indicative of and distinct from an ecosystem limited by nitrogen. A strong relationship between NPP and nitrogen was observed at the landscape scale and this relationship is suggestive of nitrogen limitation. However, spatially uniform or gradient additions of nitrogen did not result in increased NPP until the system was fundamentally changed by the loss of fixers. By the definition of nutrient limitation, an increase in productivity following an addition of the limiting material, the spatially extended system comprised of both fixers and non-fixers does not exhibit limitation by nitrogen. Yet, at the scale of the individual cell, the only limitation to NPP was nitrogen. There was a change in the constraints to NPP with a change in scale. Why were the local determinants of NPP not similarly important in constraining NPP at broader scales? How was nitrogen limitation mitigated at the landscape level?

Within this model, the principal effect of a nitrogen amendment was to increase the displacement rate of fixers by non-fixers. The resulting decrease in the fixation rate compensated for any external amendments of nitrogen. This was evident in both the gradient and the chronic amendments. By linking biogeochemical and community processes into a single model, novel results often occur. In this case, the scale dependence of nitrogen limitation was one such finding. While local nitrogen limitation was observed, at broader scales spatial heterogeneity in the supply and utilization of nitrogen ameliorated this limitation. However, non-linear thresholds of change characterize landscape processes; the loss of internal nitrogen fixation fundamentally altered ecosystem dynamics. Scaling empirical observation of nitrogen limitation from plot studies to regional scales could be problematic.

The processes occurring at population and community levels have been extensively examined by ecologists interested in self-organization of spatial patterns (Kaitala et al. 2001). In a variety of ecological models, spatial organization has been shown to develop from species interactions and was robust to a range of initial and environmental conditions. Some of the patterns shown to develop include traveling waves, organized spirals, and clumped spatial chaos in the distributions of different species (Hassell et al. 1994, Rohani et al. 1997). Host–parasitoid (Ruxton and Doebeli 1996), population fluctuations (Ranta et al. 1997), disturbance and competition (Wu and Levin 1994) and species coexistence/diversity (Levin and Paine 1974, Tilman 1994, Durrett and Levin 1998) are examples of phenomena that ecologists have linked spatial pattern formation with ecological processes. In these examples, the self-organized spatial heterogeneity has generated new insights that were not predictable from similar analyses assuming spatial homogeneity.

In summary, this research presents several new findings. First, a linked biogeochemistry-community model in a spatially explicit framework can generate self-organizing spatial patterns. While self-organization of spatially explicit models has been shown for a variety of systems, such behavior in systems that include biogeochemical processes has not been adequately considered. Second, the spatial patterns created by endogenous model processes have a functional consequence; the system regulates productivity and nitrogen content independent of external supplies of nitrogen.

Understanding the mechanisms by which nitrogen availability limits ecosystems provides insight into possible consequences of human-induced biospheric changes. One such change is the increase in available nitrogen through anthropogenic fixation (Galloway et al. 1995, Vitousek et al. 1997). At different scales the constraints to ecosystem functioning change dramatically, thus the impacts of landscape nitrogen additions will be difficult to assess from local plot scale analyses alone. Human land use/land cover alterations, which are rapidly changing the connectivity of terrestrial ecosystems at global scales (Vitousek 1994), might also impact ecosystems through alterations in fixer and non-fixer interactions. Landscape fragmentation, which disrupts the formation of self-organized heterogeneity, could affect landscape ecosystem functioning. In a spatially heterogeneous environment the interactions between ecosystem components at broad scales can be dramatically distinct from those at fine scales.

Acknowledgements – We wish to thank Matt Luck, Ann Kinzig, Nancy Grimm, and John Pastor for providing constructive feedback on our research. This research was supported in part by US-NSF (DEB 97-14833, CAP-LTER and Urban Ecology Integrative Graduate Education and Research Traineeship) and USEPA (R827676-01-0) granted through Arizona State University.

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