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Abstract approved:

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Ecosystems are highly heterogeneous systems subjected to important levels of environmental variability; however, it is common in terrestrial biogeochemical models to assume homogeneous properties of the elements of the system or constant environmental conditions. For some processes, heterogeneity in these models is treated very simplistically, but there is not much information about the advantages of including more complex representations in these models. By environmental variability I refer to the continuous changes of abiotic drivers in ecosystems, mainly climatic conditions. System heterogeneity is treated here as the diversity of elements that compose an ecosystem and respond differently to biotic and abiotic drivers. In this dissertation I performed a theoretical analysis to evaluate the consequences of ignoring heterogeneity and variability on the representation of carbon and nitrogen cycling in terrestrial biogeochemical models. For this purpose I used tools from probability theory and simulation models to test the hypothesis that ignoring heterogeneity and variability excludes a variety of system properties and behaviors that cannot be obtained with simpler models. Explicit treatments of climatic variability showed that changes in temperature variance alone can modify the amounts of respiration and carbon storage in ecosystems. Additionally, changes in temperature variance can modify predictions solely based on changes in temperature averages. This behavior

is strongly dependent on the degree and nature of nonlinearity in ecosystems. Effects of system heterogeneity on carbon and nitrogen cycling are also strongly influenced by nonlinearities. Extrapolations of average system behavior are only valid when the system is linear and the elements of the system are distributed homogeneously or symmetrically around an average value. In all other cases, the nonlinearity of the system and the distribution of its elements produce complex behaviors that are impossible to predict with simple models.

Environmental Variability and System Heterogeneity in Terrestrial Biogeochemical Models

by

Carlos A. Sierra

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Carlos A. Sierra, Author

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ENVIRONMENTAL VARIABILITY AND SYSTEM HETEROGENEITY IN TERRESTRIAL BIOGEOCHEMICAL MODELS

1. INTRODUCTION

This dissertation is primarily concerned with issues of environmental variability and system heterogeneity in terrestrial biogeochemical modeling. By environmental variability I refer to the continuous changes of abiotic drivers in ecosystems, mainly climatic conditions. System heterogeneity is treated here as the diversity of elements that compose an ecosystem and respond differently to biotic and abiotic drivers. Variability and heterogeneity have been largely simplified in terrestrial biogeochemical models, so the motivation of this dissertation is to explore the consequences of their explicit treatment.

In this chapter I will focus on exploring the issue of strict determinism in ecosystem models. It is not my intent to present here an exhaustive and rigorous analysis, but rather to provide some ideas that could help to reconcile the discrepancy in approaches between the empirical and modeling communities in ecosystem science. This chapter also serves as introduction to the whole dissertation and gives the conceptual support of the different analyses presented in subsequent chapters. Given the theoretical nature of this dissertation, it was necessary to touch on some aspects of philosophy and history of science.

1.1. Background

A little more than fifty years ago a scientific revolution started developing in the biophysical and ecological sciences. A time series of the concentration of CO_2 in the atmosphere has become as iconic as the double helix, $E = mc^2$, or even Leonardo's Mona Lisa (Moore 2002, Briggs 2007). The increasing trend it depicted introduced a new paradigm into the ecological sciences, that of a human-made, rapidly changing environment. Before this new paradigm became a dominant theme, ecosystem ecology was a small and emerging discipline mainly concerned with fluxes of matter and energy in natural systems, dealing with problems such as acid rain, lake eutrophication, and movement of pesticides and radioactive elements. Today the discipline has gained a predominant role in the natural and physical sciences, with the important task of understanding how the cycle of biogeochemical elements are being affected by human actions and how these might be affecting current and future climate.

The positioning of ecosystem ecology within the broader discipline of Earth System Science would not have been possible without the level of mathematical conceptualization that has been accomplished. Mathematical models of ecosystems are the primary tool in ecosystem science for integration of knowledge as well as for communication with other disciplines. Models of the biogeochemistry of terrestrial ecosystems are now being coupled with models of the physics and chemistry of the atmosphere and oceans. These new models are also being used for diagnosing the state of key environmental variables and prescribe possible solutions to global environmental problems.

The current generation of terrestrial biogeochemical models incorporates an intricate mix of equations for different ecosystem processes. Mechanisms for water, carbon and nitrogen cycling are described with systems of differential or difference equations that provide exact solutions for the state of the system in space and time. The approach relies heavily on their numerical implementation in computers and is highly deterministic.

The ecological sciences have a strong tradition of explicitly addressing variability and heterogeneity. Early in the history of ecology, statistics became the primary tool for analyzing field data and framing the scope of the findings. It is therefore puzzling why ecosystem models have developed in a strict deterministic framework. This mismatch of approaches between field research and modeling in ecosystem ecology is a topic that may have been overlooked and deserves more attention. It requires stepping back from our detailed work in our sub-discipline and looking at the whole discipline from above. Like the artist methodically working on the finger of an sculpture, or the musician writing an almost imperceptible oboe melody, they have to stop once in a while and look at the whole sculpture or symphony. It is also helpful in science to stop our detailed work on a specific subject and look at the state of the whole discipline to see how all the pieces fit.

1.2. Ecosystem models and classical mechanics

Some of the first ecosystem models appeared in the 1950s and 60s, representing the ecosystem as a set of pools connected through mathematical relationships. The work of Eugene and Howard T. Odum conceptualizing energy cycling in ecosystems was fundamental for the mathematical representation of ecosystems. At that time, ecosystems were represented in analogy to electrical circuits and the legacy of that work still remains in some ecosystem models. Equally important in the development of ecosystem models has been the work in the area of environmental physiology, which has provided basic equations for the energy, water, and carbon balance of ecosystems.

Deterministic ecosystem models have been highly valued due to their causal connections among variables that allow the researcher to explore whole system behavior under new conditions. This has been particularly useful for exploring the possible response of ecosystems to climatic and other environmental changes. These causal connections among variables are often defined as mechanisms, represented as equations that predict the exact consequences due to a change in the driving variables. In many cases the exact mechanisms are poorly known or are too complex for explicit mathematical treatment. In these cases models incorporate relational solutions that mimic these mechanisms. In general, mechanisms or their approximations are based on some theoretical consideration and contain parameters that need to be estimated for the specific conditions for which the model is applied. Traditionally, parameters are considered as fixed values, but may change in the spatial or temporal domain.

The work of the ecosystem modeler contrasts with the work of the field ecologist, who explicitly deals with variability of the observed data using tools from statistics such as analysis of variance and regression. The statistical models often used in observational or experimental studies are considered of lesser value if they are not based on first biological or physical principles. Rarely, empirical equations are introduced in ecosystem models, and if they are, they omit a fundamental part of the empirical model: the error term. This error term is an explicit account of unexplained variability in empirical models, but given the structure of deterministic ecosystem models it is practically impossible to include it. The same is true for the measures of variability, usually expressed as standard errors, that empirical models present for estimated parameter values

It is clear that there is a fundamental difference between the work conducted in ecosystem science between the modeling and the observational/experimental communities. Ecosystem models are powerful tools for exploring whole system behavior under different assumptions of the driving variables, but omit the variability and heterogeneity that field observations and experiments display. Is this a reconcilable paradox within the discipline? Can a new generation of ecosystem models incorporate the variability and heterogeneity found in experiments and observations?

This paradox between determinism and uncertainty has some similarities with the history of physics at the beginning of the 20th century. Before this time physics was still under the paradigms of Newtonian mechanics, but failed to explain some phenomena such as the mechanics of electrons and atoms. A significant paradigm change was introduced with Heisenberg's uncertainty principle, which led to the development of quantum mechanics. A good perspective on the state of physics at that time can be gathered from this passage from Thomas Kuhn's (1962, p. 84) Structure of Scientific Revolutions:

> *And Wolfgang Pauli, in the months before Heisenberg's paper on matrix mechanics pointed the way to a new quantum theory, wrote to a friend, "At the moment physics is again terribly confused. In any case, it is too difficult for me, and I wish I had been a movie comedian or something of the sort and had never heard of physics." That testimony is particularly impressive if contrasted with Pauli's words less than five months later: "Heisenberg's type of mechanics has again given me hope and joy in life. To be sure it does not supply the solution to the riddle, but I believe it is again possible to march forward."*

Although ecosystem ecology is not concerned with the motion of particles, there are interesting similarities with physics that deserve some attention. The set of equations commonly encountered in ecosystem models are the same type of equations used to describe the dynamics of objects in classical mechanics. In this respect one could say that ecosystem modeling is at a stage of development similar to that of Newtonian physics at the beginning of the 20th century, with the main difference that ecosystem models implement a large set of state variables and parameters in a numerical framework; i.e., with the aid of computers. In fact, the ecosystem models of today are very similar to the mechanical systems that Arthur Tansley envisioned almost 75 years ago when he compared nature with physical entities.

Heisenberg's uncertainty principle and the subsequent development of quantum mechanics introduced a fundamental change in the conceptualization of the physical world. It was realized that the exact position and momentum of particles cannot be estimated exactly and simultaneously, but rather one could make inferences about the probability of their trajectories. It was also a realization that, at certain levels of observation, deterministic predictions were pointless and probabilistic statements more informative.

There have been attempts to introduce concepts from quantum mechanics in ecology, mainly for predicting the dynamics of populations and communities. It has been argued that the relatively low success of applying these concepts was due to the lack of a 'conserved quantity' similar to the total kinetic energy of the molecules in a perfect gas (Maynard-Smith 1974). However, at the ecosystem level such variables exist. Energy, water, carbon and nutrients are quantities that follow the principles of conservation of mass and energy, therefore it is possible to apply the concepts of statistical mechanics in ecosystem ecology. Whether the exact same concepts and tools from quantum mechanics would be useful is a different question, but a change in paradigm from deterministic to probabilistic inference would be an important advancement.

1.3. Variability and uncertainty in ecosystem ecology

As mentioned above, ecology is a discipline that has always been concerned with variability and heterogeneity. In fact, the modeling and observational communities in ecosystem ecology seem to be very aware of the limitations and dangers of strict deterministic predictions (e.g., Clark et al. 2001, Raupach et al. 2005). There are a few ways in which modelers have tried to get around this problem. One is the use of uncertainty analysis, basically producing uncertainty bounds on the predictions based on different techniques such as sensitivity analysis or Monte-Carlo uncertainty estimators (Håkanson 2003). Another way for approaching uncertainty has been through model-intercomparison projects, in which different modeling teams compare their model output (e.g., Melillo et al. 1995, Cramer et al. 2001). More recently, model-data assimilation techniques have become more popular (Raupach et al. 2005, Williams et al. 2005), but are not widely applied.

The goal from all these techniques is the same, to produce an estimate of the uncertainty or variability that cannot be solely explained by the mechanisms included in the model. However, not all modeling results provide a measure of uncertainty of the predictions; and perhaps more problematic, there seems to be confusion about the type of uncertainty that the reported error bars represent: uncertainty in model structure, parameters, driving variables, or numerical implementation? Despite this confusion, it is clear that the paradigm shift is occurring, and although not all model applications currently report prediction uncertainty, a growing number do.

If prediction uncertainty is reported, in theory we can estimate the probability of an event occurring, of a data point to be observed, or the likelihood of the model being right given the observed data. With some exceptions, these types of analyses are rarely done with terrestrial ecosystem models. Even more interesting analyses about the variability of the system or the external drivers can be explored with an explicit treatment of variability in models. For instance, explicit treatments of variability can provide valuable information about the behavior of the system under nonlinear conditions. Small pushes to the system caused by environmental variability can produce significant changes in system behavior, depending on the degree and nature of nonlinearity of the system. In these cases, a basic understanding of the type of environmental variability is needed for predicting possible system behavior. Even for linear systems, a basic knowledge of variability and extreme events is greatly useful.

System heterogeneity is treated explicitly in individual-based or ‘gap’ models. These type of models follow the fate of individual trees over time and have been used successfully for predicting dynamics of populations and communities (e.g., Huston & Smith 1987, Pacala et al. 1996). They also have been used at the ecosystem level for predicting carbon dynamics (e.g., Moorcroft et al. 2001) or the effects of forest management on carbon storage (e.g., Harmon et al. 2009). However, the spatial scale of gap models differs considerably from the resolution of atmospheric models, so their use for global scale questions is very limited. Modeling every individual tree on earth is practically impossible, but important research is currently underway to scale the average behavior of gap models to large spatial domains (Moorcroft et al. 2001, Medvigy et al. 2009).

There are a significant number of tools from probability theory and other disciplines that can help ecosystem ecologists move beyond simple representations of uncertainty in their predictions. In quantum mechanics, probabilistic arguments have been used to describe general laws about particles. Perhaps explicit treatments of variability and heterogeneity can help ecosystem ecologists find general properties of ecosystems that cannot be explained by simpler, homogenous models. Or even more importantly, these ideas could expand the theoretical basis of the discipline by going beyond average representations of system behavior.

1.4. Organization of this dissertation

The main objective of this dissertation is to provide an explicit treatment of variability and heterogeneity in modeling forest biogeochemical cycling. This is accomplished by exploring questions related to ecosystem function under climate change that require explicit accounts of variability. The dissertation consists of three main chapters with separate and independent questions related to issues of variability and heterogeneity in ecosystem modeling. More specifically, variability in model drivers is explored in terms of climatic variability, with a strong emphasis on temperature. Heterogeneity of the system is explored for both a forest stand and a soil system. Throughout the document, the main working hypothesis is that the introduction of environmental variability and system heterogeneity produce behaviors that cannot be obtained when these properties are excluded from models.

1.4.1 Climatic variability

It is common in global change modeling to run an ecosystem model with constant environmental conditions and perturb it to a plausible future scenario. For example, the model can be run with the average climatic conditions for a site and be compared with a run of the average condition predicted for some time in the future. The change to the new climatic condition can also be accomplished by a linear interpolation, or a prescribed scenario predicted by a climate model. These three approaches generally ignore possible changes in the variability of the system (Figure 1.1). At the regional level, climate variability can increase, decrease or remain constant, with implications for the frequency and magnitude of extreme events. The combination of changes in the average and variance of the climate, may expose the system to novel conditions that can have important impacts in system behavior and cannot be predicted by assuming changes in the average climate only.

In this dissertation, changes in the variance of climatic conditions were explored to evaluate the behavior of carbon and nitrogen cycling in forest ecosystems. Chapter 2 contains an analysis of the effects of running an ecosystem model with and without climatic variability. The main focus is on exploring possible effects in the accumulation of carbon and the net fluxes over time. A more detailed analysis of the consequences of temperature variability is performed in Chapter 3, focusing in the soil system and the heterotrophic component of soil respiration.

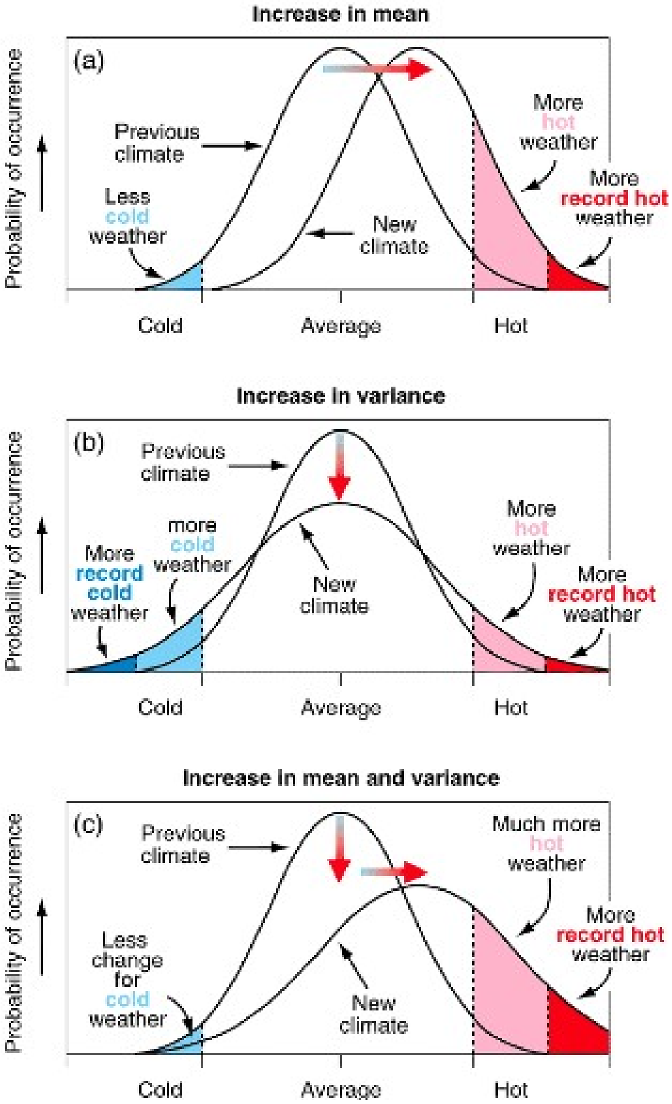

FIGURE 1.1 – Schematic representation of three conceptual approaches to climatic change. Extracted from IPCC (2001).

1.4.2 System heterogeneity

Many ecosystem models assume that the system is homogeneous. For example, leaf physiology is commonly extrapolated directly to entire landscapes and biomes without introducing spatial variability. Similarly, soils are usually considered homogeneous units with the same physical and chemical characteristics over large spatial domains. Heterogeneity can be introduced in ecosystem models representing the entire system as a mosaic of discrete units with different process rates. Interactions among the different units can also be incorporated, creating a level of heterogeneity and connectivity that differs substantially from a simple homogeneous system (Figure 1.2).

Interactive mosaics allow the estimation of the variability of important ecological variables such as net carbon fluxes. In Chapter 2 we focus on the estimation of ranges of variability of carbon fluxes due to the effects of a heterogenous system composed of trees with different recruitment, growth, mortality and decomposition rates. This is accomplished with a gap model that represents a stand of trees growing on a grid with interactive cells. In Chapter 4 we perform a systematic analysis comparing the differences of assuming a homogeneous, a mosaic, and an interactive system. In that chapter, we focus on soil organic matter, evaluating the effects of substrate heterogeneity on the mineralization of carbon and nitrogen.

Interactions of both climate variability and system heterogeneity are evaluated in Chapters 2 and 4. The focus of Chapter 2 is in understanding the interactions of climate variability and gap dynamics that produce variability of net carbon fluxes. Chapter 4 presents a more detailed analysis of the interactions between temperature variability and substrate heterogeneity in soils as it applies to carbon and nitrogen mineralization.

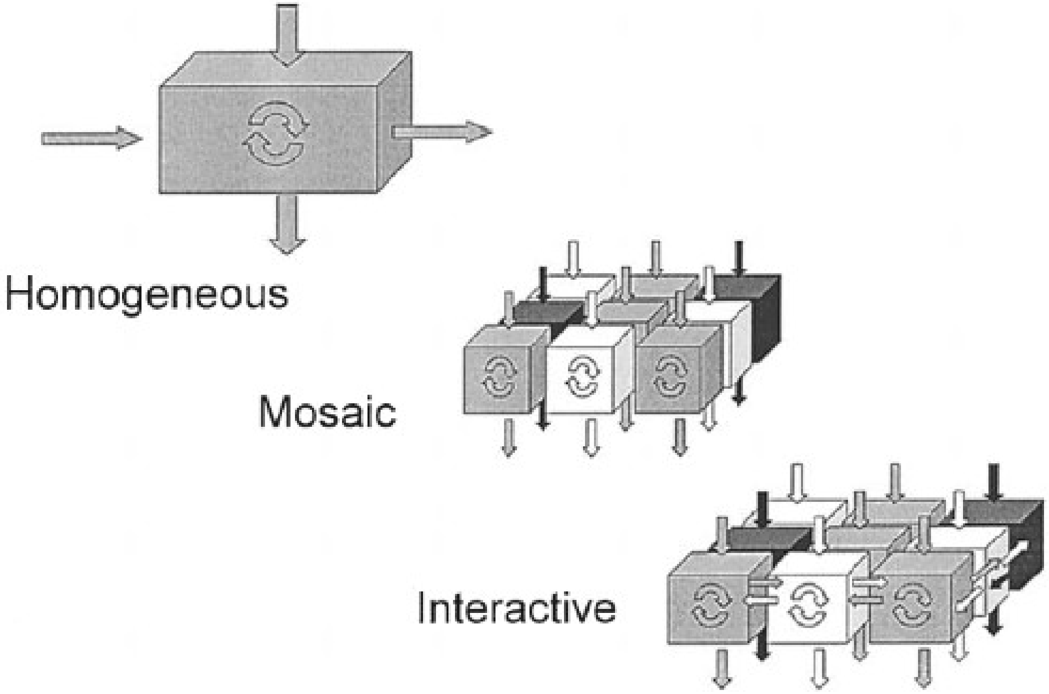

FIGURE 1.2 – Schematic representation of three conceptual approaches to heterogeneity in ecological systems. Extracted from Lovett et al. (2005).

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2. INTERANNUAL VARIATION OF CARBON FLUXES FROM A TROPICAL, A TEMPERATE, AND A BOREAL EVERGREEN FOREST: THE ROLE OF FOREST DYNAMICS AND CLIMATE

2.1. Abstract

Interannual variation of carbon fluxes can be attributed to a number of biotic and abiotic controls that operate at different spatial and temporal scales. Type and frequency of disturbance, forest dynamics, and climate regimes are important sources of variability. Assessing the variability of carbon fluxes from these specific sources can enhance the interpretation of past and current observations. Being able to separate the variability caused by forest dynamics from that induced by climate will also give us the ability to determine if the current observed carbon fluxes are within an expected range or whether the ecosystem is undergoing unexpected change. Sources of interannual variation in ecosystem carbon fluxes from three evergreen ecosystems, a tropical, a temperate coniferous, and a boreal forest, were explored using the simulation model STANDCARB. We identified key processes that introduced variation in annual fluxes, but their relative importance differed among the ecosystems studied. In the tropical site, intrinsic forest dynamics contributed $\sim 30\%$ of the total variation in annual carbon fluxes. In the temperate and boreal sites, where many forest processes occur over longer temporal scales than those at the tropical site, climate controlled more of the variation among annual fluxes. These results suggest that climate-related variability affects the rates of carbon exchange differently among sites. Simulations in which temperature, precipitation, and radiation varied from year-to-year (based on historical records of climate variation) had less net carbon storage than simulations in which these variables were held constant (based on historical records of monthly average climate); a result caused by the functional relationship between temperature and respiration. This suggests that under a more variable temperature regime, large respiratory pulses may become more frequent and high enough to cause a reduction in ecosystem carbon stores. Our results also show that the variation of annual carbon fluxes poses an important challenge in our ability to determine whether an ecosystem is a source, sink, or neutral in regard to CO_2 at longer time scales. In simulations where climate change negatively affected ecosystem C stores, there was a 20% chance of committing Type II error, even with 20 years of sequential data.

Keywords: Ecosystem carbon fluxes, carbon sequestration, climate variability, forest dynamics, carbon sources and sinks, hypothesis testing, ecosystem modeling, old-growth forests.

2.2. Introduction

Terrestrial ecosystems modulate interannual variability in atmospheric CO_2 across the globe (Bousquet et al. 2000, Rodenbeck et al. 2003, Canadell et al. 2007). Inverse simulations of atmospheric CO_2 concentration have identified the magnitude and direction of carbon fluxes at continental scales (Gurney et al. 2004, Jacobson et al. 2007, Stephens et al. 2007). However, it is less clear where the terrestrial biosphere is a carbon source or sink at finer spatial scales. Given that conservation and management of terrestrial ecosystems for carbon sequestration is only logistically feasible in areas much smaller than continents, it is important to improve our understanding on the controls of annual variation in terrestrial carbon budgets at smaller spatial scales.

Within any ecosystem, year-to-year variation in carbon fluxes limits our ability to assess whether an ecosystem is a consistent carbon source or sink. For example, current estimates of carbon fluxes from tropical forests are highly variable; ranging from a moderate source of -2.15 Mg C ha^{-1} yr^{-1} to a large sink of 5.97 Mg C ha^{-1} yr^{-1}, and do not provide any consistent evidence for either a significant source or sink at decadal scales

(Sierra et al. 2007). It is possible that these forests are in a dynamic carbon balance as predicted by classical ecological theory (Odum 1969), in which case the available measurements correctly support the null hypothesis of neutrality, i.e., long-term NEP = 0 in undisturbed ecosystems. However, it is also possible that current observations incorrectly support the null hypothesis (Type II error), in which case external factors such as global change may be in fact altering the equilibrium of these ecosystems (Grace et al. 1995, Phillips et al. 1998). Whichever the case, interannual variability plays a major role in identifying and understanding potential long-term controls on ecosystem carbon budgets.

Several studies have reported significant ranges of interannual variation in carbon flux estimates for a variety of forest types (e.g., Loescher et al. 2003, Chen et al. 2004, Hollinger et al. 2004, Dunn et al. 2007, Richardson et al. 2007), and have identified changes in climate as the main control over variability in ecophysiological processes (mainly production and respiration rates). In some cases, climate can act in concert with ecosystem processes, synergistically enhancing net uptake (Dunn et al. 2007), or fostering net carbon loss (Loescher et al. 2003). Even though it is recognized that species-level processes are important drivers of interannual variability, there is a paucity of research linking variability of species-specific rates of growth, establishment, mortality, and decomposition to annual ecosystem carbon fluxes (Sierra and Harmon 2008). Furthermore, interactions among climatic variables and these intrinsic forest dynamics can lead to more complex, non-linear behaviors not fully explored or understood. Here we focus on how intrinsic forest dynamics and their interactions with climate control interannual variability in net carbon fluxes of old-growth forests. By intrinsic forest dynamics we refer here to the interaction between rates of growth, recruitment, mortality, and decay of the species comprising a plant community within a site. We focus on old-growth forests because their carbon flux is assumed to be in equilibrium according to classical ecological theory (Odum 1969), but current environmental change may be altering this equilibrium state. Departures from equilibrium may be easier to detect in the old-growth phase than earlier in succession when rates of carbon uptake or release are intrinsically high.

The objective of this study was to separate and estimate the degree of variability in carbon fluxes due to internal forest dynamics versus climate, and use these results to explore their possible interactions under future climate change. For this latter analysis, we used a modeling approach and compared our results with observations of carbon fluxes compiled in a recently published global dataset (Luyssaert et al. 2007a).

2.3. Methods

In this study we used the simulation model STANDCARB, which is a hybrid between a gap and an ecosystem model (Harmon and Domingo 2001, Harmon and Marks 2002, Smithwick et al. 2003). It simulates living and dead C pools of forest stands and can be used to examine the effects of climate, forest dynamics, and species succession on carbon dynamics. This model was implemented similarly as the ZELIG model (Urban et al. 1991) in which calculations are made over a grid of cells to simulate interactions between trees such as competition for light. Each cell can be colonized by 4 different layers of plants: herbs, shrubs, lower trees, and upper trees. The lower tree layer represents advanced regeneration and the upper layer dominant trees. Live pools are divided into seven parts within each layer, and six dead pools are derived from the live parts (Harmon and Marks 2002). Dead pools in turn form three stable pools derived from decomposing foliage, wood, and belowground plant parts. The model produces annual estimates of total carbon stores (TCS_i), which is the sum of carbon stores in the live, dead, and soil pools. Carbon fluxes are calculated as the difference in total carbon stores between the current (i) and the previous ($i-1$) year $\Delta\mathrm{C}/\Delta\mathrm{t} = \mathrm{TCS}_i - \mathrm{TCS}_{i-1}$. A detailed model description can be found in Appendix A as well as in Harmon and Domingo (2001), Harmon and Marks (2002), and Smithwick et al. (2003). We used STANDCARB to simulate carbon dynamics of three contrasting evergreen forest types: a tropical forest, a temperate coniferous forest, and a boreal evergreen forest. For the tropical forest, parameters related to growth, recruitment, mortality, and decay were chosen to reproduce the behavior of four distinctive functional species groups, late and early successional trees, palms, and legumes. For the temperate coniferous forest we chose parameters to simulate two common species found in conifer dominated forests of the Pacific Northwest, Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*). For the boreal forest, we simulated the plant community common in mixed conifer-hardwood forests of northern Maine, white pine (*Pinus strobus*), paper birch (*Betula papyrifera*), balsam fir (*Abies balsamea*), red spruce (*Picea rubens*), eastern hemlock (*Tsuga canadensis*), northern white cedar (*Thuja occidentalis*), and red maple (*Acer rubrum*).

Simulations were performed over a spatial grid of 20 x 20 cells, with 17 m cell width and with 10 replicates per simulation, representing 10 plots of ~11 ha each. We used existing climate records from these three forest types to simulate climate variability over a 2000 year period assuming no long-term trend. For the tropical forest we used 14 years of climatic data from the Porce region of Colombia (6° 45′ N, 75° 06′ W), and for the temperate forest we used 34 years of data from the H.J. Andrews LTER site in western Oregon (44° 12′ N, 122° 15′ W). The boreal forest was simulated using 50 years of climatic data from Millinocket, Maine to represent processes at the nearby Howland Research Forest (45° 12′ N, 68° 44′ W).

Three different sets of simulation experiments were run in STANDCARB to separate the effects of forest dynamics and climate variation, hereafter called (1) constant mortality, (2) constant climate, and (3) variable climate scenarios. First, in the constant mortality scenario, the model was run using a constant mortality rate independent of competition among cells, but having random variation in the climatic data series. Long-term climatic data series were created by adding random variates (anomalies) to monthly climatic averages. Anomalies were generated using the observed monthly and annual standard deviations from the local datasets, assuming normal distributions. Second, in the constant climate simulations, the model was run with mortality represented as a competition driven processes with a stochastic component (see Appendix A for details). The long-term average mortality rate was equal to that in the previous simulation set. The climatic data series used in this scenario consisted only of monthly climate averages. Third, in the variable climate simulation set, we combined both the variation introduced by a variable climatic dataset with the variation introduced by stochastic and competition driven mortality. Results from these simulation experiments were used to create hypothetical probability distribution functions (PDFs) of average carbon fluxes at steady-state. We created 95% confidence intervals of the average carbon flux by estimating the interval that contains 95% of the area under the PDF.

The simulated time series of annual carbon fluxes were then used to sample random data points and test whether or not the selected series would reject the null hypothesis of equilibrium; i.e. average $\Delta \mathrm{C}/\Delta \mathrm{t} = 0$. Consecutive data points were randomly selected in the interval 1001-2000 years, after the ecosystems reached steady-state, in intervals from 2 to 50 years. This sampling procedure was repeated 100 times for each interval of consecutive data, from 2 to 50 years. For each time interval of consecutive points, we tested the null hypothesis $\Delta \mathrm{C}/\Delta \mathrm{t} = 0$ with a *t*-test, and used the 100 repetitions to calculate the proportion of times in which the null hypothesis was either rejected or not rejected. The standard deviation in the *t*-test was adjusted for serial correlation using the factor $\sqrt{(1+r_1)/(1-r_1)}$, where r_1 represents the first order autocorrelation coefficient (Zwiers and von Storch 1995, Ramsey and Schafer 2002). Given that we know a priori that in our simulations the null hypothesis is true, we interpreted the proportion of rejections as the probability of incurring a Type I Error, i.e., rejecting the null hypothesis when it is true.

TABLE 2.1 – Summary statistics, average ± standard deviation, of the simulations with constant and variable climate for the three forest types evaluated.

Forest type	Constant mortality	Constant climate	Variable climate
Tropical	0.005 ± 1.262	-0.001 ± 0.257	0.001 ± 0.887
Temperate	0.045 ± 1.832	0.001 ± 0.116	0.004 ± 1.375
Boreal	-0.001 ± 0.780	0.002 ± 0.087	-0.004 ± 0.455

In a fourth set of simulations, we created new climate time series for each site by increasing temperature 6°C across 100 years, and incorporating the natural variability found in the empirical datasets. Simulations were run using the climatic data from the variable climate scenario for 1000 years to allow the ecosystems to reach steady-state before perturbing the system with the new climatic time series containing the temperature increase. We used the results of this set of simulations to also test the hypothesis ΔC/Δt = 0 as above, and calculate the probability of incurring in Type II error, i.e., not rejecting the null hypothesis when it is false.

2.4. Results

All simulations reproduced the pattern of successional development predicted by classical ecosystem models (Odum 1969, Bormann and Likens 1979). At early stages of development, our modeled ecosystems accumulated carbon at high rates until reaching a maximum, then declined slightly to reach steady-state (Bormann and Likens 1979) where the long-term average net carbon flux (over 100s of years) was ∼0 Mg C ha^{-1} yr^{-1} (Figure 2.1, Table 2.1).

The highest level of interannual variation was observed under the constant mortality scenario, where climate was the only factor responsible for the variability of carbon fluxes (Table 2.2). Varying internal forest dynamics (i.e., mortality) under a constant climate

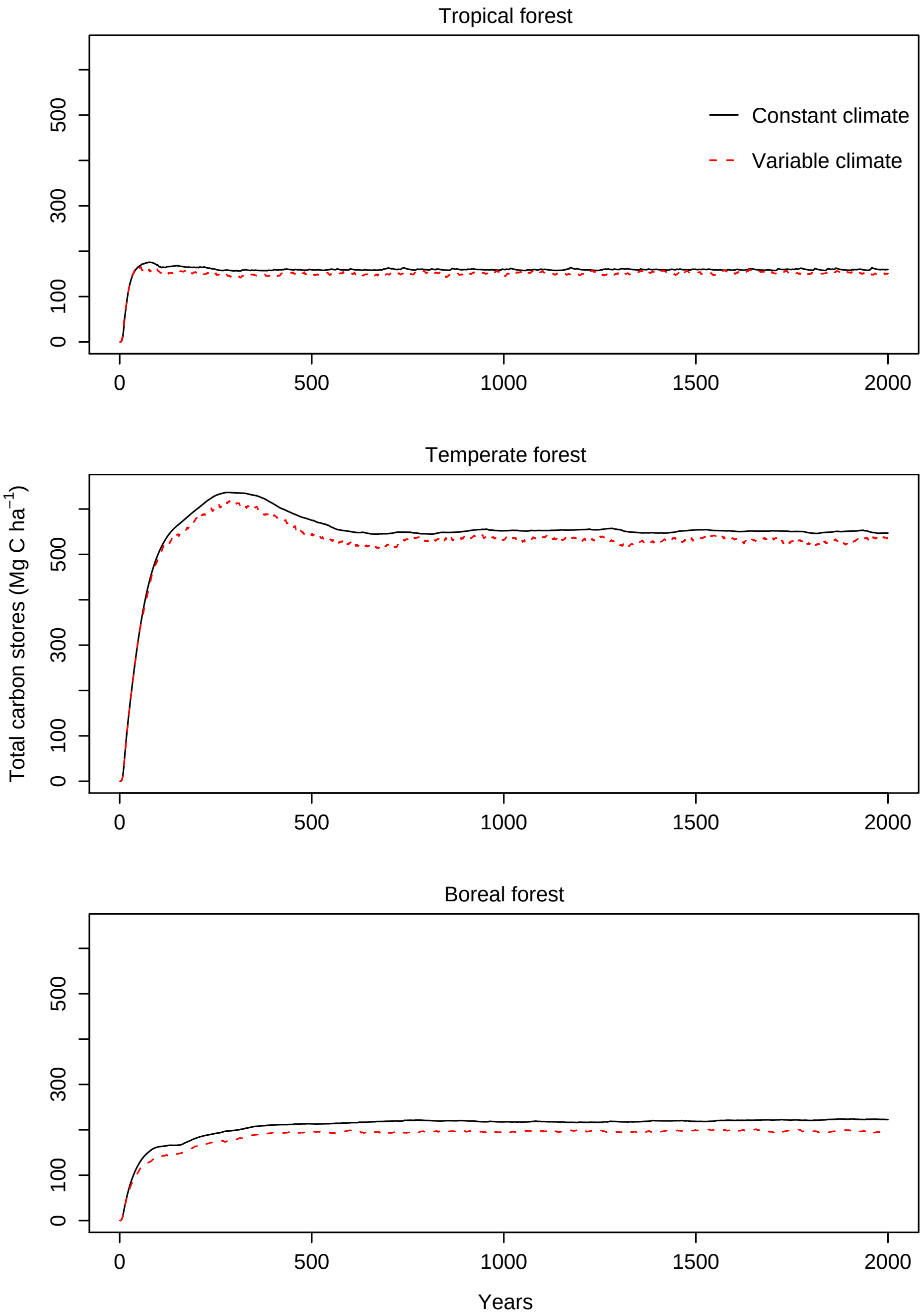

FIGURE 2.1 – Simulation results of total carbon stores for a tropical (upper panel), a temperate (middle panel), and a boreal forest (lower panel). Black continuous lines represent simulations in which climate was held constant. Red dotted lines represent simulation in which climate was variable according to observed climatic records.

TABLE 2.2 – Variation of annual carbon fluxes attributable to climate (σ_c^2), mortality (σ_m^2), and their interaction (σ_{cm}^2) in a tropical, a temperate, and a boreal forest. Percentage values compare contributions from climate, forest dynamics (i.e., mortality), and their interaction to overall variability, calculated as: % Climate alone = $100\sigma_c/\sigma_{cm}$; % Forest dynamics = $100\sigma_m/\sigma_{cm}$, and; %Climate interaction = $100\,(1-(\sigma_m/\sigma_{cm}))$.

Source of variability	Tropical	Temperate	Boreal
σ_c^2	1.595	3.357	0.636
σ_m^2	0.066	0.013	0.08
σ_{cm}^2	0.787	1.891	0.207
Climate alone (%)	142	133	175
Forest dynamics (%)	29.0	8.3	19.6
Climate interaction (%)	71.0	91.7	80.4

had only minor effects on carbon flux variation, but played a key role in shaping flux variation under a variable climate. Variability due to internal forest dynamics was higher in the tropical site than in the temperate site, which in turn was higher than the boreal site (Tables 2.1 and 2.2). However, variability due to climate did not follow this trend. The highest variability due to climate was found in the temperate coniferous forest (Figure 2.2).

For the three sites simulated, Total Carbon Stores at steady-state were lower using the variable rather than the constant climate scenario (Figure 2.1). This difference in carbon stores was observed in the live, dead, and soil organic matter pools (Appendix D), rather than just one single pool. This suggests that respiration, a process common to all pools, was more sensitive than other processes to the variation in the climatic data series. In STANDCARB, respiration is modeled with a Q_{10} function to represent the effect of temperature on the rates of autotrophic and heterotrophic respiration (Ryan 1991). Respiration is an increasing convex function of temperature, therefore its expected value using a random variable does not provide the same results as the value of the function using the expected value of the random variable ($f(E(x)) \neq E(f(x))$, see Appendix B for a mathematical proof) (see also Rastetter et al. 1992, Ruel and Ayres 1999, Peters et al.

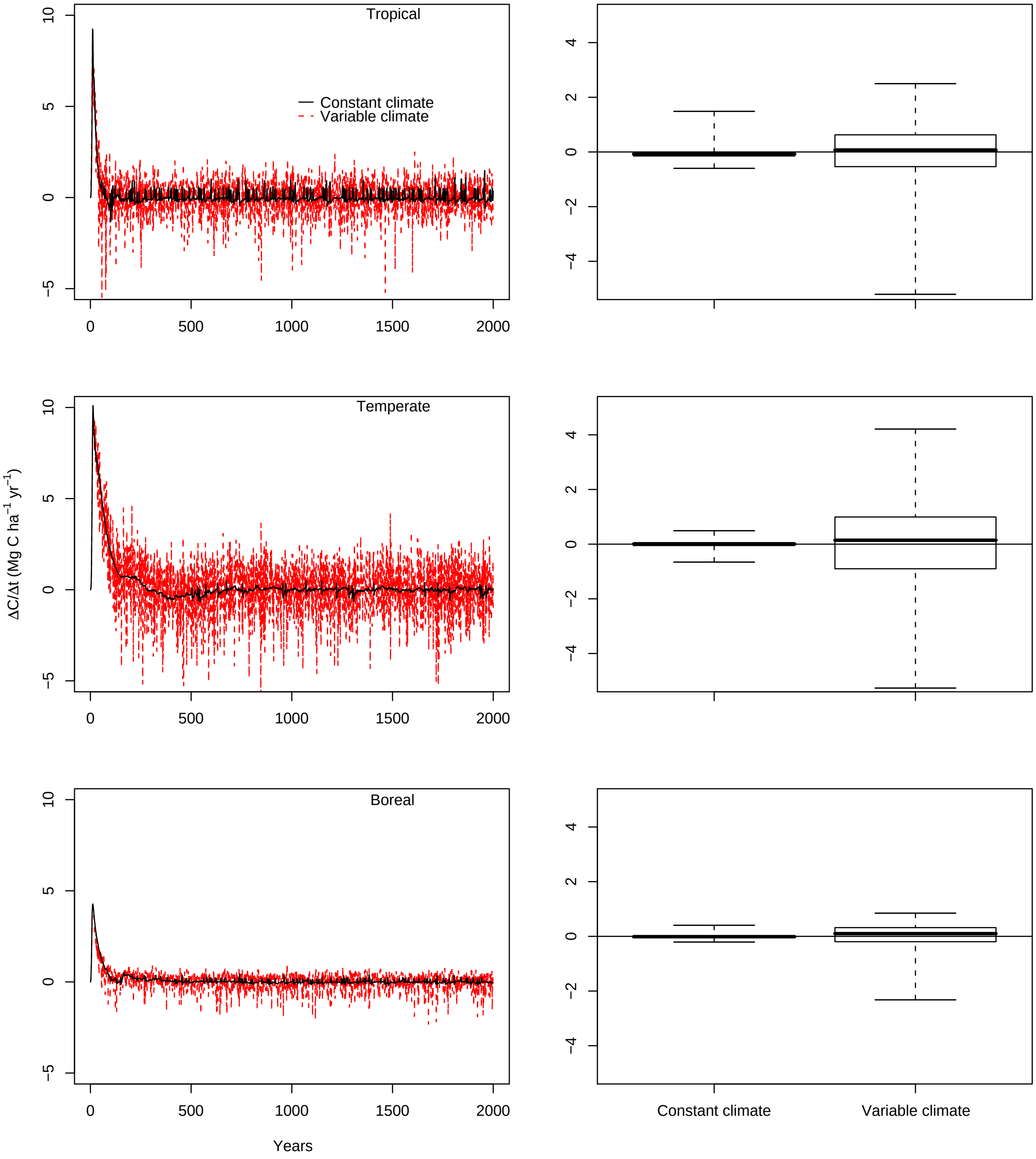

FIGURE 2.2 – Simulation results of annual net carbon fluxes (ΔC/Δt) for a tropical (upper row), a temperate (middle row), and a boreal forest (lower row). Carbon fluxes are represented as time series in the left column and box-plots in the right column. Boxes enclose upper and lower quartiles, and lines extend to maximum and minimum values.

2004, Ross 2006). Although STANDCARB also models the relationship between temperature and photosynthesis, its functional relationship is not strictly convex or concave in the interval of temperatures being examined.

2.4.1 Hypothetical ranges of variation

At steady-state, carbon fluxes vary in a range of values around 0 Mg C ha^{-1} yr^{-1} as a result of internal forest dynamics and climate (Figure 2.2). We used these simulation results to produce hypothetical ranges of variation of average carbon fluxes from the three different forest types (Figure 2.3). We assumed that, at steady-state, average carbon fluxes are approximately zero and normally distributed. When considering variability due to forest dynamics alone, we were 95% confident that average carbon fluxes in the tropical forest at steady-state ranged ±0.5 Mg C ha^{-1} yr^{-1}. Combining the effects of forest dynamics and climate variation, this 95% confidence interval increased to ±1.74 Mg C ha^{-1} yr^{-1}. For the temperate forest the difference between the two confidence intervals was higher, increasing from ±0.23 to ±2.7 Mg C ha^{-1} yr^{-1} (Figure 2.3). Confidence intervals for the boreal site were low compared to the other two sites, with forest dynamics introducing variation in the range of ±0.17 Mg C ha^{-1} yr^{-1}, and climate in the range of ±0.89 Mg C ha^{-1} yr^{-1}.

2.4.2 Consequences for hypothesis testing

The probability of incurring a Type I Error decreased as the length of the time series evaluated increased. This probability was below the confidence level of the hypothesis test ($\alpha = 0.05$) only after ∼10 years of consecutive flux data for the tropical forest, ∼20 years for the temperate forest, and ∼35 years for the boreal forest (Figure 2.4). For time series shorter than 10 years the probability of incurring a Type I error was between 5 and 17%.

An increase in average temperature of 6°C over 100 years caused a decline in TCS for the three ecosystems (Figure 2.5). The decline in TCS was more evident for the

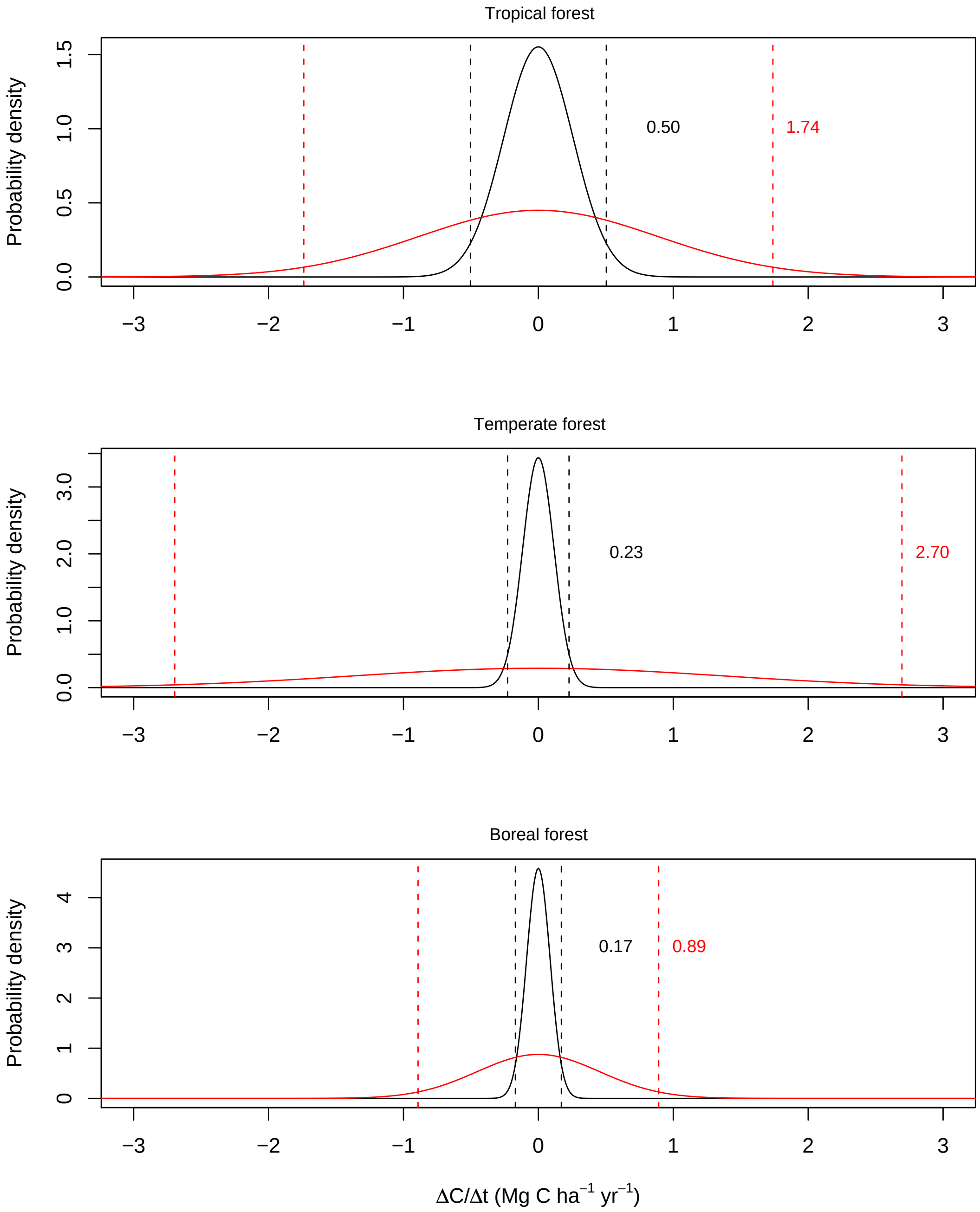

FIGURE 2.3 – Hypothetical ranges of variation of annual net carbon fluxes (ΔC/Δt) considering forest dynamics (black lines) and the interaction between climate and forest dynamics (red lines). Continuous lines represent probability density functions and dotted lines enclose 95% confidence intervals. Values next to dotted lines are upper 95% confidence limits.

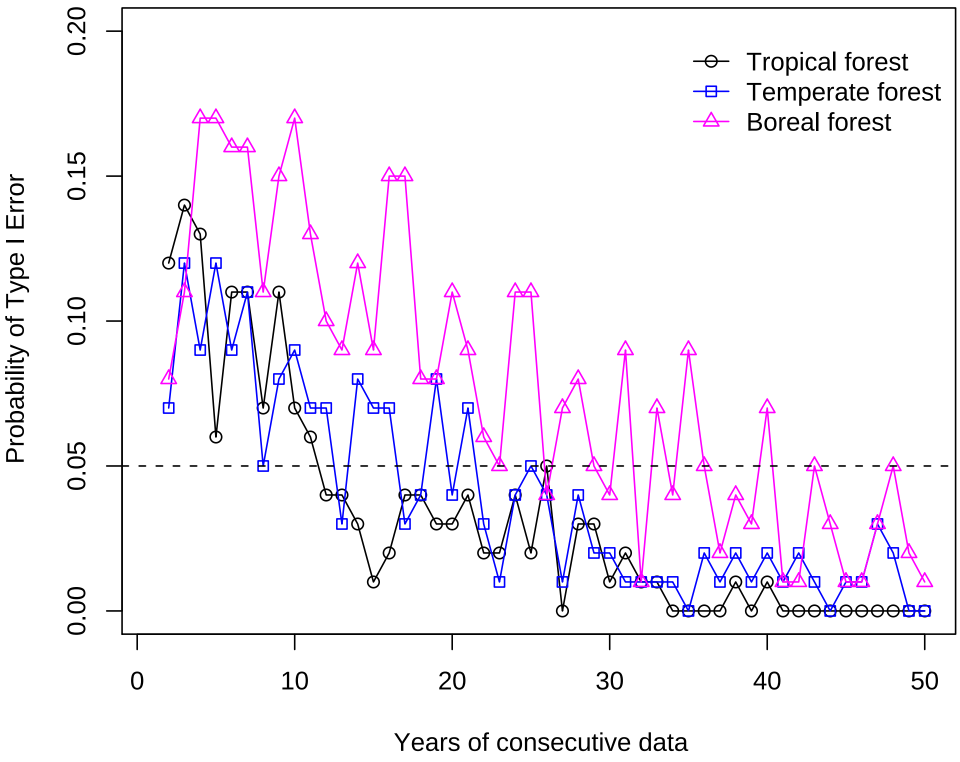

FIGURE 2.4 – Probability of Type I Error after sampling consecutive years of the time series presented in Figure 2.2 when the forest reaches equilibrium (years 1001 to 2000). For each number of consecutive years, Type I Error was calculated as the number of times that the hypothesis H0: NEP = 0 was rejected from a total of 100 t-tests with $\alpha = 0.05$ (dotted line).

temperate forest than for the tropical site. However, trends in ecosystem carbon fluxes were not as evident as for TCS given the large degree of observed interannual variability (Figure 2.5). These simulations indicate that there are high probabilities of not rejecting the null hypothesis when the alternative hypothesis is true (Figure 2.6). In other words, our results suggest that even with more than 10 years of consecutive flux data there are high chances of not observing a significant and real emission of carbon from these ecosystems.

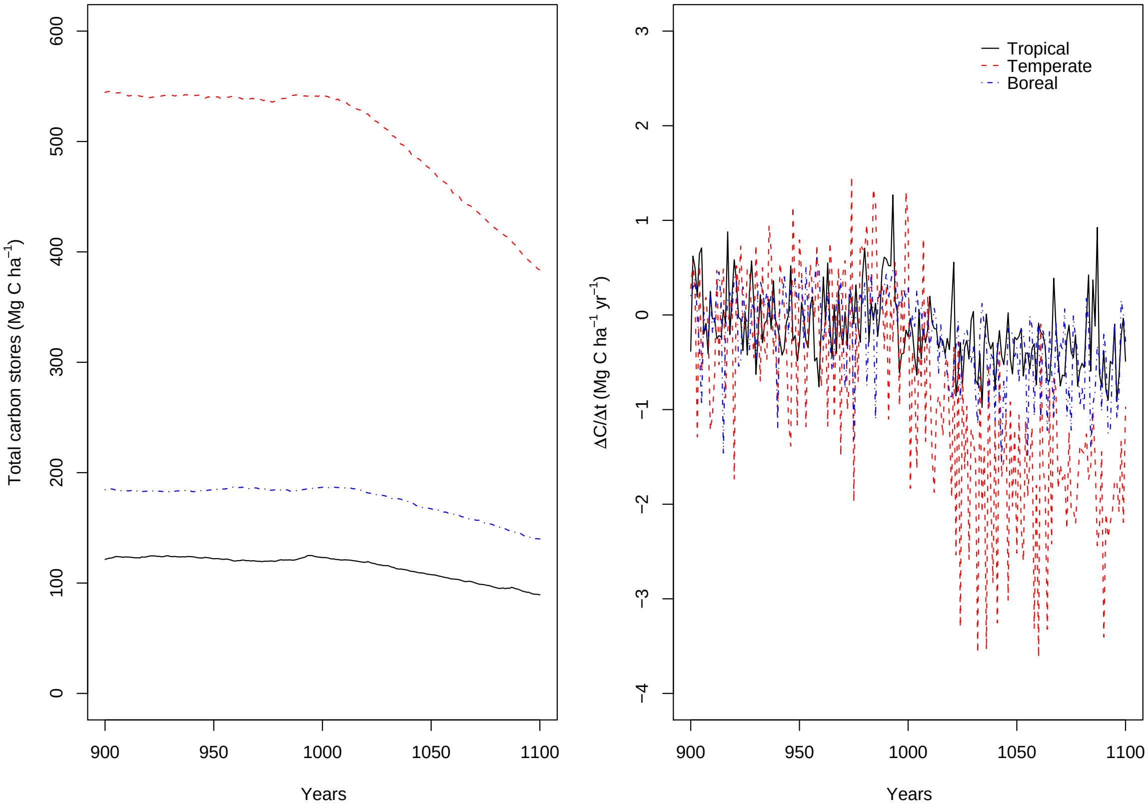

FIGURE 2.5 – Simulation results of Total Carbon Stores (TCS, in Mg C ha^{-1}) and annual net carbon fluxes ($\Delta C/\Delta t$, in Mg C ha^{-1} yr^{-1}) for a set of simulations in which temperature was increased by an average of 6°C in 100 years. In all cases the model was run for 1000 years to reach steady-state before applying the climate change function.

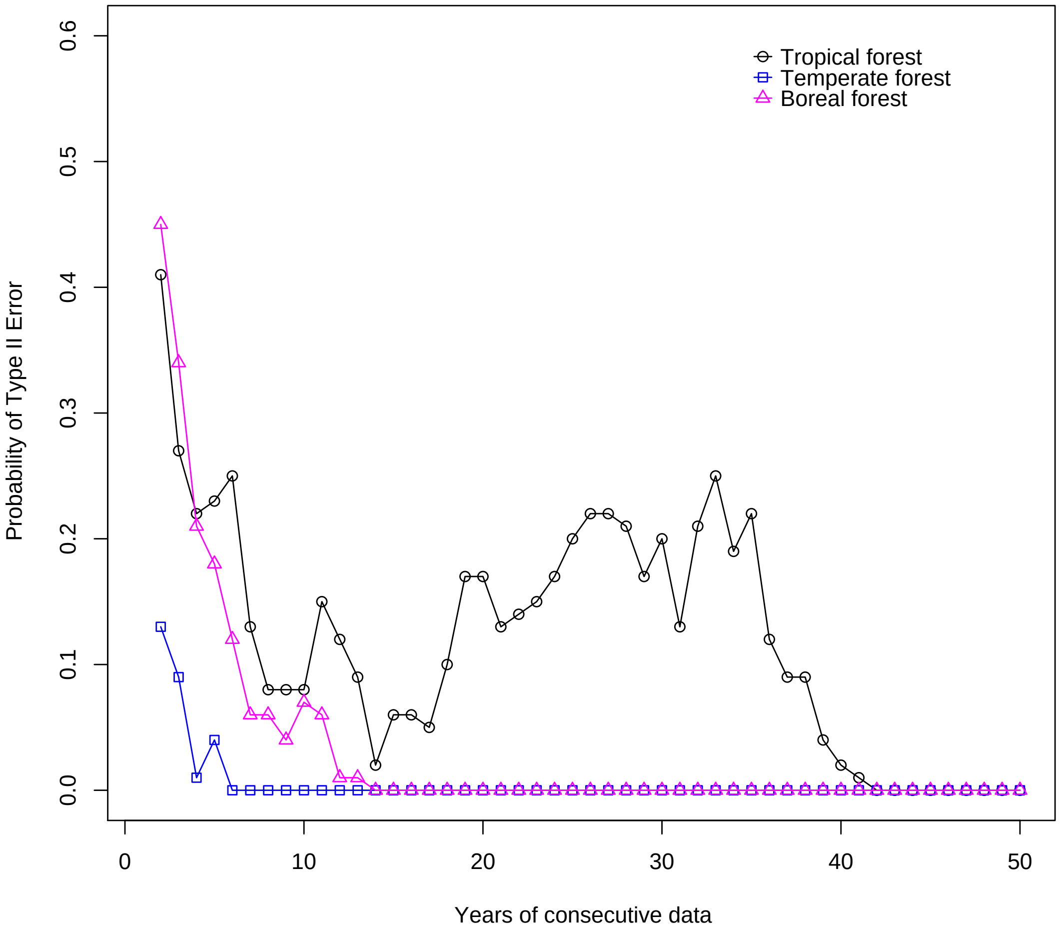

FIGURE 2.6 – Probability of Type II Error after sampling consecutive years of the time series presented in Figure 2.5 when the forests experienced a temperature increase of 6°C for 100 years (years 1001 to 1100). For each number of consecutive years, Type II Error was calculated as the number of times that the hypothesis H0: NEP = 0 was not rejected from a total of 100 t-tests with $\alpha = 0.05$.

2.5. Discussion

We used a hybrid ecosystem-gap model to examine the level of interannual variation of carbon fluxes attributable to internal forest dynamics versus climate in forests at their equilibrium phase. Although modeling is just one approach to this problem, we believe it can provide important insights that can complement and guide observational studies and field experiments. Here, we focused on long-term process as opposed to short-term physiological dynamics common in many biogeochemical models. Results from other models can be compared with the results presented here to evaluate uncertainties associated with processes that are not represented explicitly in STANDCARB.

It is also important to point out that the predictions obtained in this study are not necessarily predictions of the carbon balances of these particular sites into the future. Our aim was to model three contrasting evergreen ecosystems with different internal forest dynamics and climate, and to observe the resulting emergent behaviors of the interannual variability in carbon exchange.

2.5.1 Forest dynamics and carbon fluxes

In this analysis we found that internal forest dynamics can contribute as much as 30% to the total interannual variation of ecosystem carbon fluxes (Table 2.2). Although this contribution varies among forest types and is scale dependent (smaller plots could have larger variability), it is a source of variability that is often ignored in analyses of long-term carbon flux data. Climate obviously played a dominant role in explaining interannual carbon fluxes, but forest dynamics can potentially modulate or amplify the signal attributable to climate. The comparison between constant mortality and variable climate clearly shows a modulation effect (Table 2.1). Furthermore, should climate remain relatively constant for a series of years, some level of variation in carbon fluxes can be expected because of stochastic mortality alone, even in systems that are supposed to be in steady-state.

The paradigm that old-growth forests are carbon neutral (Odum 1969, Bormann and Likens 1979) has often been challenged (e.g., Grace et al. 1995, Malhi et al. 1999, Luyssaert et al. 2008). However, our results suggest that old-growth forests in a state of dynamic equilibrium can have a significant range of variation around an average carbon flux of 0 Mg C ha^{-1} yr^{-1} (Figure 2.2). Consequently, forests can behave as carbon sources or sinks for short periods of time (years to decades), without departing from steady-state in the long-term. This system behavior can complicate the interpretation of short-term data or observations with relatively high measurement uncertainties.

Forest dynamics play a significant role in determining the structure of forest ecosystems and the level of spatial heterogeneity of the overstory, creating what is known as the 'forest mosaic' (Shugart 1998) or the 'shifting mosaic steady-state' (Bormann and Likens 1979). Individual patches may respond differently to environmental conditions according to their successional stage. For example, a recently opened gap will respond to a temperature increase with a larger amount of carbon release than a closed-canopy because the photosynthetic component is reduced in the gap. Consequently, the overall response of the ecosystem to a change in the environment will likely depend on the structure of the forest mosaic, and the relative contribution by the different patches in terms of photosynthesis and respiration.

The simulation results showed a consistent reduction of the variability in carbon fluxes due to intrinsic forest dynamics from the tropical to the boreal sites (Figure 2.3). This trend is an indication that internal forest dynamics play a larger role in 'faster' systems such as tropical rain forests. It also suggests that short-term climatic fluctuations will play a larger role in determining carbon fluxes in 'slower' systems such as boreal forests (here we consider a system 'fast' or 'slow' in terms of the relative magnitude of different process rates among ecosystems).

2.5.2 Interannual climate variability and carbon fluxes

Variability in environmental conditions occurs over daily, seasonal, annual, and even longer time scales. Reichle et al. (1975) hypothesized that ecosystems maintain a dynamic equilibrium with a varying environment through multiple non-linear interactions among ecosystem components. Similar ideas are embedded in the concepts of resilience and stability (Holling 1973, 2001). Specifically, there are multiple homeostatic mechanisms by which ecosystems will maintain a dynamic equilibrium with the environment. In terms of energy or carbon storage, this dynamic equilibrium depends directly on the frequency and amplitude of environmental variations and disturbances. Hypothetically, the maximum carbon storage in an ecosystem will tend to decrease from the maximum potential storage as frequency and severity (amplitude) of environmental fluctuations and disturbances increase (O'Neill et al. 1975, Reichle et al. 1975). The results observed in Figure 2.1, in which TCS were lower in the variable climate scenario, support this hypothetical behavior.

Recent syntheses and local studies have shown that climate plays an important role in controlling the variation of carbon fluxes at small spatial and temporal scales (Goulden et al. 1996, Law et al. 2002, Luyssaert et al. 2007a, Luyssaert et al. 2007b, Richardson et al. 2007). In general, climatic variables can explain up to 80% of the short-term variation in carbon fluxes, e.g., 30 minute flux averages within a site (Clark et al. 1999, Loescher et al. 2003, Hollinger et al. 2004), but explain $< 50\%$ when scaled to longer time intervals or across sites (Law et al. 2002, Luyssaert et al. 2007a). From the perspective of hierarchical theory (Allen and Starr 1982), processes controlled by high frequency environmental factors should be constrained by factors operating at lower frequencies. Processes related to forest dynamics such as individual turnover rates operate at lower frequencies than many climatic variables; therefore they can constrain the direct effects caused by short-term environmental fluctuation over long periods of time. Other factors that may constrain carbon fluxes at higher hierarchical levels are plant species succession, nutrient accumulation or depletion, and cycles in herbivore and pathogen populations.

Analyses of long-term climate records have shown that regional increases in temperature are also accompanied by short-term high-frequency variation (e.g., Esper et al. 2002, Luterbacher et al. 2004). Future temperature increases at the regional level will be most likely accompanied by a significant level of interannual variation. Our analysis showed that carbon fluxes can also show an important level of interannual variation under long-term temperature increase. Detection of systematic trends in carbon fluxes can be problematic because most of our current knowledge on the state of the global carbon cycle is derived from studies that measure carbon fluxes rather than trends in total carbon stocks TCS (Friend et al. 2007, Luyssaert et al. 2007a), with both methods potentially subject to significant sources of measurement error (Loescher et al. 2006). We found that for systems in dynamic equilibrium and then exposed to a systematic climatic disturbance, the probability of detecting a statistically significant and consistent trend in carbon fluxes could take as much as 20 to 30 years of continuous data collection. A decline in carbon storage was most pronounced for the temperate coniferous site where respiration rates are generally low but can increase dramatically with increases in temperature (Figure 2.5). For the tropical site where temperatures and respiration rates are already high the probability of not observing the effects of temperature increase are very low (Figure 2.6). These results reflect our focus on statistically testing the null hypothesis of flux equilibrium at three separate measurement sites. Multiple measurements within a site and other analyses such as model-data assimilation, boundary-layer approaches, or complete inventory methods may provide additional insight into forest carbon balances at shorter time scales. In the long-term, however, time series of carbon fluxes should at least cover the phase of decadal or multi-decadal oscillations in climate such us those related with ENSO and the North Atlantic Oscillation.

2.5.3 Building on Odum's equilibrium concept

The concept of equilibrium in ecosystem ecology (e.g., Odum 1969) can be interpreted narrowly as a static view of the relationship between an ecosystem and its external environment. However, more explicit treatments of equilibrium concepts typically recognize some level of variability at the equilibrium stage. Bormann and Likens (1979) concept of shifting mosaic steady state recognizes this level of variability, as well as the concepts of resilience and stability as defined by Holling (1973). The concepts of engineering and ecological resilience focus on the existence of one or multiple stability domains (Gunderson 2000), however, in both concepts there is a level of variability around the stable state(s) that can be quantified within the framework proposed here. The ranges of variation identified in this manuscript are simply a quantification of these stability concepts in a probabilistic framework. For example, the ranges of variability of NEP could be interpreted as the width of the valleys of attraction in the common representation of the resilience concept. Evidence supporting gradual or sudden changes in the state of an ecosystem away from the expected range of stability would be indicative of an important disruption of a stable state, and perhaps a shift to an alternative stable state (Gunderson 2000, Scheffer et al. 2001). So the value of the concept of equilibrium (or steady state, or stable state) resides in its applicability for testing alternate hypotheses about ecosystem change (Scheffer et al. 2001).

2.5.4 Other implications

Measurements of carbon fluxes in forest ecosystems demonstrate an important degree of variability (Table 2.3). Many short-term individual studies are often used to infer a source or sink of carbon over the decadal-scale or longer-term. Our analysis shows that short-term measurements are subject to either Type I or Type II Error. To avoid erroneous interpretations of current measurements it has to be acknowledged that ecosystem functions are intrinsically variable. When determining whether an old-growth ecosystem is a significant carbon source or sink, it would be more informative if the null hypothesis of a near equilibrium carbon flux were stated (and tested) in terms of an expected range instead of a single static quantity. A null hypothesis stated as H0: NEE = 0, does not consider the inherent variability that would occur naturally in the system. Sierra et al. (2007) proposed an alternative way to state this hypothesis using Bayesian statistics considering that carbon fluxes vary spatially and temporally. Equilibrium under this proposed method is represented as a null hypothesis in which the average carbon flux lies within an arbitrary range around zero (H0: NEP $\sim N(\mu, \sigma^2)$). It is convenient to use Bayesian statistics and arbitrary a priori information to test this hypothesis since different ranges of variation around equilibrium can be used. The degree of variation of carbon fluxes among ecosystems could differ due to dissimilarities in climate and disturbance regimes, and also as a consequence of intrinsic properties of the populations of species occupying the system.

For example, observed carbon fluxes in unmanaged tropical, temperate, and boreal forests show a high degree of variability (Table 2.3). The variability observed in these studies is not only caused by forest dynamics and climate, but also by a number of environmental factors within biomes and uncertainties associated with measurements. We compared these observations with the ranges of variability found in this study for the three different biomes using the Bayesian approach proposed in Sierra et al. (2007). The approach consists of finding the probability of the carbon flux given the observed data P(NEP | NEP*). The hypothetical ranges of variation were used as prior information about the expected range for NEP. The posterior probabilities obtained in this comparison provided little evidence for carbon fluxes in old-growth forests outside the range predicted for forests in equilibrium (Figure 2.7). For tropical forests the probability of the average NEP being higher than the upper bound of the hypothetical range (1.74 Mg C ha^{-1} yr^{-1}) is only 4.3%. For temperate forests the probability of NEP higher than 2.70

TABLE 2.3 – Estimates of NEP for different late successional-unmanaged forests in the boreal, temperate, and tropical biomes. Extracted from Luyssaert et al. (2007) database.

Plot/site name	Climatic region	Weighted NEP	Uncertainty NEP	Latitude	Longitude
Tropical forests					
Porce	Tropical Humid	-0.91	3.50	6.75 N	75.10 W
Jacaranda/K34	Tropical Humid	0.50	4.95	2.60 S	60.20 W
Guyaflux	Tropical Humid	1.51	1.05	5.28 N	52.91 W
Cuieiras/C14	Tropical Humid	4.72	0.53	2.58 S	60.10 W
Caxiuana	Tropical Humid	5.60	2.10	1.72 S	51.45 W
Tapajos 67	Tropical Semi-arid	-1.12	0.28	2.81 S	54.95 W
Tapajos 83	Tropical Semi-arid	-0.63	1.21	3.00 S	54.95 W
Mean		1.38	0.91		
Temperate forests					
Andrews 12	Temperate Humid	-1.29	3.50	44.26 N	122.18 W
Andrews 11	Temperate Humid	-0.90	3.50	44.23 N	122.18 W
Cascade Head 10	Temperate Humid	1.68	3.50	45.07 N	123.89 W
Cascade Head 12	Temperate Humid	1.94	3.50	45.04 N	123.90 W
Cascade Head 11	Temperate Humid	3.47	3.50	45.08 N	123.90 W
Wind River	Temperate Humid	3.87	0.53	45.52 N	121.57 W
Mean		1.46	1.27		
Boreal forests					
Fyedorovskoye	Boreal Humid	-2.31	0.35	56.45 N	32.92 E
Sodankylä	Boreal Humid	-0.63	0.21	67.36 N	26.64 E
Niwot Ridge	Boreal Humid	0.71	1.05	40.03 N	105.53 W
Yenisey Abies	Boreal Humid	2.70	1.05	61.02 N	89.76 E
Thompson NSA (NOBS)	Boreal Semi-arid	0.004	0.09	55.90 N	98.47 W
Prince Albert SSA (SOBS)	Boreal Semi-arid	0.64	0.25	53.92 N	104.68 W
Howland	Boreal Humid	1.90	0.08	45.20 N	68.74 W
Mean		0.43	0.23		

Mg C ha^{-1} yr^{-1} is 1.2%, and for boreal forests the probability of NEP higher than 0.89 Mg C ha^{-1} yr^{-1} is 2.2%. For the temperate forests, however, the probability of a carbon source is less than 10%, and the obtained probability distribution may be indicative that these forests have been moved to an alternate state.

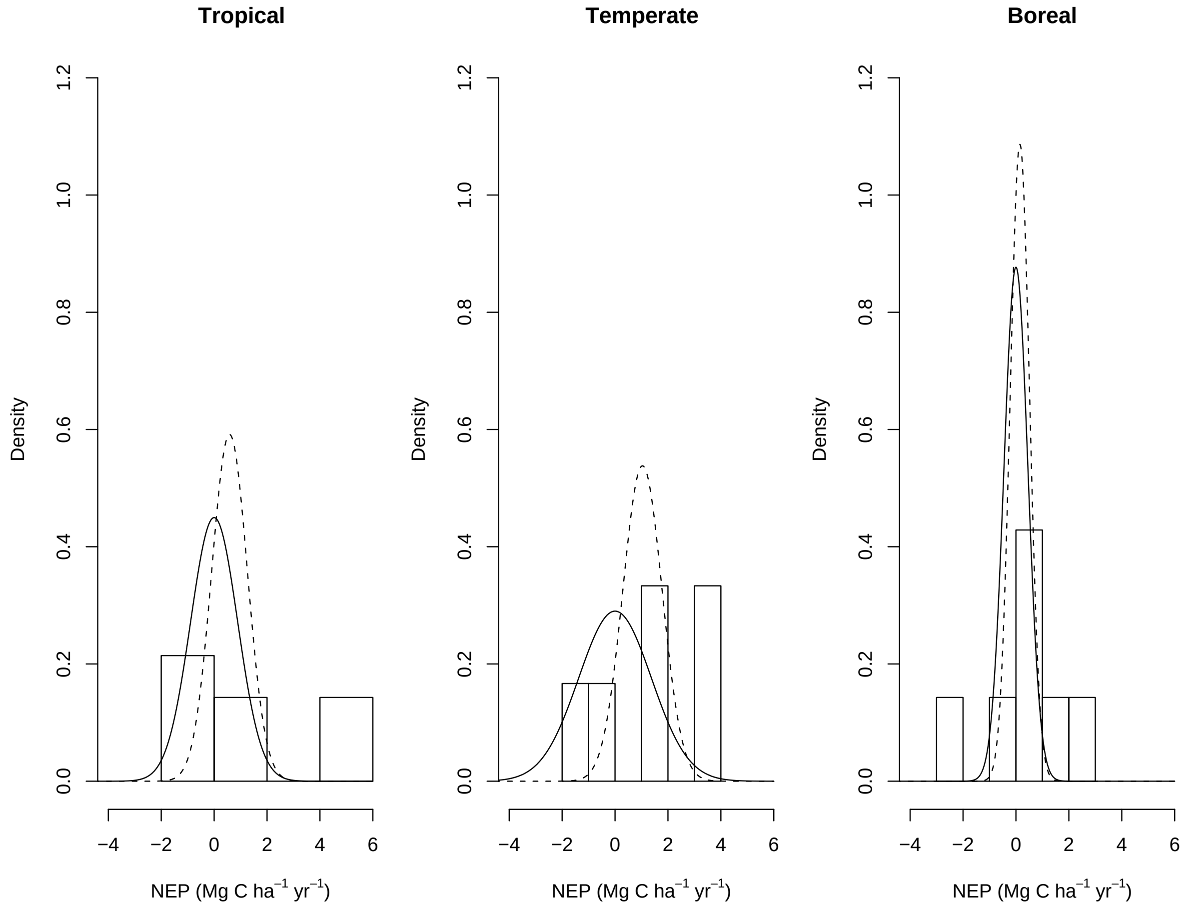

FIGURE 2.7 – Comparison between measured Net Ecosystem Production (NEP) in unmanaged boreal (n = 6), temperate (n =7), and tropical (n = 8) forests and the hypothetical ranges of variation found in this study. Histogram bars represent the measured data for different sites within the biomes, the continuous line represent the hypothetical ranges from this study and the dashed line represent the posterior distribution of NEP based on the data and the hypothetical ranges. Data extracted from Luyssaert et al. (2007) database.

Spatial heterogeneity in ecosystems that results from forest dynamics and temporal climatic variations can interact in a complex fashion that is sometimes underestimated in current models, experiments, and analysis of global change effects on ecosystems (Moorcroft 2006, Norby et al. 2007). Behaviors such as modulation or amplification of the carbon flux can emerge as a result of interactions between spatial heterogeneity and variability of climatic drivers. In many cases, field and modeling experiments exclude these sources of variation and therefore exclude the possibility of these behaviors emerging. For example, experimental manipulations in which an environmental factor is changed to a level predicted for the future, such as increasing temperatures or excluding rainfall to a specific level, do not correspond to more realistic scenarios in which long-term environmental change itself displays a certain degree of temporal variation. Similarly, simplifying the analysis by minimizing spatial variation (e.g., using the big-leaf approach in biogeochemical modeling) reduces the domain of responses by excluding spatial interactions. Our results highlight how internal ecosystem processes and complexity can modulate or amplify responses to external climatic drivers in ways that are poorly characterized in many field and modeling experiments.

2.6. Conclusions

Interannual variability of ecosystem carbon fluxes (NEE, NEP, or NECB) can be explained by both climate and intrinsic forest dynamics. In systems such as tropical forests where process rates are faster than in other ecosystems, forest dynamics were responsible for a larger fraction of the interannual variation in carbon fluxes. As a result, forests at steady-state and under relatively constant environmental conditions can behave either as a source or sink of carbon for short periods of time. Therefore, the concept of equilibrium in a carbon balance should be thought as a range of variation around an average carbon flux of zero.

Our simulations indicate less carbon storage under a variable climate scenario than under constant climatic conditions. This behavior, which is controlled by the non-linear relationship between temperature and respiration, caused larger and more frequent respiratory fluxes under elevated temperatures. Given that the shape of this relationship is consistent across a large number of evergreen and coniferous forests (Law et al. 2002), it can be inferred from our results that an increase in temperature variability will also lead to larger in situ respiratory fluxes and reduced carbon stores.

A temperature increase of 6°C over 100 years caused a consistent decline in carbon storage for the three simulated forests. However, this climatic forcing was not easy to detect in terms of carbon fluxes. Depending on the characteristics of the site, it could take more than 10 years of consecutive flux data to observe a consistent carbon source.

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3. AMPLIFICATION AND DAMPENING OF SOIL RESPIRATION BY CHANGES IN TEMPERATURE VARIABILITY

3.1. Abstract

Accelerated release of carbon from soils is one of the most important possible feedbacks related to anthropogenically induced climate change. Analyses studying the mechanisms for soil carbon release through decomposition have focused on the effect of changes in the average temperature, with little attention to changes in temperature variability. Anthropogenic activities are likely to modify both the average state and the variability of the climatic system; therefore, the effects of future warming on decomposition should not only focus on trends in the average temperature, but also variability expressed as a change of the probability distribution of temperature. Using analytical and numerical analyses we tested common relationships between temperature and respiration and found that the variability of temperature plays an important role determining respiration rates of soil organic matter. Changes in temperature variability, without changes in the average temperature, can either increase or decrease the amount of carbon released through respiration over the long-term. Furthermore, simultaneous changes in the average and variance of temperature can either amplify or dampen the sensitivity of soil organic matter to temperature. A potential consequence of this effect of variability would be lower respiration in places where the average temperature is expected to increase but its variance decreases.

Keywords: Jensen's inequality, soil respiration, climate change, environmental variability, MSC plots.

3.2. Introduction

One of the most important feedbacks of terrestrial ecosystems to climate change is the potential release of soil carbon as temperature increases, especially at high latitudes (Field et al. 2007). The amount of carbon stored in soils worldwide exceeds the amount of carbon in the atmosphere by a factor of two to three (Houghton 2007), and there is concern that a large portion of this carbon will be released to the atmosphere as the global average temperature increases (Schimel et al. 1994, Kirschbaum 1995, Trumbore 1997, Davidson and Janssens 2006). The temperature sensitivity of organic matter decomposition has been a topic of major debate (e.g., Giardina and Ryan 2000), and although this debate is still active, for the most part it is clear that temperature has a significant role controlling the rates of organic matter decomposition. Less clear though, is how different carbon pools respond to temperature changes and under what circumstances other factors such as substrate or moisture limit the rates of organic matter decomposition (Davidson and Janssens 2006).

Most of the analyses studying the temperature sensitivity of decomposition have focused on changes in the average temperature, with little attention to changes in temperature variability. Anthropogenic activities are predicted to modify both the average state and the variability of the climatic system (Räisänen 2002, Brönnimann et al. 2007, IPCC 2007); hence, the effects of future warming on decomposition should not only focus on trends in the average, but more broadly on changes in the probability distribution of temperature. The frequency of hot or cold days and extreme events over long periods of time can potentially determine the frequency of large respiration pulses and subsequently the total amount of C stored in an ecosystem. For this reason it would be convenient to analyze the temperature sensitivity of decomposition in a probabilistic framework.

Recent modeling studies have found important differences in carbon accumulation just by adding random white noise to the temperature time series used to run the simulations (Chapter 2, Notaro 2008). Using a Dynamic Global Vegetation Model (DGVM), Notaro (2008) found a reduction of 20% in total carbon from terrestrial ecosystems when climatic variability (random noise) was added to the average temperature. A similar behavior was found in the predictions from Chapter 2 (Figure 2.1), and we attributed this result to the nonlinearity of the functional relationship between temperature and respiration. Respiration is commonly modeled by convex functions dependent on temperature, supported theoretically by enzyme kinetics theory (Davidson and Janssens 2006, Davidson et al. 2006). Given the convexity of these functions it is reasonable to obtain a higher average respiration when variability is added to the average temperature; this is explained by Jensen's inequality (Jensen 1906, Ruel and Ayres 1999, Ross 2006).

In this study, we explore the effects of changes in climatic regimes, i.e., simultaneous changes in the mean and variance of temperature, on the potential amount of carbon release from ecosystems through soil respiration. To facilitate the analysis, two research questions are explored separately: 1) would changes in temperature variance alone have effects on the amount of soil carbon respired from an ecosystem? 2) Would simultaneous changes in the average and variance of temperature produce complex behaviors in terms of soil respiration? To address these questions we used analytical and numerical analyses. The first question was addressed using an analytical analysis of random variables with different variances. A numerical analysis was used to address both questions. Numerical simulations were performed with a set of simulation models of respiration with stochastic representations of realistic temperature time-series. In the latter analysis, three contrasting ecosystems were used for comparison purposes.

In the remainder of this introduction, we present Jensen's inequality and its consequence for predicting the effects of temperature variability on soil respiration. The results section of this manuscript presents separately the analytical and numerical analyses. The methods sections describes in detail the procedure used for the numerical analysis and describes the datasets employed. Results from both analyses are explored together in the discussion section.

3.2.1 Jensen's inequality

Jensen's inequality is a mathematical property of convex (or concave) functions. It is particularly useful for predicting the consequences of using either a series of values from a random variable or the average of these numbers in a non-linear function. According to Jensen's inequality, if T is a random variable (e.g., temperature), and $f(T)$ a convex function on an interval I, then

$$E[f(T)] \geq f(E[T]), \tag{3.1}$$

where E is the expected value operator. If the function is concave the sign of the inequality is reversed (Jensen 1906, Ross 2006). In other words, evaluating the function with the expected value of the random variable will produce a lower amount than taking the expected value of the function's evaluations at each value of the random variable.

We will illustrate the inequality as it applies to soil respiration. Suppose we are interested in calculating the average rate of soil respiration as a function of soil temperature with the function $R = Q_{10}^{(T-T_0)/10}$ (the modified Van't Hoff equation, see details below), which is a convex function on I. Suppose further that we have a series of 1000 temperature measurements to estimate respiration with this function. We have two alternatives to calculate the average respiration rate: 1) take the average of all the temperature values and then evaluate the function ($f(E[T])$), or 2) calculate all values of respiration corresponding to each temperature value and then calculate the average respiration rate ($E[f(T)]$). Jensen's inequality tell us that method (1) provides a higher value for the respiration rate (Figure 3.1).

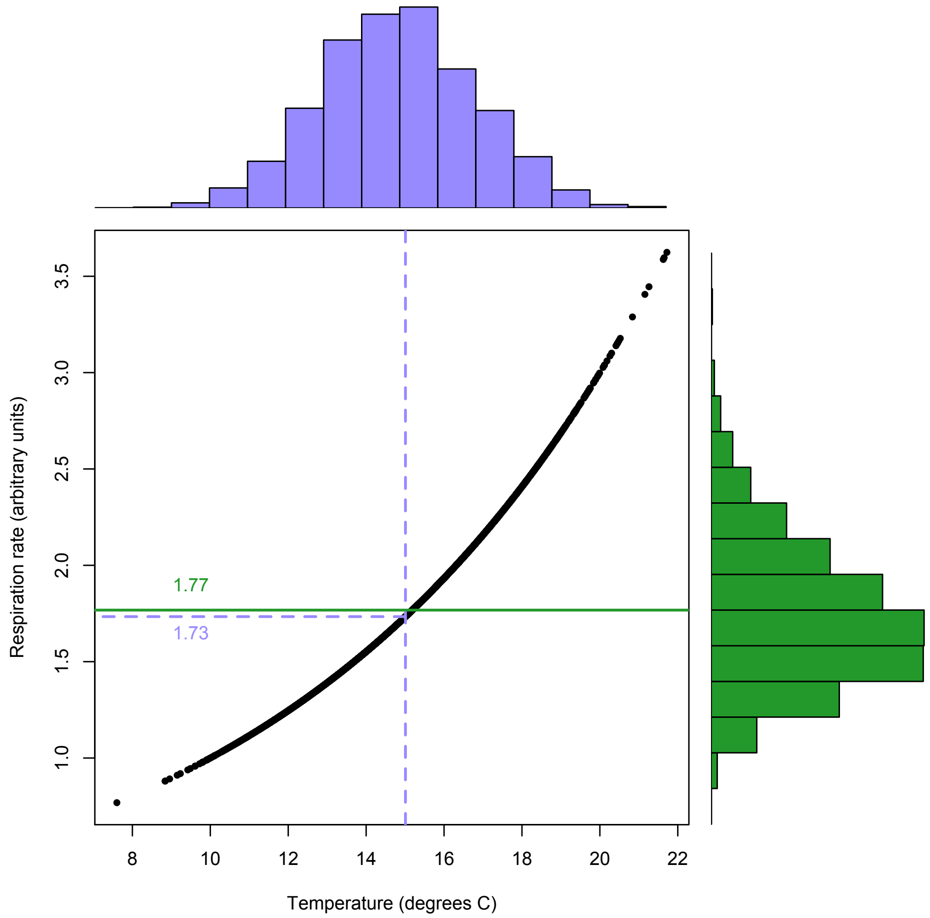

FIGURE 3.1 – Graphical representation of Jensen's inequality to estimate the average respiration rate using a series of 1000 values of soil temperature. If all the 1000 temperature numbers (top histogram) are averaged out we obtain a value of 15 degrees Celcius, which corresponds to a respiration rate of 1.73 (arbitrary units). If all the temperature values are used to calculate the corresponding respiration rate we obtain 1000 values of respiration (points on graph and right histogram), which give an average respiration rate of 1.77. The function used in this case was $R = 3^{(T-10)/10}$.

Although the differences in the average respiration rates may seem small (Figure 3.1), important differences result for the cumulative amount of C respired over a long period of time (e.g., Notaro 2008, Chapter 2).

3.2.2 Functional relationships between temperature and respiration

Historically, the theory behind the temperature sensitivity of organic matter decomposition has been supported by the equations that relate chemical reaction rates with temperature. The Van't Hoff and Arrhenius equations (Table 3.1, equations 3.2 and 3.4) have been widely used to predict changes in decomposition rate constants and respiration rates with changes in temperature. An increase in the respiration rates as temperature increases is expected under this theory, and it can be easily shown that these functions are convex within the interval of temperatures where most biological processes take place (Table 3.1).

The Van't Hoff equation, originally developed in the study of chemical thermodynamics, is commonly used to predict the rates of organic matter decay or respiration R as a function of temperature (T in Celcius), and two empirical parameters $\alpha > 0$, and $\beta > 0$

$$R = \alpha e^{\beta T}. \tag{3.2}$$

Convexity can be evaluated by calculating the second derivative of the function (if the second derivative of the function is non-negative on an interval, then it is convex in that interval). Since $\alpha > 0$, then

$$R'' = \alpha \beta^2 e^{\beta T} > 0, \; \forall \, T \in (-\infty, \infty). \tag{3.3}$$

The Arrhenius equation is a modification of the Van't Hoff equation and relates the respiration rate to the energy required for enzyme reactions to proceed (activation energy E_a), as well as temperature (T in Kelvin), the universal gas constant ($\Re = 8.31$ J K^{-1}

mol^{-1}), and a constant $\alpha > 0$. The Arrhenius equation is expressed as

$$R = \alpha e^{(-E_a/\Re T)}. \tag{3.4}$$

Since the metabolic rate of most organisms take place in the temperature interval (in Kelvin) $I = [273, 313]$ (Gillooly et al. 2001), and values for E_a are usually two orders of magnitude higher than values for T, then

$$R'' = e^{(-E_a/\Re T)} \left[\left(\frac{E_a}{\Re T^2} \right)^2 - \frac{\alpha E_a}{\Re T^3} \right] > 0 \Longleftrightarrow E_a \gg T. \tag{3.5}$$

Convexity is also a property of other empirical equations used to represent the relationship between respiration and temperature, such as the modified Van't Hoff equation and the Lloyd and Taylor (1994) equation (Table 3.1).

TABLE 3.1 – Empirical equations commonly used to describe the relationship between temperature T and soil respiration R, with their second derivatives and range of convexity. Equations extracted from Luo and Zhou (2006).

Equation	Second derivative	Range of convexity on T	Comments
$R = ae^{bT}$	ab^2e^{bT}	$-\infty < T < \infty$, if $a > 0$ and $b \neq 0$	Van't Hoff's exponential function. a and b are empiricial coefficients.
$R = R_0 Q_{10}^{\frac{T-T_0}{10}}$	$R_0 \left(\frac{\ln Q_{10}}{10}\right)^2 Q_{10}^{\frac{T-T_0}{10}}$	$-\infty < T < \infty$, if $R_0 > 0$ and $Q_{10} \neq 0$	Modified Van't Hoff. R_0: respiration rate at temperature T_0. Q_{10}: relative increase by a 10°C change in temperature.
$R = ae^{(-E_a/\Re T)}$	$e^{(-E_a/\Re T)} \left[\left(\frac{E_a}{\Re T^2}\right)^2 - \frac{aE_a}{\Re T^3}\right]$	$-\infty < T < \infty$, if $E_a \gg T$	Arrhenius equation. E_a: activation energy, $\Re$: universal gas constant. T in Kelvin.
$R = R_{10}e^{\left(\frac{E_a}{283.15\Re}\right)\left(1-\frac{283.15}{T}\right)}$	$R_{10}e^{\left(\frac{E_a}{283.15\Re}\right)\left(1-\frac{283.15}{T}\right)} \left[\frac{2E_a}{\Re T} + \left(\frac{-E_a}{\Re T}\right)^2\right]$	$0 < T < \infty$, if $R_{10} > 0$	Modified Arrhenius or Lloyd and Taylor (1994) equation. R_{10}: respiration at 10°C.
$R = ae^{bT+cT^2}$	$ae^{bT+cT^2}[2c + (b + 2cT)^2]$	$-\infty < T < \infty$, if $a > 0$	Second order exponential function.
$R = a(T + 10)^b$	$a(b^2 - b)(T + 10)^{b-2}$	$-\infty < T < \infty$, if $a > 0$ and $b \neq 1$	Power function of Kucera and Kirkham (1971).

3.2.3 Temperature variability and respiration in a changing climate

If the relationship between temperature and respiration is convex for a given ecological or biological system, we can use Jensen's inequality to make practical inferences concerning biogeochemical studies:

1. Modeling studies using average temperature as a driving variable will obtain lower values of respiration than if they were using temperature from weather records.
2. Incubation experiments at constant temperatures will result in lower respiration rates than experiments in which temperature is allowed to vary but without changing the average value.

These are important implications for artificial systems such as laboratory incubations and biogeochemical models; however, implications of Jensen's inequality for natural systems are hard to envisage since temperature is far from constant in nature.

Jensen's inequality suggests that changes in climatic variability may play an important role determining the rates of organic matter decomposition and subsequent carbon release. This effect of variability though, may depend on the magnitude and direction of the change in variance as well as the change in the average climate. Assuming that temperature is normally distributed around a given mean value, a change in variability is associated with either an increase or decrease in both hot and cold days. We hypothesize that this change in variance would result in different rates of decomposition over the long-term given the convexity of the relationship between temperature and respiration. Furthermore, we hypothesize emergent and predictable behaviors of simultaneous changes in the mean and variance of temperature.

3.3. Methods

3.3.1 Sites and datasets

For the numerical analysis we used soil temperature data from three contrasting ecosystems, an arctic tundra grassland, a temperate rain forest, and a tropical rain forest.

Soil temperature data at 20 cm depth from the Toolik lake Long-Term Ecological Research (LTER) site in Alaska (68° 38'N, 149° 43'W, elevation 760 m asl) were obtained from the site's webpage. The dataset contains daily temperature records from June 1, 1998 to December 31, 2006, with a grand mean of −2.5°C and 11% of observations missing.

From the H.J. Andrews LTER site in Oregon we used soil temperature data measured at the PRIMET meteorological station (44° 12' N, 122° 15' W, elevation 430 m asl). The record contains daily soil temperature values measured at 10 cm depth, starting on December 26, 1994 until January 24, 2007. The average temperature for this period was 11.8°C, with only 2% of observations missing. Detailed information about the soil temperature record can be found at the H.J. Andrews' website.

Unpublished high-frequency soil temperatures from La Selva Biological station in Costa Rica (10° 26' N, 83° 59' W) were also used. Three platinum resistance thermometers were used to collect information at 5 cm depth with 2 second execution. Data were averaged to obtain 30 minute time series. The record extends from January 1, 1998 to December 31, 2000, with only 1% of missing observations and a global average of 23.7°C.

3.3.2 Data processing and modeling experiments

The time series from the three sites were filtered with a nine-day moving average to obtain an estimate of short-term variability. In particular, if T_t represents the daily temperature observations, then

$$\tau_t = \frac{1}{9} \sum_{j=-4}^{4} T_{t-j}, \tag{3.6}$$

where τ_t is a symmetric moving average of the data, a low-pass filter that captures the seasonal trend. An estimate of the short-term variability is then given by the residuals $\hat{\epsilon_t} = T_t - \tau_t$, which are basically white noise, i.e., $E(\hat{\epsilon_t}) = 0$, with variance σ_ϵ^2. The average annual trend can then be defined as $\bar{\tau_d} = \frac{1}{N}\sum_{n=1}^{N} \tau_{d,n}$, where $d = t - 365(n-1)$ is the Julian day, n is a year counter, and N the total number of years in the time series.

We used $\bar{\tau_d}$ and σ_ϵ^2 to simulate a reference climatic regime for the three sites, as well as departures to new climatic regimes. These changes in climatic regimes were performed within the framework provided by Mean versus Standard deviation Change (MSC) diagrams (Sardeshmukh et al. 2000, Scherrer et al. 2008). Within this framework it is possible to represent independent and simultaneous changes in the mean and variance of temperature time series (see Figure 3.2 for details). For the purpose of this analysis we defined time series of reference climatic regimes as

$$\tilde{T_t} = \bar{\tau_d} + \epsilon_t \tag{3.7}$$

where $\tilde{T_t}$ is a simulated time series lengthened to a decade, i.e., $t = \{1, ..., 3650\}$. The term ϵ_t is a series of simulated Gaussian white noise, obtained as $\epsilon_t \sim$ iid N(0, σ_ϵ^2). Notice that the values of $\bar{\tau_d}$ are recycled 10 times until the end of the simulation.

New climatic regimes were simulated as a change in the mean and variance of the reference climatic regime by modifying the ϵ_t term in equation 3.7. A combination of values of mean m and standard deviation s were used to simulate time series with $\epsilon_t \sim$ iid N(m, s^2), where $m = \{0.1, 0.2, ..., 2\}$ and $s = \{0.1, 0.2, ..., 3\}$. These values of m and s were chosen such that their combination can fill a wide domain of possibilities in the MSC plots. In other words, these combinations produce 600 different climatic regimes that are possible as the regional climate changes at each site. Notice that values of m only reproduce warming from the starting conditions of the reference regime.

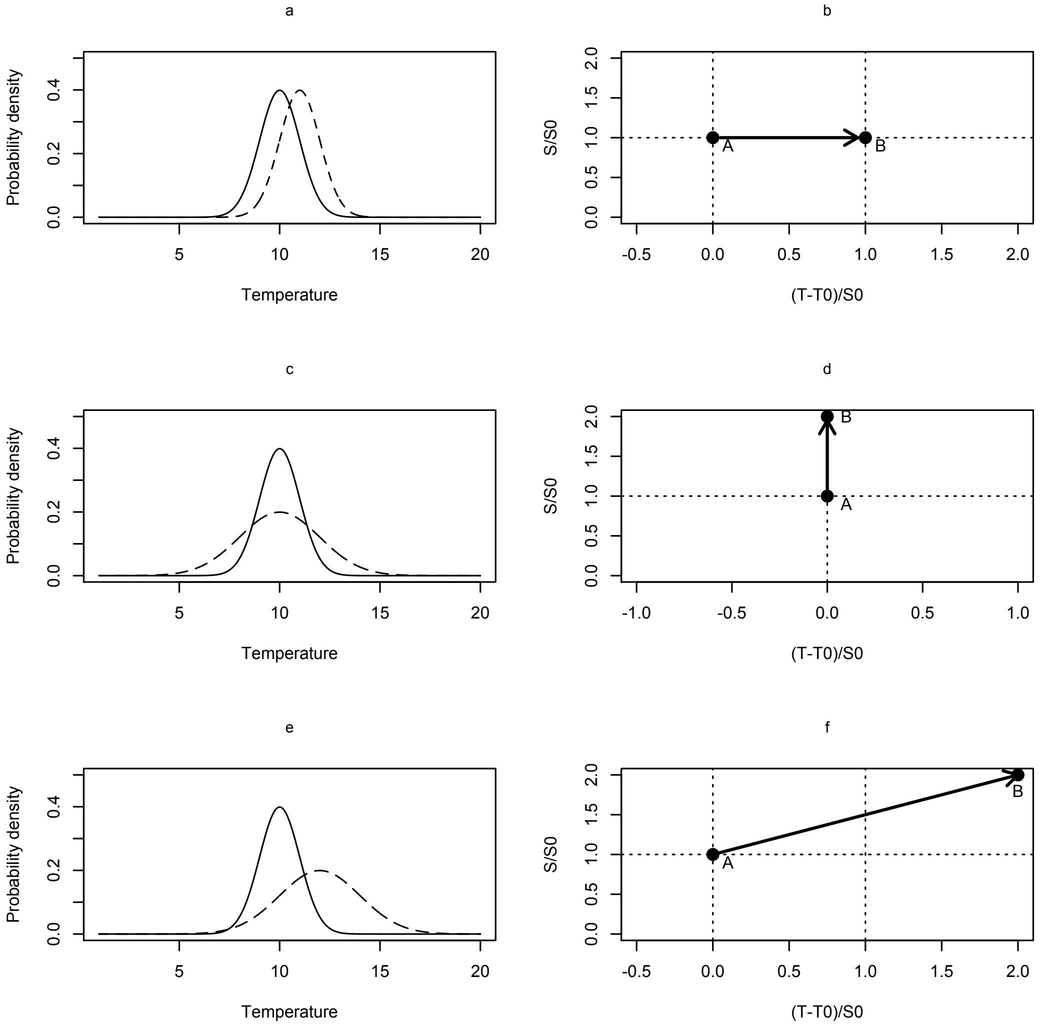

FIGURE 3.2 – Graphical representation of changes in the mean and standard deviation on a Gaussian climate distribution A with mean T0 and standard deviation S0 resulting in distribution B with mean T and standard deviation S. (a) Probability density functions (pdfs) where the mean from distribution A (continuous) changes to distribution B (dashed), (b) distributions A and B from (a) in a standardized MSC plot showing standardized changes in the mean (T -T0)/S0 against standardized standard deviation S/S0, (c) pdfs where the standard deviation from distribution A changes to distribution B. (d) standardized MSC plot of (c), (e) pdfs where both the mean and the standard deviation from A change to B, (f) standardized MSC plot of (e).

3.3.3 Respiration models

The simulated temperature regimes were used to run common empirical functions that relate temperature and respiration in terrestrial ecosystems. The modified Van't Hoff model (Table 3.1) was used for the three ecosystems with an arbitrary value of the reference respiration $R_0 = 1$ at $T_0 = 0$, that is

$$R_t = Q_{10}^{\frac{\tilde{T}_t - 10}{10}}. \tag{3.8}$$

Since we are only interested in observing emergent patterns after using different climatic regimes we did not use site specific parameters in this function. The usefulness of this function, in addition to its familiarity to ecologists, is that it allows us to test for different levels of convexity with different values of Q_{10}; i.e., as Q_{10} gets higher so does the second derivative of the function R''. We ran the model for $Q_{10} = 2$, 3, and 4.

We also simulated respiration using the empirical functions implemented in the DAYCENT and CENTURY models (Del Grosso et al. 2005), given by

$$R_t = F(T_{soil})F(RWC) \tag{3.9}$$

where respiration R_t is represented as the combined effect of soil relative water content (RWC) and temperature (T_{soil}). These individual effects are represented as

$$F(T_{soil}) = 0.56 + (1.46 \arctan(\pi 0.0309(T_{soil} - 15.7)))/\pi, \tag{3.10}$$

$$F(RWC) = 5(0.287 + (\arctan(\pi 0.009(RWC - 17.47)))/\pi). \tag{3.11}$$

Since we are only interested in exploring the effects of temperature variability, a constant water content of $RWC = 75\%$ was assumed, so $F(RWC) = 3.06$ in all simulations.

The benefit of using equation (3.10) is that it has an inflection point at $T = 15.7$, which means the relationship between respiration and temperature changes from convex to concave at this value. The implication for the three ecosystems being modeled is that the range of temperatures for the arctic tundra is below this inflection value whereas the range for the tropical forest is above. For the temperate forest site, this inflection point lies in the middle of its temperature range.

Equations (3.8 and 3.9) were used to calculate total cumulative respiration for the whole simulation period (10 years) and compare differences between the reference (A) and the new (B) climatic regime with the index

$$\delta R = \frac{\sum_{t=1}^{3650} R_t^B - \sum_{t=1}^{3650} R_t^A}{\sum_{t=1}^{3650} R_t^A}. \tag{3.12}$$

Results from all 600 simulations comparing the reference regime and a new climatic regime from all posible combinations of m and s are presented in a single MSC plot. Calculations were performed in the R environment for computing (R Development Core Team 2008).

3.4. Results

3.4.1 Analytical analysis: Geometric argument

A real-valued function $f(x)$ is said to be convex on an interval I if

$$f[\lambda x + (1-\lambda)y] \leq \lambda f(x) + (1-\lambda)f(y), \tag{3.13}$$

for all $x, y \in I$, and λ in the open interval (0, 1). Consider now the closed interval $[a, b]$ which is contained in the interval $[c, d] \in I$; both intervals with an average value $\bar{x}$,

$c = a - h$, $d = b + h$, and

$$\bar{x} = \lambda a + (1 - \lambda)b = \lambda c + (1 - \lambda)d, \tag{3.14}$$

(Figure 3.3). Using the definition of convexity in equation (3.13) we can show that

$$f(\bar{x}) \leq \lambda f(a) + (1 - \lambda)f(b) \leq \lambda f(c) + (1 - \lambda)f(d). \tag{3.15}$$

This inequality can be confirmed graphically in Figure (3.3) and analytically in Appendix C. Geometrically, this inequality implies that the end points of two intervals with the same mean produce different means after convex transformation.

A change in variability of a random variable such as temperature implies a change in the interval of possible values that this variable can take. Equation (3.15) suggests that changes in the variance alone, without changes in the average value of a random variable, produce different values of the average of all the function evaluations. Although this geometric argument is informative, the implications can be better studied in a probabilistic setting.

3.4.2 Analytical analysis: Probabilistic argument

Assume that respiration is a function of temperature $R = f(T)$, which is a strictly convex function on an interval I, so by definition $f''(T) > 0$, $\forall T \in I$. Let's now assume that there are two random variables T_1 and T_2 that are normally distributed with equal mean but with different variance, so $T_1 \sim N(\mu, \sigma_1^2)$ and $T_2 \sim N(\mu, \sigma_2^2)$. Let's also assume that $\sigma_1^2 > \sigma_2^2$. For simplicity, T_1 and T_2 can be transformed to $z_1 = (T_1 - \mu)/\sigma_1$ and $z_2 = (T_2 - \mu)/\sigma_2$, respectively. The expected value of $E[f(T_1)] = E[f(\sigma_1 z_1)]$, and $E[f(T_2)] =$

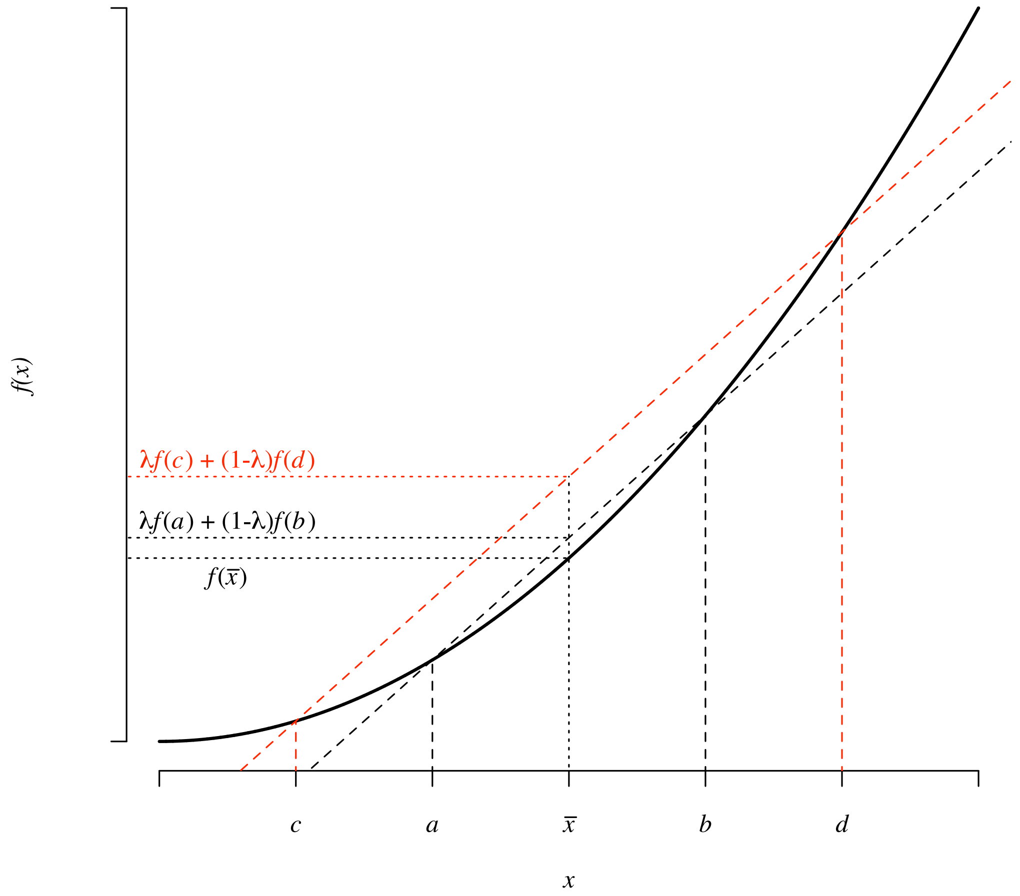

FIGURE 3.3 – Graphical representation of the inequalities in equation (3.15). $\bar{x}$ is the center point of both intervals $[a, b]$ and $[c, d]$, and $\lambda = 1 - \lambda$.

$E[f(\sigma_2 z_2)]$ can be calculated as

$$\begin{aligned} E[f(\sigma_1 z_1)] &= \int_{-\infty}^{\infty} f(\sigma_1 z_1) \frac{1}{\sqrt{2\pi}} \exp\left(\frac{-z_1^2}{2}\right) dz, \\ &= \frac{1}{\sqrt{2\pi}} \left[\int_{0}^{\infty} f(\sigma_1 z_1) \exp\left(\frac{-z_1^2}{2}\right) dz + \int_{-\infty}^{0} f(\sigma_1 z_1) \exp\left(\frac{-z_1^2}{2}\right) dz\right], \\ &= \frac{1}{\sqrt{2\pi}} \left[\int_{0}^{\infty} (f(\sigma_1 z_1) + f(-\sigma_1 z_1)) \exp\left(\frac{-z_1^2}{2}\right) dz\right]. \end{aligned} \tag{3.16}$$

Similarly,

$$E[f(\sigma_2 z_2)] = \frac{1}{\sqrt{2\pi}} \left[\int_{0}^{\infty} (f(\sigma_2 z_2) + f(-\sigma_2 z_2)) \exp\left(\frac{-z_2^2}{2}\right) dz\right]. \tag{3.17}$$

According to the properties of convexity it can be shown that $f(\sigma_1 z_1) + f(-\sigma_1 z_1) > f(\sigma_2 z_2) + f(-\sigma_2 z_2)$ (equation 3.15); therefore,

$$E[f(T_1)] > E[f(T_2)]. \tag{3.18}$$

Equation (3.18) confirms the hypothesis initially posed, changes in temperature variance alone can produce differences in respiration. The magnitude and functional relation of the effect of different variance can be evaluated by calculating the difference $\Delta = E[f(T_1)] - E[f(T_2)]$. For simplicity, we will calculate Δ for the specific case of the exponential function $R = \exp(T)$, assuming σ_1^2 is η times σ_2^2 ($\sigma_2^2 = \sigma_1^2/\eta$), which gives

$$\begin{aligned} \Delta &= E[f(\sigma_1 z_1)] - E[f(\sigma_2 z_2)], \\ &= \frac{1}{\sqrt{2\pi}} \left[\int_{-\infty}^{\infty} f(\sigma_1 z_1) \exp\left(\frac{-z_1^2}{2}\right) dz - \int_{-\infty}^{\infty} f(\sigma_2 z_2) \exp\left(\frac{-z_2^2}{2}\right) dz\right], \\ &= \frac{1}{\sqrt{2\pi}} \left[\sqrt{2\pi} \exp(-\sigma_1) - \sqrt{2\pi} \exp(-\sigma_2)\right], \\ &= \exp(-\sigma_1) - \exp(-\sigma_1/\eta). \end{aligned} \tag{3.19}$$

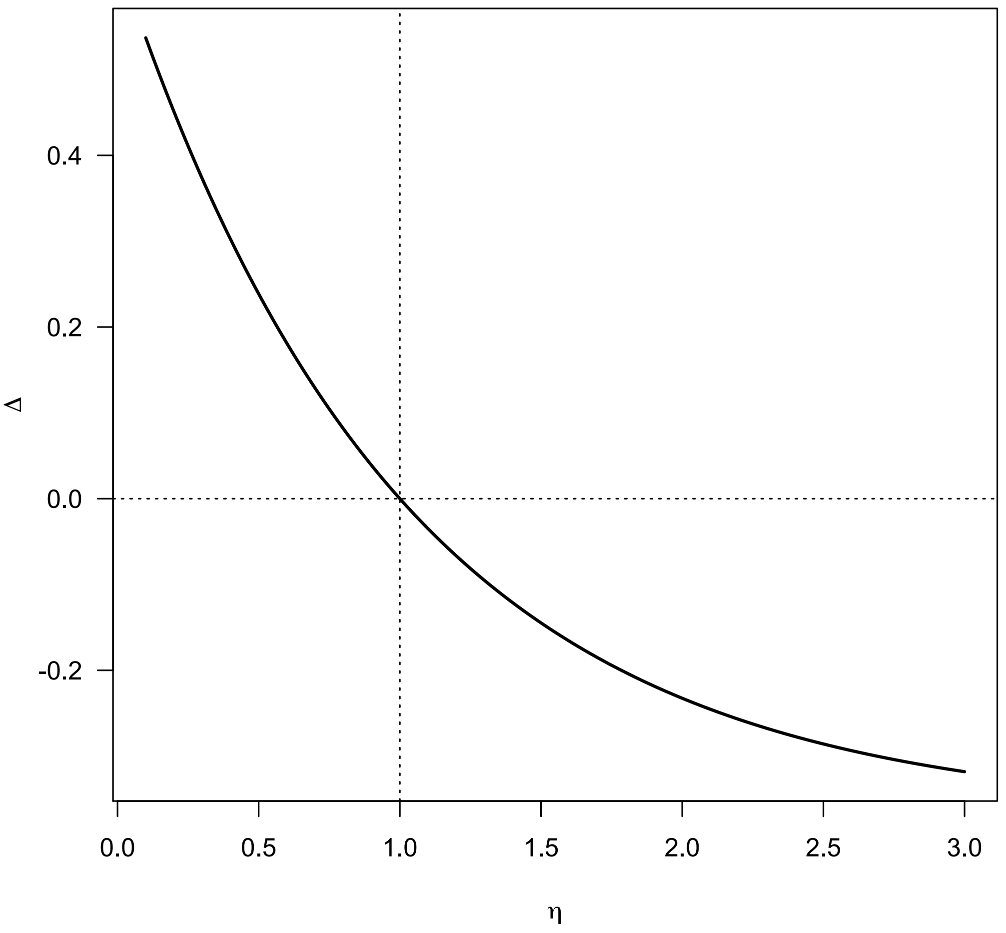

FIGURE 3.4 – Relationship between η (proportional change in temperature variance) and Δ (difference in average respiration) for an exponential function $R = \exp(T)$.

Equation (3.19) summarizes the effects of a change in the variance of T over R. It shows that the value of η affects the magnitude of the difference in expected values. This can be visualized in Figure (3.4), which shows that for an exponential function an increase in variance (from σ_1^2 to σ_2^2, and $\eta < 1$) produces an increase in the average respiration ($\Delta > 0$), and a decrease ($\Delta < 0$) when variance diminishes ($\eta > 1$).

3.4.3 Numerical analysis

The results obtained using the modified Van't Hoff model (equation 3.8) were similar for the three ecosystems modeled, so we will focus on the results for the H.J. Andrews forest only. The differences between the reference and the set of new climatic regimes, evaluated with δR, confirm the hypotheses initially posed. First, the results from the simulations show that changes in the variance of temperature alone can increase the amount of carbon respired (Figure 3.5). This can be observed in the MSC plot by changes along the vertical axis at a fixed value of 0 in the horizontal axis. For example, an increase of about 6% of carbon respired over 10 years can be achieved by a 2.5 times increase in the standard deviation. Second, the MSC plot shows that respiration is more sensitive to proportional changes in the average temperature than to changes in variance. The same 6% increase in respiration obtained with a 2.5 times increase in standard deviation could have been achieved by increasing the average temperature by a factor of 0.5. Third, simultaneous changes of the average and the variance of temperature show that increases in variance amplify the effects of increases in the average. In contrast, decreases in variance dampen the effects of the increase in the average temperature. This can be observed in the MSC plot by changes in δR in the vertical direction at any fixed point in the horizontal axis.

The degree to which δR responds to changes in variance was highly dependent on Q_{10} (Figure 3.6). As the value of Q_{10} decreases the convexity of the function decreases (value of the second derivative gets smaller) and the effect of variability on respiration becomes less important. This behavior was consistent for the three ecosystems studied.

The pattern observed in Figure (3.5) was also consistent seasonally (Appendix D). Differences between seasons for each value of m and s were almost in a 1:1 correspondence (Figure 3.7). This same pattern was consistent for different values of Q_{10}, but the sensitivity of respiration to temperature variability decreased as Q_{10} got smaller (data not shown), similar to what was described previously.

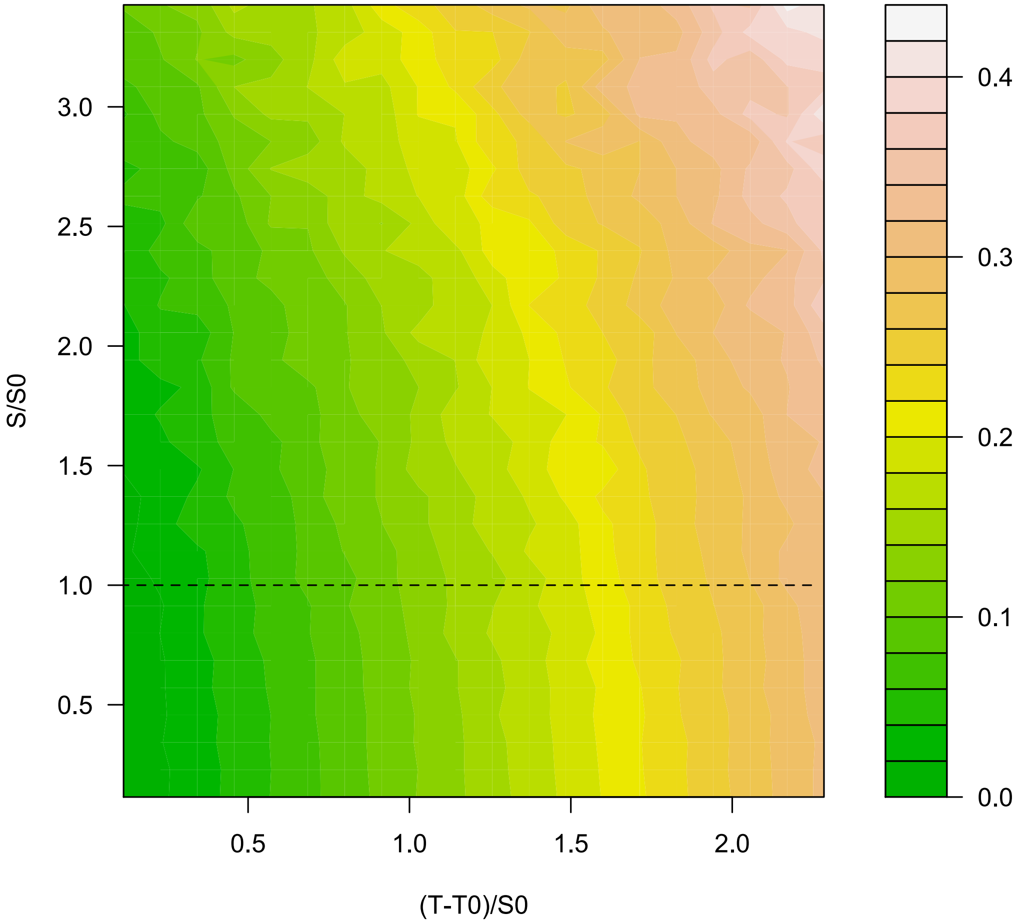

FIGURE 3.5 – MSC plot for H.J. Andrews using the modified Van't Hoff equation with $Q_{10} = 4$. Colors represent values of δR, i.e., the proportional increase in respiration over 10 years from one climatic regime over the other. The dashed horizontal line represents simulations in which variance remained constant relative to the reference climatic regime. S/S0 > 1 represents increase in variance and (T-T0)/S0 > 0 represents increase in average temperature.

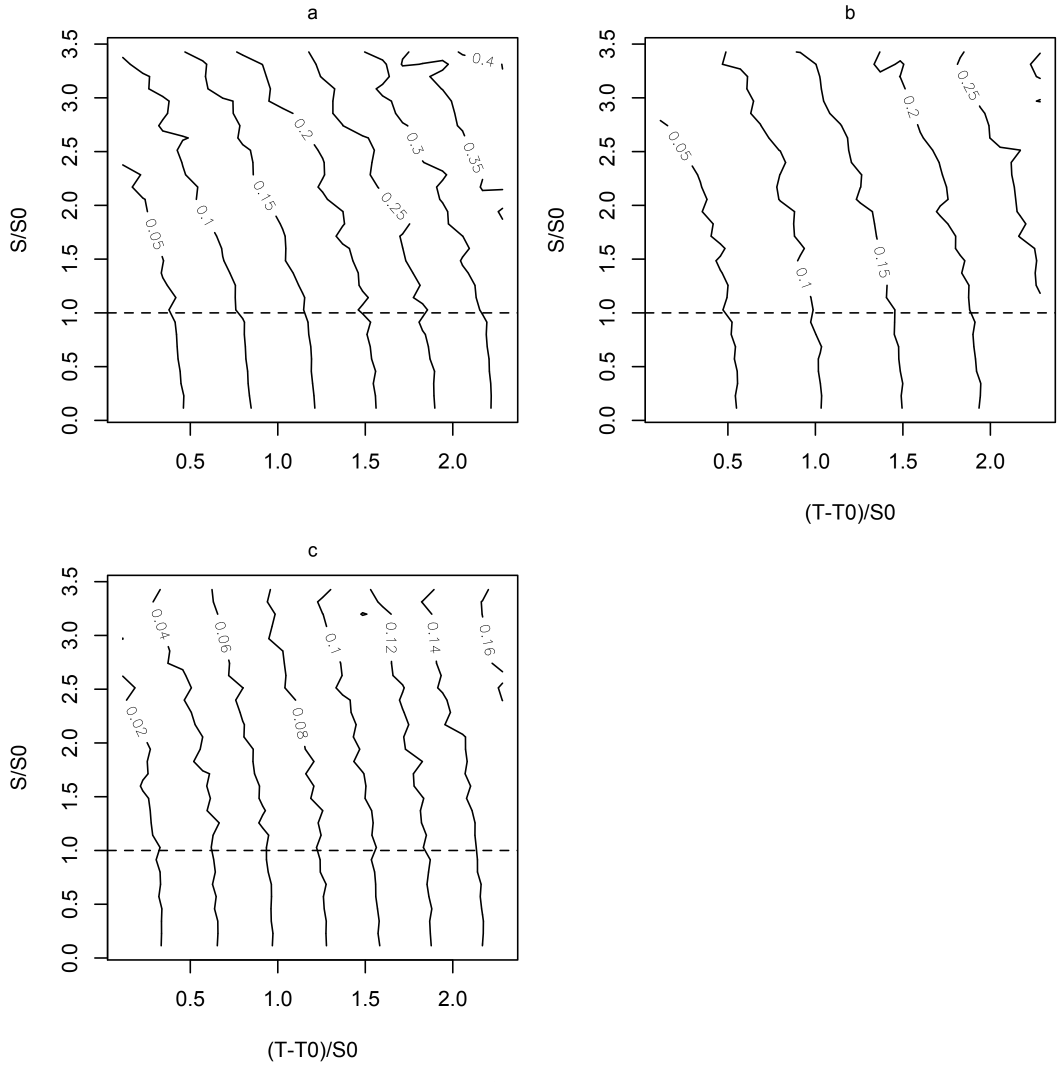

FIGURE 3.6 – MSC plots for H.J. Andrews using the modified Van't Hoff equation and $Q_{10} = 4, 3, 2$, for panels a, b, and c, respectively. Contours represent values of δR, i.e., the proportional increase in respiration over 10 years from one climatic regime over the other.

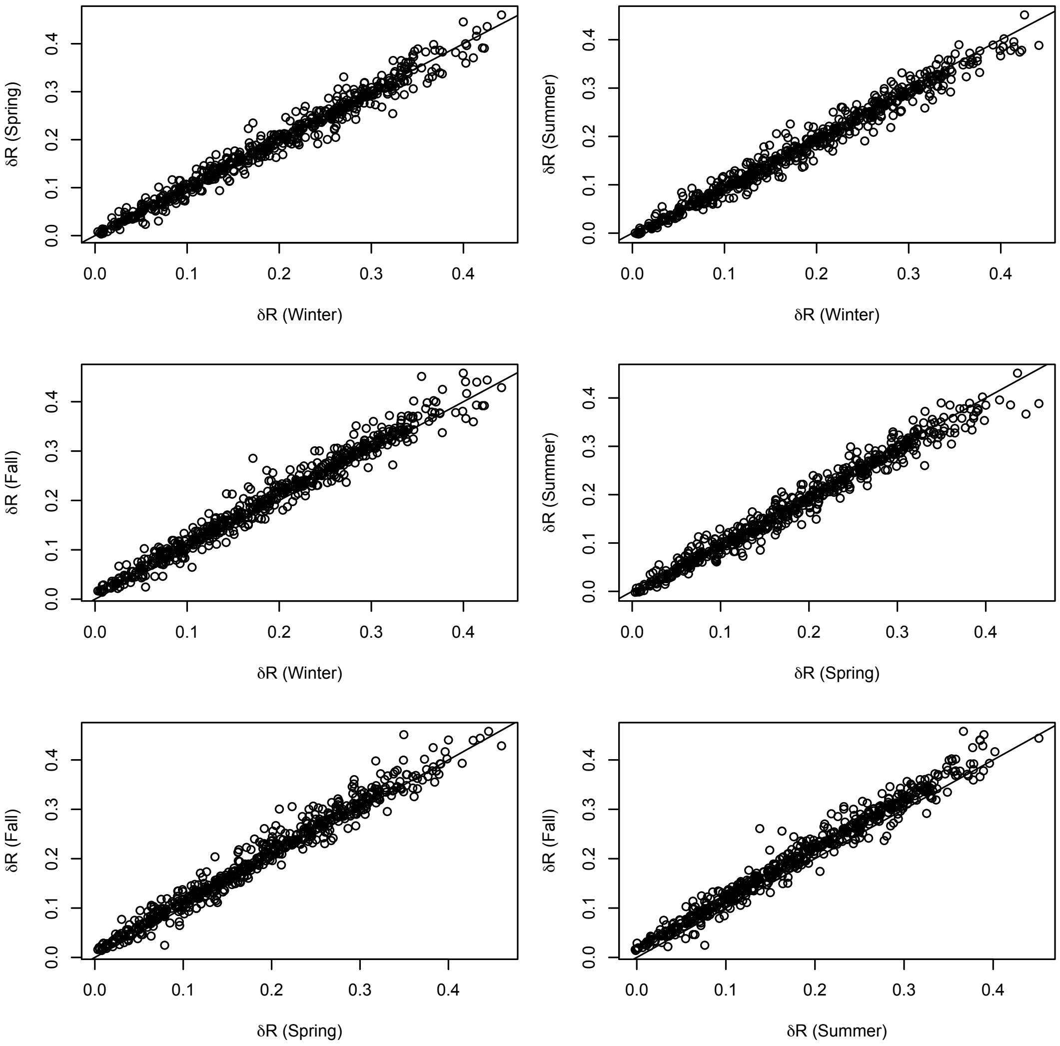

FIGURE 3.7 – Comparison of values of δR at H.J. Andrews between seasons. Each point corresponds to the same location in the MSC plots for the two seasons being compared. The continuous line represents a 1:1 correspondance. Winter: December, January and February; Spring: March, April and May; Summer: June, July and August; Fall: September, October and November

The approach used in the DAYCENT and CENTURY models (equation 3.9) produced different results for the three ecosystems analyzed. For the arctic tundra site the pattern observed was similar to the overall patterns observed with the Van't Hoff equation (Figure 3.8a). For the H.J. Andrews though, the DAYCENT approach shows no sensitivity of respiration to temperature variance (Figure 3.8b). For the tropical forest the results are the converse, showing a dampening effect with increases in the average temperature and amplification with decreases in the average (Figure 3.8c).

3.5. Discussion

The results from this analysis provided strong support to the hypotheses initially posed. First, we found that changes in the variance of temperature alone can either decrease or increase the amount of soil respiration in terrestrial ecosystems. This was confirmed by both the analytical and numerical analyses. Second, changes in temperature variance can either amplify or dampen the effects of changes in the average temperature on soil respiration. These effects are predictable and depend on the degree of convexity or concavity between temperature and respiration (value of the second derivative of the relationship) and the magnitude of the change in variance (η in equation 3.19).

3.5.1 Climate variability and change

Changes in climate variability and its effects on ecosystems have been studied less intensively than changes in the mean climate. The ongoing modification of the climatic system by changes in albedo, aerosols and prominently greenhouse gases, affects not only the mean state of the climate system but also its variability (Räisänen 2002, IPCC 2007, Brönnimann et al. 2008). Changes in temperature variability may result in changes in the frequency of events apart from the mean state such as unusual warm or cold events. Significant attention has been given to extreme climatic events such as heat waves or floods

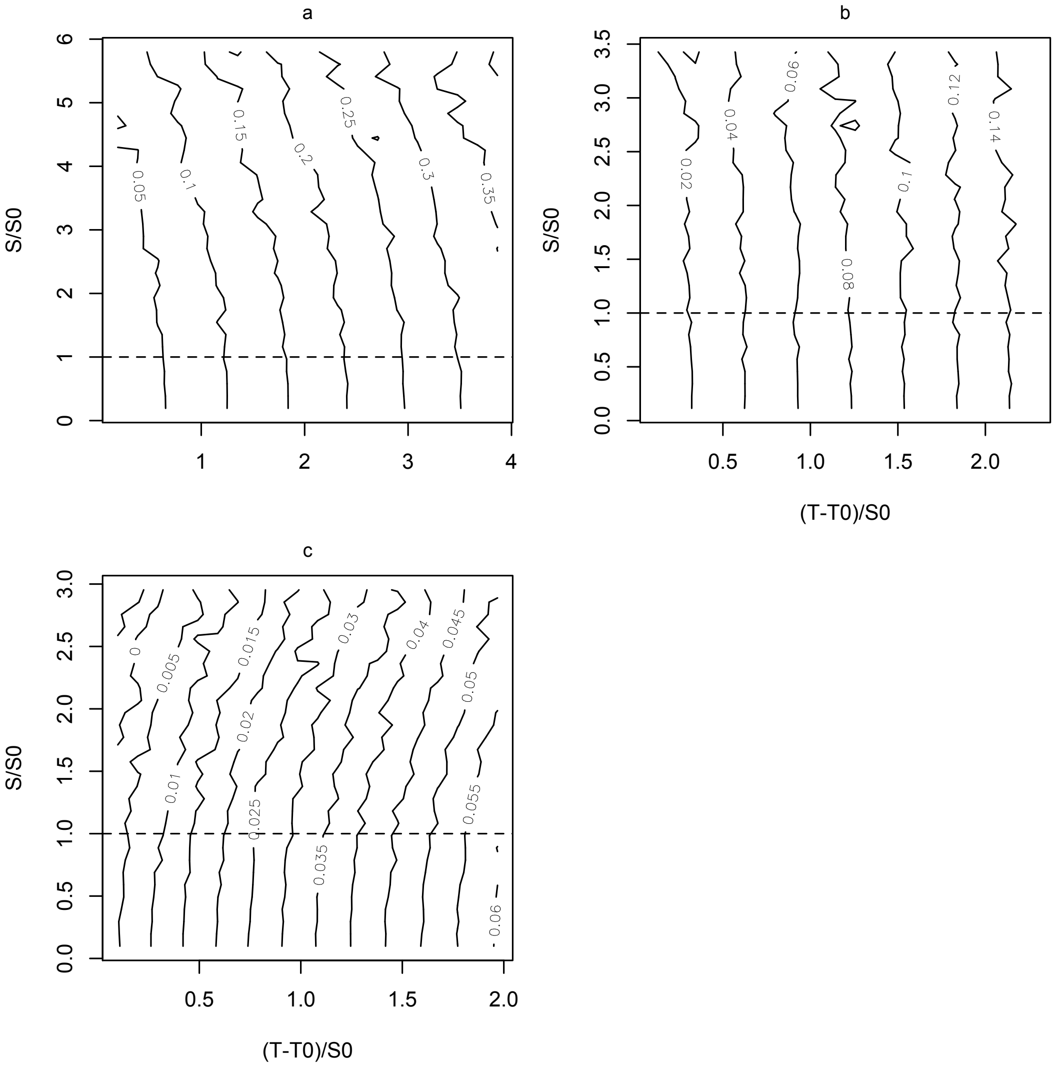

FIGURE 3.8 – MSC plots for Toolik lake (a), H.J. Andrews (b), and La Selva (c) using the DAYCENT and CENTURY approach. Contours represent values of δR, i.e., the proportional increase in respiration over 10 years from one climatic regime over the other.

for their dramatic effects on populations. However, less extreme but still unusual events can have important implications for the functioning of ecosystems over the long-term (Jentsch et al. 2007).

Important changes have been observed in temperature variability for different regions in the recent past. In Europe, where climate records are longer than in other continents, important changes in the variance of temperature have been described. Della-Marta and Beniston (2007) report an increase in the variance of summer maximum temperature of 6°C for the period 1880-2005 in Western Europe. This increase in variance accounts for at least 40% of the increase in the frequency of hot days after accounting for the increase in the average temperature. Although significant changes in temperature variability have not been observed for Central Europe over the past decades, most climate models predict increases in summer temperature variability for the 21st century (Scherrer et al. 2007).

Changes in climate variability are not expected to be homogenous globally. A comparison of 19 atmosphere-ocean general circulation models (AOGCMs) showed that as a consequence of doubling CO_2, temperature variability is expected to decrease during the winter of the extratropical Northern Hemisphere (Räisänen 2002). Conversely, the AOGCMs show that temperature variability is expected to increase during the summer in low latitudes and northern midlatitudes. A more recent analysis using an updated version of one climate model confirms these results, which also suggest decreases in temperature variability for fall, spring and winter in the northern hemisphere (Stouffer and Wetherald 2008).

These expected changes in temperature variability most likely will have consequences on the total amount of carbon emitted to the atmosphere from terrestrial ecosystems. Our results showed that changes in variance produce a variety of effects on respiration in addition to the predicted effects of changes in average temperatures alone. At a global scale, differences in temperature sensitivities of respiration and in the magnitude of change in temperature variance for different regions will produce a variety of responses. For example, at high latitudes in the Northern Hemisphere, where the mean temperature is expected to increase and the variance is expected to decrease, respiration would probably be lower than the predicted by changes in mean temperature alone. These regions are expected to contribute the most to the positive feedback between temperature and respiration, but this effect may be overestimated in simulation models. At low latitudes, where both the mean and variance of temperature are expected to increase, the amount of respiration would be higher than the predicted by changes in mean temperature alone. These predictions obviously depend on the assumption of a convex relationship between respiration and temperature.

3.5.2 Convexity of respiration functions

The relationship between temperature and respiration historically has been described using empirical convex functions (Table 3.1). Although there have been important criticisms to simple empirical models and more mechanistic representations are currently being discussed (e.g., Luo and Zhou 2006, Davidson et al. 2006), it is clear from the many modeling approaches that these two variables have a convex relationship, independent of the type of model employed. In some cases, however, this relationship shows a change to concavity at higher values of temperature, which could be explained by the interacting effects of water content and substrate availability (Del Grosso et al. 2005, Davidson et al. 2006), among other factors.

Independent of the type of model being used, the number of pools represented, or the main drivers included in the model, the results obtained in this study will apply to all predictions of future respiration if its relationship with temperature is other than a simple straight line. They also apply to all temperature ranges where most biological process take place, except where the respiration function changes from convex to concave. As the simulations in the temperate forest showed, a change in convexity can cause the effects of concavity at one part of the temperature range to compensate the effects of convexity in the other part of the range.

In general, simulation models use one single equation to described the relationship between temperature and respiration, with the modified Van't Hoff model being the most common. Although there is important work trying to predict Q_{10} values for different ecosystem types (e.g., Chen and Tian 2005, Fierer et al. 2006), this modeling approach only considers one single functional relationship between temperature and respiration. For some systems it is possible that this relationship is other than convex or changes to concavity at some point in the temperature range; therefore, more effort should be directed to understand local scale relationships to be incorporated in models and whether these relationships are generalizable within and across major biomes.

3.5.3 Implications

Although ecologists are well aware of the importance of climate variability (e.g. Ruel and Ayres 1999, Pasztor et al. 2000, Knapp et al. 2002, Jentsch et al. 2007), studies looking at the effects of climate change on ecosystem function have given perhaps too much attention to changes in the average climate, but not to the full probability distribution of the climate system. The findings of this study can greatly modify past predictions about the effects of future average temperatures on ecosystem respiration, especially for large temporal and spatial scales. However, soil respiration not only depends on temperature but also on moisture and substrate availability. New climatic regimes will be associated with different soil moisture regimes and different plant phenologies that control substrate supply. There has been a considerable amount of work showing the effects of variable soil moisture on respiration through drying/wetting cycles (see Borken and Matzner 2009 for a review). If combined with the results from this study, changes in both temperature and precipitation variance would likely produce complex behaviors not currently incorporated in simulation models.

The effects of new climatic regimes with different variances would not only affect the mineralization of C measured as soil respiration, but also the production of dissolved organic and inorganic forms of C as well as other elements such as N. Autotrophic respiration is also likely to be affected by changes in the variance of temperature since they usually correlate well with a modified Van't Hoff model (Ryan 1991). In general, any ecosystem process that is related with a climatic variable through a convex or concave function is likely to be subject to the effects of variance presented here (see Drake 2005 for an example of temperature variability effects on growth rates of zooplankton).

To our knowledge, very few published laboratory or field experiments have looked at the effects of temperature variability on respiration (however see Lomander et al. 1998). These type of experiments, in addition to corroborate what is presented here, would allow one to test the interacting effects of temperature, moisture and substrate variability. Vegetation models also need to be improved so they can predict the complexities of new climatic regimes. Probabilistic modeling is a very useful approach for this purpose as shown here and by others modeling the effects of precipitation variability (Daly et al. 2008).

3.6. Conclusions

Using analytical and numerical analyses as well as empirical models that relate temperature and respiration, we found that changes in the variance of temperature alone can potentially increase the amount of respiration from terrestrial ecosystems over decadal time scales. Furthermore, simultaneous changes in temperature variance can either amplify or dampen the net effect of mean temperature increase, depending on whether the change in variance is positive or negative, or the respiration function is concave or convex. An important consequence of this behavior is that the increase in mean and decrease in variance expected for high latitude regions would result in lower amounts of respiration than that estimated from changes in mean temperature alone.

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4. SUBSTRATE HETEROGENEITY AND ENVIRONMENTAL VARIABILITY IN THE DECOMPOSITION PROCESS

4.1. Abstract

Soil organic matter is a complex mixture of material with heterogeneous biological, physical, and chemical properties. However, traditional analyses of organic matter decomposition assume that a single decomposition rate constant can represent the dynamics of this heterogeneous mix. Terrestrial decomposition models approach this heterogeneity by representing organic matter as a substrate with three to six pools with different susceptibilities to decomposition. Even though it is well recognized that this representation of organic matter in models is less than ideal, there is little work analyzing the effects of assuming substrate homogeneity or simple discrete representations on the mineralization of carbon and nutrients. Using concepts from the continuous quality theory developed by Göran I. Ågren and Ernesto Bosatta, we performed a systematic analysis to explore the consequences of ignoring substrate heterogeneity in modeling decomposition. We found that the compartmentalization of organic matter in a few pools introduces approximation error when both the distribution of carbon and the decomposition rate are continuous functions of quality. This error is generally large for models that use three or four pools. We also found that the pattern of carbon and nitrogen mineralization over time is highly dependent on differences in microbial growth and efficiency for different qualities. In the long-term, stabilization and destabilization processes operating simultaneously result in the accumulation of carbon in lower qualities, independent of the quality of the incoming litter. This large amount of carbon accumulated in lower qualities would produce a major response to temperature change even when its temperature sensitivity is low. The interaction of substrate heterogeneity and temperature variability produces behaviors of carbon accumulation that cannot be predicted by simple decomposition models. Responses of soil organic matter to temperature change would depend on the interacting effects of the sensitivity of different pools to decomposition, the amount of carbon stored in the pools, the variability of climatic drivers, and the degree and nature of the nonlinearities in the system.

Keywords: continuous quality theory, representation error, organic matter decomposition, coupled carbon and nitrogen cycling, ecological heterogeneity, temperature sensitivity of decomposition.

4.2. Introduction

The decomposition of soil organic matter is a process as important as plant photosynthesis in terms of the cycling of carbon and driving other important biogeochemical cycles (Swift et al. 1979, Schlesinger 1997). At a global scale, the magnitude of carbon release to the atmosphere by the decomposition of organic matter is relatively similar to the amount of carbon that plants fix in their biomass. However, relatively little attention has been given to the study of decomposition. In a search on the Ecology and Environmental Sciences database of *Web of Science*$^{\copyright}$ we found 53% more studies containing the term *photosynthesis* than *decomposition*; and 74% more studies containing the term *net primary production* than the term *heterotrophic respiration.* This disparity in number of publications is perhaps an indication of the current lack of understanding in many belowground processes associated with carbon and nutrient cycling. Another indication is the crude representation of decomposition processes, in contrast with photosynthetic processes, in terrestrial biogeochemical models (Davidson & Janssens 2006, Luo & Zhou 2006, Manzoni et al. 2009).

Organic matter in soils is a highly heterogenous mix of detritus from plants, as well as a mix of macro- and microorganisms with the products of their metabolic activity

(Swift et al. 1979). Despite its heterogeneity, soil organic matter is often represented as a single homogenous pool or a mix of a few homogenous pools. Some models such as FAEWE, PnET-II, or TEM only represent one soil carbon pool, while some of the most popular models, such as Biome-BGC, CASA or CENTURY, contain 3 pools (Parton et al. 1987, Potter et al. 1993, Burke et al. 2003, Luo & Zhou 2006). Although significant progress in the understanding of terrestrial biogeochemical cycling has been achieved by the use of these models in the past decades, it is still unclear what are the implications of simple categorizations of soil organic matter when it is well known that it is highly heterogeneous.

There are several reasons to believe that substrate heterogeneity is an important factor for predicting the amounts of carbon and nutrient release from soils. One is that a heterogeneous substrate is composed of material with different chemical and physical characteristics and different levels of accessibility to decomposers. The total amount of substrate that can be consumed by decomposers therefore depends on the relative proportions of substrate at different levels of accessibility. If the proportion of inaccessible substrate is higher, less carbon can be consumed than if the proportion of inaccessible substrate is lower or if the substrate is homogeneously distributed in all levels of accessibility. The rates at which carbon and other elements can be mineralized would therefore depend on the different proportions of accessible substrate. Another reason is that substrates with different properties will respond differently to environmental drivers such as temperature and moisture, so the total response of the system to a change in the environment will depend on the relative proportions of material with different characteristics. Additionally, internal interactions within the soil may constantly change the physical and biophysical make up of the substrate leading to complex behaviors over time.

In this chapter we explore the consequences of treating substrate heterogeneity explicitly in a decomposition model. We also explore the consequences of this heterogeneity for interactions between soil organic matter and temperature. Our main hypothesis is that substrate heterogeneity produces a set of system behaviors that cannot be predicted by assuming a single homogenous pool. We will focus on the mineralization of carbon and nitrogen since these are highly relevant ecosystem process. For this purpose, we make extensive use of the continuous quality theory developed by Ågren and Bosatta (1998).

In the first part of this manuscript we present a systematic analysis of the consequences of introducing heterogeneity in a cohort of organic matter subject to decomposition. Then we extend the analysis to multiple cohorts with heterogeneous inputs, and lastly we study the interactions of substrate heterogeneity with an abiotic driver: temperature.

4.3. Substrate heterogeneity

Although it is well recognized that organic matter is a highly heterogeneous mix of material with different chemical and physical properties (Swift et al. 1979), models representing organic matter decomposition usually separate it in a few discrete categories (Burke et al. 2003, Luo & Zhou 2006). This categorization is often based on the resistance of organic matter to decomposition, therefore each category is associated with a specific decomposition rate constant. Some authors have pointed out the limitations of this compartmentalization approach and suggested that, more realistically, organic matter should be distributed in a continuum of quality ranging from high to low decomposition resistance (Carpenter 1981, Bosatta & Ågren 1991).

4.3.1 Number of pools and approximation error

If soil organic matter is distributed in a continuous range of qualities, a compartmentalization into discrete categories can introduce error in its representation within decomposition models. The error is conceptually similar to the error obtained with numerical approximations of a definite integral by a Riemman sum (Figure 4.1). The decomposition rate for each pool generally describes the average decomposition rate within the pool, which geometrically is similar to the midpoint approximation of the Reimman method. The absolute error for approximating the area under a curve using the midpoint method is $E = \frac{(b-a)}{24} h^2 f''(\xi)$, where a and b are the lower and upper limits of integration, $h = (b-a)/m$ is the width of the compartments, and m the total number of compartments or pools. This error also depends on the second derivative of a point ξ within each compartment. As the number of compartments m increases, h decreases as well as the absolute error ($E = O(h)$ as $h \to 0$).

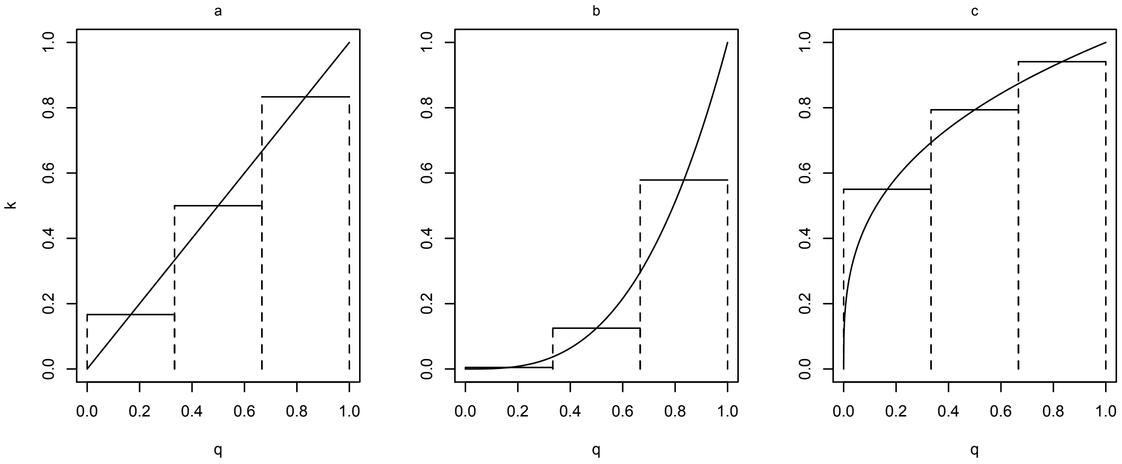

FIGURE 4.1 – Approximation error by representing decomposition rates with three discrete pools within the quality continuum. Hypothetical relationships between quality q and decomposition rate k are presented as a) linear ($k = q$, $f''(q) = 0$), b) convex ($k = q^3$, $f''(q) > 0$), and c) concave ($k = q^{1/3}$, $f''(q) < 0$).

The choice of arbitrary discrete pools with constant decomposition rates necessarily implies lumping specific amounts of organic matter within these categories. Since abrupt discontinuities may not necessarily represent accurately the distribution of carbon in organic matter, another representation error is introduced here (Figure 4.2). Similarly, this error depends on the number of pools and is equal to $E = \frac{(b-a)}{24} h^2 g''(\xi)$.

In its simplest representation, the decomposition of organic matter follows an expo-

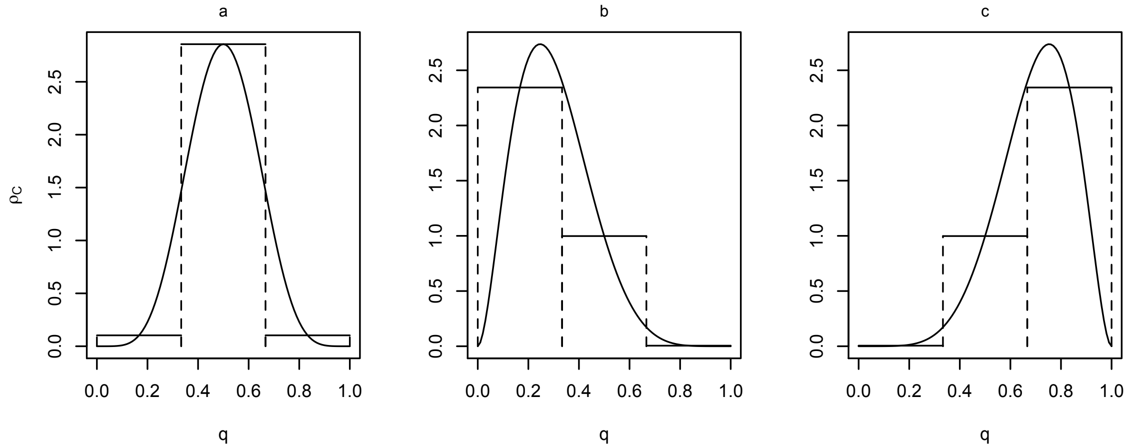

FIGURE 4.2 – Approximation error by representing the distribution of carbon in soil organic matter ρ_C with three discrete pools within the quality continuum. Hypothetical relationships between quality q and ρ_C are presented as a) symmetric centered on an average quality value, b) asymmetric skewed towards low quality quantities, and c) asymmetric skewed towards high quality.

nential mass loss over time (Olson 1963). When the total amount of carbon is partitioned in m number of pools with specific decomposition rates k for each pool i, the decomposition process can be represented as

$$C_{t,i} = C_{t=0,i} \exp(-k_i t), \tag{4.1}$$

where $C_{t,i}$ is the amount of carbon in the pool i at time t. The total amount of carbon at any given time is then

$$C_t = \sum_{i=1}^{m} C_{t,i}. \tag{4.2}$$

Both terms in equation (4.1) depend on the number of pools in which total carbon is partitioned; therefore, the representation error imbedded in both propagates to the total amount of carbon at each time step as

$$E^2_{C_{t,i}} \propto \left(\frac{(b-a)}{24} h^2 f''(\xi_1) \right)^2 + \left(\frac{(b-a)}{24} h^2 g''(\xi_2) \right)^2, \tag{4.3}$$

or

$$E^2_{C_{t,i}} = O(h^2) \quad \text{as} \quad h \to 0. \tag{4.4}$$

Two important consequences can be inferred from equation (4.3). First, the two sources of error depend on the degree of convexity or concavity of the functions being approximated. As the concavity or convexity increases, measured by the second derivative of the function, the error increases. Second, when the relationship between quality and decomposition rate is linear, $f''(q) = 0$, so there is no approximation error for k and the total error is dominated by the error incurred approximating the distribution of $C_{t=0}$. As a consequence, the approximation error can only be zero when both functions can be described by straight lines.

As expressed in equation (4.4), the error in modeling decomposition decreases as h tends to zero; i.e., as the number of pools increases. The relative error for any different number of pools can be calculated easily using equation (4.1) and different values of m. We calculated the relative approximation error for different combinations of the functional forms presented in Figures (4.1) and (4.2). This error was calculated for $t = 5$, before all the remaining organic matter was completely decomposed. The results show that the approximation error is large when only a few pools are considered. For example, when only three pools are considered, the approximation error can be as large as 30-40% (Figure 4.3).

4.3.2 Coupled carbon and nitrogen dynamics in heterogeneous substrates

Models of organic matter decomposition are of primary importance for predicting carbon fluxes from soils as well as the cycling of other elements such as nitrogen and phosphorus. Most models use a limited number of pools that introduce approximation error as suggested above. However, there are models that represent organic matter as a continuous variable, as opposed to abrupt compartmentalizations. One of the most relevant is the continuous quality model (Ågren & Bosatta 1998). This model has been

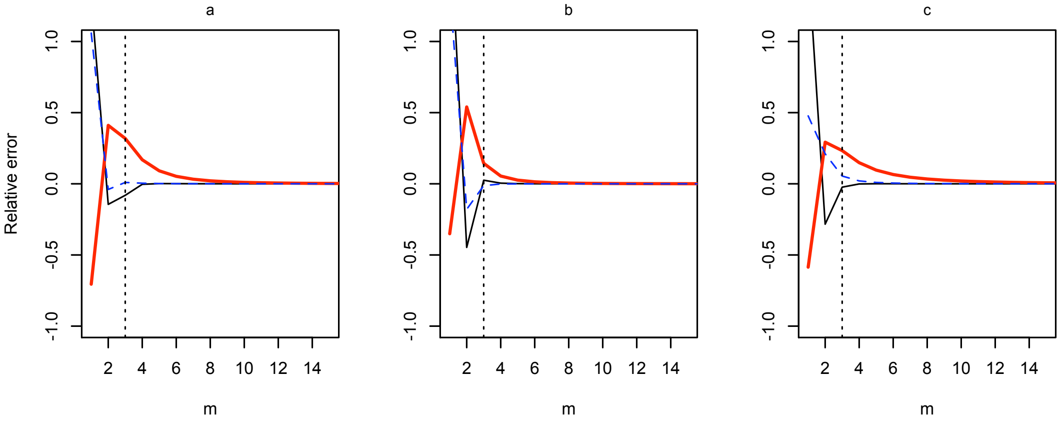

FIGURE 4.3 – Approximation error in modeling the decomposition of organic matter by different number of pools m. The relative error was calculated as $(C^{m}_{t=5} - C^{500}_{t=5})/C^{500}_{t=5}$, where $C^{m}_{t=5}$ is the amount of carbon remaining after 5 time steps using m number of pools and $C^{500}_{t=5}$ the same amount using 500 different pools. a) Combination of a linear decomposition rate and a symmetric distribution (thin black), an asymmetric distribution skewed towards low quality (thick red), and asymmetric skewed towards high quality (dashed blue). b) Same combinations as in (a) but with a convex function between q and k. d) Same combinations but with a concave function. The vertical line indicates the predicted values when decomposition is modeled with only 3 pools.

widely used for theoretical predictions of ecosystem behavior, mostly using analytical solutions of systems of differential equations centered on the first moment (i.e., the mean) of the distribution of qualities.

We implemented the continuous quality model in a numerical framework to explore the effects of different representations of substrate heterogeneity in the cycling of C and N. One of the advantages of our approach is that we can represent different shapes of the distribution of carbon in the quality continuum without restricting our analysis to the first (mean) or second moments (variance) of these distributions.

4.3.3 Model description

Göran I. Ågren and Ernesto Bosatta developed a mathematical theory for carbon and nutrient cycling using the concept of quality continuum. Their continuous-quality theory has been developed over the years and it is well described in Bosatta & Ågren

(1985, 1991), and Ågren & Bosatta (1998). Here we briefly present the main equations used to implement the continuous quality theory in a numerical framework. We begin by presenting the conceptual dynamic equations for carbon and nitrogen and then we present particular solutions for this system. Specific details about the solutions presented here can be found in Ågren & Bosatta (1998).

The dynamic equation for carbon is given by

$$\frac{\partial \rho_C(q,t)}{\partial t} = -\frac{f_C u(q) \rho_C(q,t)}{e(q)} + \int_0^\infty f_C D(q,q') u(q') \rho_C(q',t)\, dq', \tag{4.5}$$

and for nitrogen by

$$\frac{\partial \rho_N(q,t)}{\partial t} = -\frac{f_C u(q)}{e(q)} \rho_N(q,t) + \int_0^\infty f_N(q) D(q,q') u(q') \rho_C(q',t)\, dq', \tag{4.6}$$

where $\rho_C(q,t)$ and $\rho_N(q,t)$ are the density functions of carbon and nitrogen, and $\rho_C(q',t)\, dq$ is the amount of carbon in the interval of qualities $[q, q+dq]$. Additionally, f_C and f_N are the concentration of carbon and nitrogen in the decomposer biomass, which here are assumed to be constant or homeostatic (Sterner & Elser 2002). The decomposer growth rate as a function of litter quality is represented by $u(q)$, with an efficiency $e(q)$ that represents the production-to-assimilation ratio of the decomposers. $D(q,q')$ is a function that represents how carbon is moved from quality q' to q. The first term in both equations (4.5 and 4.6) represent the net amount of carbon and nitrogen that is taken up by the decomposers from the soil organic matter. The second term represents how carbon and nitrogen is transferred within the range of qualities. Since changes in quality do not imply gains or losses of substrate (conservation of mass), $\int_0^\infty D(q,q')dq = 1$, we can simplify equation (4.5) to obtain the time derivative of the amount of carbon

$$\frac{dC(t)}{dt} = \int_0^\infty -\frac{f_C u(q)\rho_C(q,t)}{e(q)} + f_C u(q)\rho_C(q,t)\,dq \tag{4.7}$$

$$= -\int_0^\infty \frac{1-e(q)}{e(q)} f_C u(q)\rho_C(q,t)\,dq \tag{4.8}$$

$$= -\int_0^\infty k(q)\rho_C(q,t)\,dq, \tag{4.9}$$

where

$$k(q) = f_C u(q)\frac{1-e(q)}{e(q)}. \tag{4.10}$$

A simple solution for equation (4.9) can be obtained assuming that decomposers do not modify the quality of the substrate, in which case

$$\rho_C(q,t) = \rho_C(q,0)\exp(-k(q)t), \tag{4.11}$$

and

$$C(t) = \int_0^\infty \rho_C(q,t)dq. \tag{4.12}$$

Notice that equation (4.11 and 4.12) are the continuous equivalents of equations (4.1 and 4.2), but in this case the decomposition rate k is expressed in terms of the growth rate and the efficiency of the decomposers (equation 4.10).

The solution of equation (4.6) can be obtained similarly as above for carbon, assuming initial conditions for the N:C ratio in litter given by $r_0 = N(0)/C(0)$, which yields

$$\rho_N(q,t) = \rho_C(q,t)\left[\frac{f_N}{f_C} - \left(\frac{f_N}{f_C} - r_0\right)\exp\left(-f_C u(q)t\right)\right], \tag{4.13}$$

and

$$N(t) = \int_0^\infty \rho_N(q,t)\,dq. \tag{4.14}$$

The dependency of e and u on q can be represented by the following equations

$$e(q) = e_0 + e_1 q^{\alpha}, \tag{4.15}$$

$$u(q) = u_0 q^{\beta}, \tag{4.16}$$

with q expressed in relative terms; i.e, $q \in [0, 1]$. The coefficients α and β represent the rate at which e and u increase with quality. One interpretation of β is that it can represent the degree of physical protection of organic matter (Bosatta & Ågren 1985, Ågren & Bosatta 1996). As the quality increases, the material can become more physically accessible increasing its surface area. A value of $\beta = 3$ captures this physical protection.

4.3.4 Numerical implementation

Given that the set of equations above provides an analytical solution to the dynamic problem (equations 4.5 and 4.6), the numerical implementation of this model does not incur errors associated with finding a solution for the system of partial differential equations. However, this numerical implementation may introduce approximation error, but as shown in Figure (4.3), with a large number of pools the approximation error is basically zero.

The first step for the numerical implementation of the model was defining quality as a vector of length m (number of pools), such $\mathbf{q} = \{q_1, q_2, \ldots q_m\}$. Then we can define the initial conditions for the distribution of carbon in vector form $\rho_{\mathbf{C}}(\mathbf{q}, 0)$ calculating the density for each element of $\mathbf{q}$ from a known probability density function. Initial conditions for nitrogen are then given by the vector $\rho_{\mathbf{N}}(\mathbf{q}, 0) = r_0 \rho_{\mathbf{C}}(\mathbf{q}, 0)$. Total amounts of carbon and nitrogen at each time step are calculated as

$$C(t) = \sum_{q=1}^{m} \rho_{C_q}, \tag{4.17}$$

$$N(t) = \sum_{q=1}^{m} \rho_{N_q}. \tag{4.18}$$

For each quality q, ρ_{C_q} and ρ_{N_q} are calculated with equations (4.11) and (4.13), respectively. To assure a negligible approximation error, we ran the model for $m = 500$.

4.3.5 Distribution of carbon and decomposition rates in the quality continuum: effects on carbon and nitrogen release

There are two important characteristics that help to define how heterogeneous a substrate is. One is the way different amounts of carbon are distributed along the quality axis, and the other is how decomposition resistance changes with quality. The combination of these two characteristics can potentially create behaviors in the dynamics of carbon and nitrogen that might be impossible to predict by modeling decomposition with a homogeneous substrate.

Different combinations of the shapes of the relationships between quality and decomposition resistance, and quality and carbon density, were considered in this analysis. Different parameter combinations of the model described above were used to define quality in various forms (Table 4.1, Figure 4.4). The purpose of these different definitions was to explore how different function shapes can affect litter decomposition and the subsequent mineralization of carbon and nitrogen.

Since the decomposition rate k is a familiar concept to ecologists and it encapsulates the effect of decomposers on the decomposition process (equation 4.10), we chose four different functional forms of the relationship between decomposition rate and quality to represent substrate heterogeneity. For comparison purposes, the first functional form considered was a constant decomposition rate for all qualities. This is similar to assuming

TABLE 4.1 – Functional relationships considered for representing the efficiency $e(q)$ and growth rate $u(q)$ of decomposers. See also Figure 4.4.

Function shape	$e(q) =$	$u(q) =$	Comments
Constant	0.2	0.25	Efficiency and growth rate are independent of quality.
Linear	0.2	$0.5q$	The growth rate of decomposers only depends on quality. No physical protection.
Convex	$0.2q^{2.4}$	$0.5q^3$	Efficiency grows faster for lower than for higher qualities (Figure D-8). Organic matter is physically protected.
Concave	$0.2q^{0.5}$	$0.5q^3$	Efficiency grows faster for higher than lower qualities (Figure D-8). Organic matter is physically protected.

a homogeneous substrate that decomposes at a single rate (Figure 4.4). Biologically, this assumption is equivalent to a process in which the efficiency and the growth rate of decomposers is always constant and independent of quality (Table 4.1).

The second functional form chosen was a linear and increasing relationship between decomposition rate and quality (Figure 4.4). The assumption is that decomposition resistance increases linearly as quality decreases. This shape is obtained by assuming that decomposer efficiency is constant for all qualities and decomposer growth rates increase linearly with quality (Table 4.1). In this case $\beta = 1$, which is equivalent to assuming that the accessibility of the substrate increases linearly with quality (Bosatta & Ågren 1985, Ågren & Bosatta 1996). Physical protection of organic matter was represented by setting $\beta = 3$, which is the parameter chosen for the other functional forms considered.

Convex and concave relationships between quality and decomposition rate were also considered to contrast the rates at which decomposition resistance decreases with increases in quality (Figure 4.4). For lower qualities the resistance to decomposition can decrease

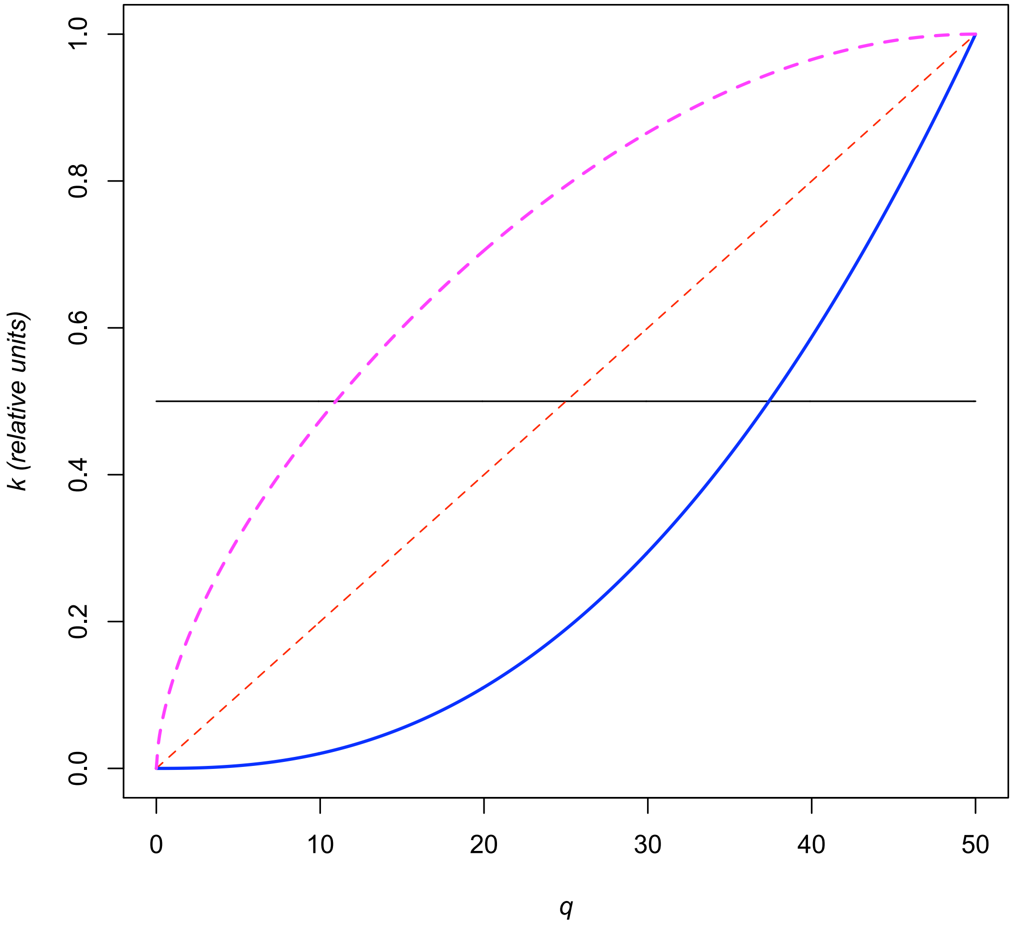

FIGURE 4.4 – Hypothetical shapes of the relationship between quality and decomposition rate. Quality q is in arbitrary units while k is in relative units. Constant: thin black, linear: thin-dashed red, convex: thick blue, concave: thick-dashed purple. See Table 4.1 for details about assumptions for each functional shape.

rapidly, which leads to a concave functional form. In contrast, if decomposition resistance decreases slowly as quality increases the functional form is convex. These functional shapes were obtained by representing the efficiency of decomposers as either concave or convex functions of quality (Table 4.1).

These functional forms were combined with different assumptions about the initial distribution of carbon among different qualities (Figure 4.5). For this purpose we used different probability density functions to assign values of carbon density to all the m ranges of quality. First, we considered the assumption that all carbon is centered around an average value of quality μ_1 with variance σ_1^2, which can be represented with a density function $S_1 = f(q) \sim N(\mu_1, \sigma_1^2)$. The second distribution of qualities assumed was also centered on an average value μ_1 but with larger spread, such that its variance was twice as large as the variance considered in the first distribution assumed; i.e., $\sigma_2^2 = 2\sigma_1^2$ and $S_2 = f(q) \sim N(\mu_1, \sigma_2^2)$ (Figure 4.5).

We also assumed that the initial amount of carbon in the substrate can be skewed towards either lower or higher qualities. To represent these assumptions we used the Beta probability distribution, scaled to an arbitrary range of qualities (Figure 4.5). These two distributions mirror each other, so $S_3 = f(q) \sim \mathrm{B}(a, b)$ and $S_4 = f(q) \sim \mathrm{B}(b, a)$. Values for a and b were chosen such that $\sigma_3^2 = \sigma_4^2 = \sigma_2^2$.

The combination of these assumptions provided insights into the effects of substrate heterogeneity on the temporal dynamics of carbon and nitrogen during decomposition of a single cohort of organic matter (Figures 4.6 and 4.7). We observed that an increase in variance of the distribution of qualities did not affect the behavior of the release of C and N (Figure 4.6). However, more interesting behaviors were obtained with the different functional forms for the relationship between decomposition rate and quality. The assumption of constant decomposition rate for all qualities provided the same results as the assumption of a linear increase of decomposition rate with quality. This result sug-

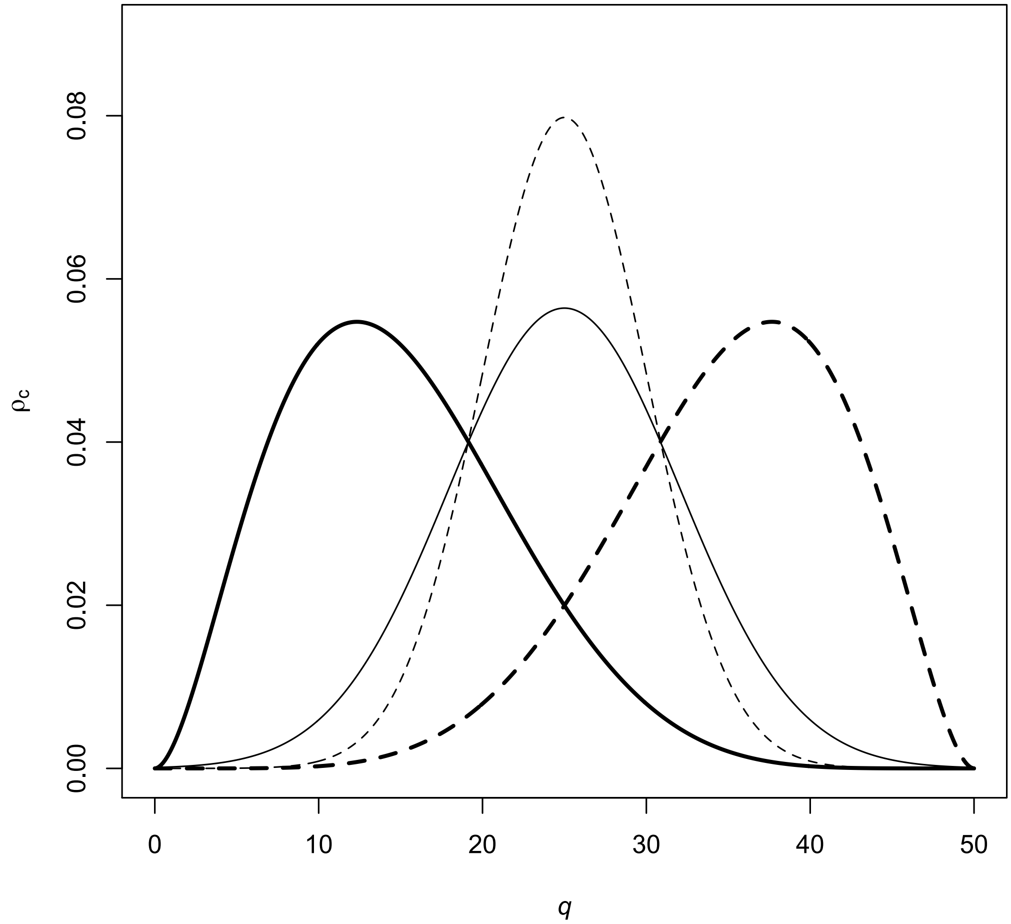

FIGURE 4.5 – Density functions representing the initial distribution of carbon $\rho_c(q,0)$ in the quality continuum. Quality q takes arbitrary values between 0 and 50. Thin dashed line: $N(\mu_1,\sigma_1^2)$, thin continuous line: $N(\mu_1,2\sigma_1^2)$, thick continuous line $\mathrm{B}(a,b)$, thick dashed line $\mathrm{B}(b,a)$; $m=500$.

gests that the assumption of a homogeneous substrate can be valid when decomposition rate increases linearly with quality, provided that the distribution of the substrate in the quality continuum is symmetric (see below). Relative to the constant and linear assumptions, convexity or concavity of the relationship between k and q can lead to slow or fast carbon release, respectively (Figure 4.6a, b). The same was true for nitrogen, with a convex function leading to nitrogen immobilization (demand driven N accumulation) and a concave function leading directly to mineralization without an immobilization phase. This result is a consequence of the differences in decomposer efficiencies represented in the two functional forms (Table 4.1).

Introduction of skewness in the distribution of the initial amount of carbon provided additional interesting insights. The results showed that with asymmetric distributions the constant and linear shapes produce different behaviors in the mineralization of carbon and nitrogen (Figure 4.7). This result suggests that the assumption of an homogeneous substrate does not hold when carbon is skewed to recalcitrant or labile fractions, even when quality and decomposition rates are linearly related. Another interesting result is that the asymmetry of the distribution of carbon determines how fast element mineralization proceeds. If the substrate is skewed towards low quality substrate, element mineralization proceeds slowly, and the opposite behavior is true for substrate skewed to high quality. This behavior is the result of the weighting of the decomposition rates by the distribution of carbon in different qualities. In addition, the skewness of the substrate contributes to determine the timing and the amount of nitrogen mineralization (Figure 4.7).

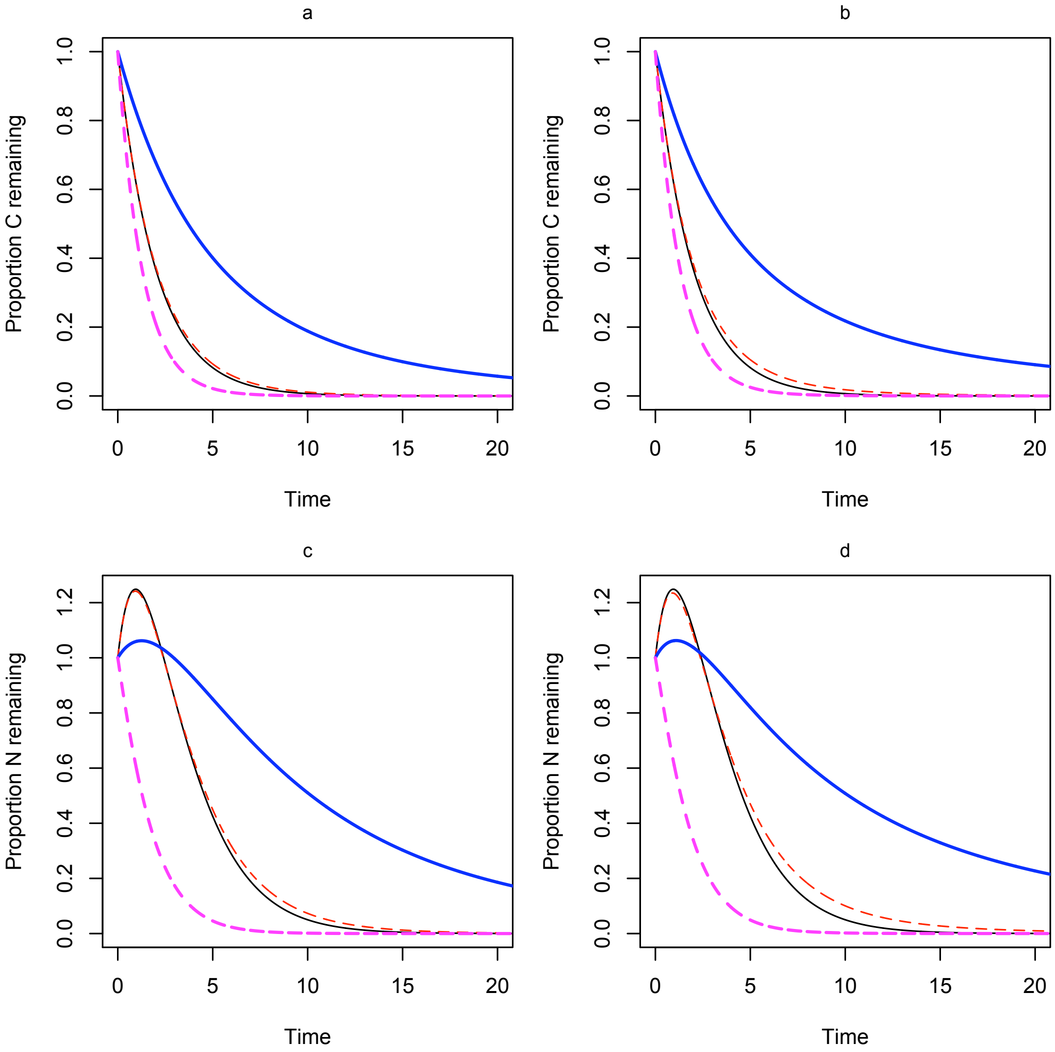

FIGURE 4.6 – Temporal dynamics of carbon and nitrogen for two different assumptions about the initial distribution of carbon in different qualities. Panels a) and c) $N(\mu_1, \sigma_1^2)$; b) and d) $N(\mu_1, 2\sigma_1^2)$. The shape of the function between quality and decomposition rate is represented with different colors in all panels: constant: thin black, linear: thin-dashed red, convex: thick blue, concave: thick-dashed purple.

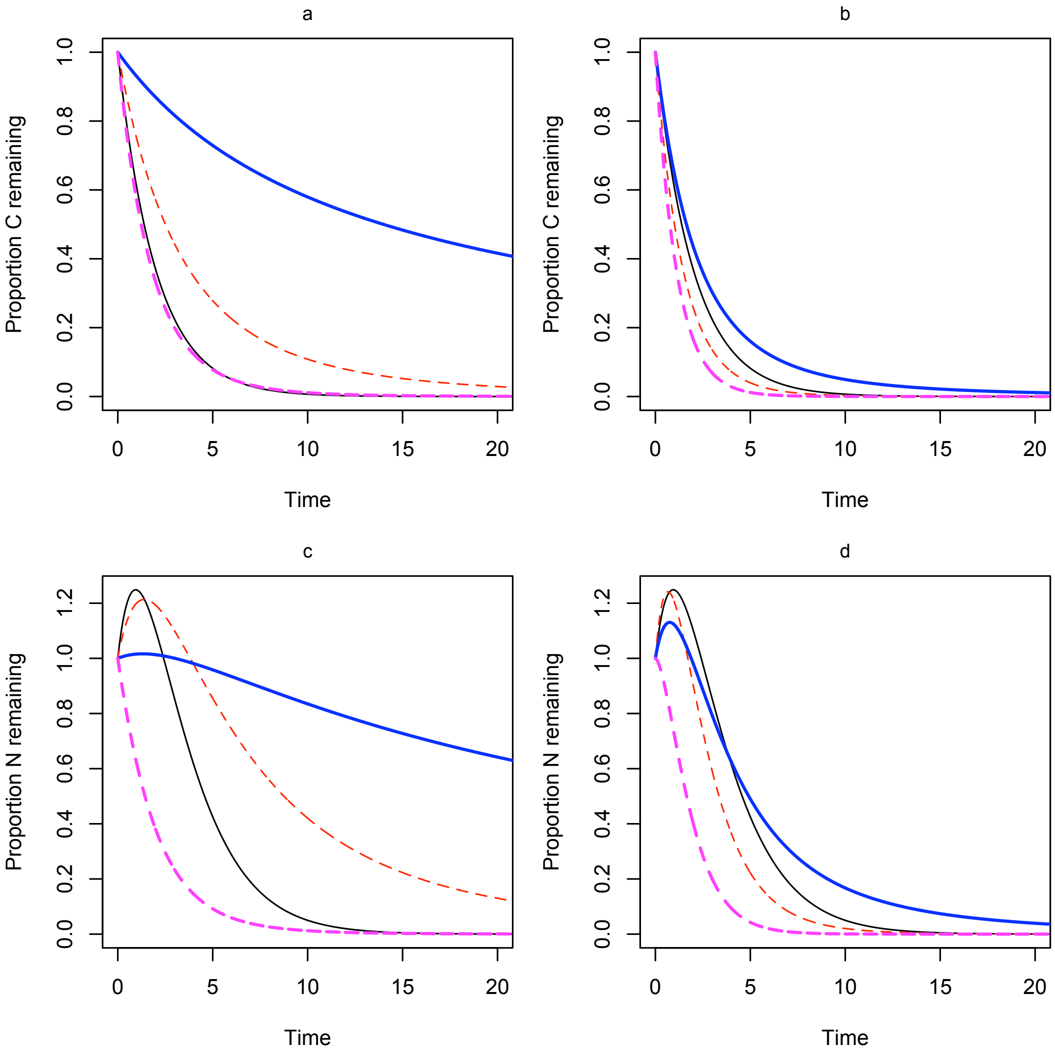

FIGURE 4.7 – Temporal dynamics of carbon and nitrogen for two different assumptions about the initial distribution of carbon in different qualities. Panels a) and c) asymmetric distribution skewed towards lower qualities $\mathrm{B}(a, b)$; b) and d) asymmetric skewed towards higher qualities $\mathrm{B}(b, a)$. The shape of the function between quality and decomposition rate is represented with different colors in all panels: constant: thin black, linear: thin-dashed red, convex: thick blue, concave: thick-dashed purple.

4.3.6 The C:N ratio

In all simulations above the initial C:N ratio of the substrate was 100:1. As time proceeds the C:N ratio for each quality class can be calculated as

$$\frac{\rho_C(q,t)}{\rho_N(q,t)} = \frac{1}{\frac{f_N}{f_C} - \left(\frac{f_N}{f_C} - r_0\right)\exp(-f_C u(q)t)}. \tag{4.19}$$

When $q \neq 0$ the C:N ratio of the final substrate approaches the C:N ratio of the decomposers, since

$$\lim_{t\to\infty} \frac{\rho_C(q \neq 0,t)}{\rho_N(q \neq 0,t)} = \frac{f_C}{f_N}. \tag{4.20}$$

When $q = 0$ the growth rate of the decomposers is zero for all of the assumptions above, except when we assume a constant growth rate for all quality classes (Figure 4.4, Table 4.1); therefore the C:N ratio of the lowest quality class is the same as the ratio of the initial substrate since

$$\lim_{t\to\infty} \frac{\rho_C(q = 0,t)}{\rho_N(q = 0,t)} = \frac{1}{r_0} = \frac{C(0)}{N(0)}. \tag{4.21}$$

The lowest quality class, which has a decomposition rate $k = 0$ in most assumptions being considered in this analysis, remains undecomposed so the final C:N ratio of the whole cohort reflects the C:N ratio of the class that does not decompose. Although the amount of carbon and nitrogen remaining in this class is small, the total final C:N ratio is highly sensitive to the C:N ratio of the lowest quality class.

4.3.7 Quality transformations during decomposition

In the previous sections we have assumed that the quality of the substrate does not change over time. This assumption is problematic because it is well known that decomposers transform organic matter in a myriad of different chemical compounds (Swift et al. 1979, Sollins et al. 1996). It is also well known that, over time, a portion of the original organic matter that enters the soil is sequentially transformed into recalcitrant compounds. Recalcitrant organic matter is highly resistant to degradation by microbes and enzymes with prolonged turnover times in soils.

In addition to microbial transformations, other physical and chemical factors interact to produce *stable* organic matter. Stabilization is the integrated effect of different biological, physical, and chemical mechanisms that protect organic matter from mineralization (Sollins et al. 1996, Lützow et al. 2006). A substrate could be stable but not necessarily recalcitrant if it is physically or chemically protected; nevertheless, a stable substrate is highly resistant to degradation and has long turnover times.

Simultaneous to stabilization is the process of destabilization (Sollins et al. 1996). This process yields material that is more susceptible to microbial consumption and is controlled by the same factors that lead to stabilization but acting in opposite directions. Although destabilization is a process as important as stabilization it has not received as much attention (e.g., Baldock et al. 2004, Lützow et al. 2006). In theory, a model of decomposition should include both processes simultaneously.

The continuous quality theory presented above (section 4.3.3) is adequate to represent changes in quality due to microbial transformations that lead to recalcitrance, but falls short in representing the more broad process of organic matter stabilization and destabilization in soils. Solutions to the dynamic system (equations 4.5 and 4.6) have been developed using dispersion models that depend on the growth rate and efficiency of the decomposers (Ågren & Bosatta 1998, Bruun et al. 2009). Although it would be useful to introduce physical and chemical controls on these dispersion functions the solution to the system of PDEs might be analytically intractable.

Here we take a different approach for representing transformations in litter quality during the decomposition process. Our main assumption is that the substrate is continually being transformed in quality, but not necessarily as a direct effect of decomposer activity. The change in quality is represented as a Markov process, in which quality is considered as a state variable with finite transition probabilities within the quality domain.

4.3.8 The Markov process

Transformations in the quality of organic matter at each time step are represented as a Markov process (Bharucha-Reid 1960), in which a transition matrix is used to calculate the amounts of substrate that are transferred among quality classes.

Assume that at each time step the transition from quality j to quality i is given by the transition matrix $\mathbf{P}$

$$\mathbf{P} = \begin{pmatrix} p_{11} & p_{12} & \cdots & p_{1j} & \cdots & p_{1m} \\ p_{21} & p_{22} & \cdots & p_{2j} & \cdots & p_{2m} \\ \vdots & \vdots & \ddots & \vdots & \cdots & \vdots \\ p_{i1} & p_{i2} & \cdots & p_{ij} & \cdots & p_{im} \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots \\ p_{m1} & p_{m2} & \cdots & p_{mj} & \cdots & p_{mm} \end{pmatrix}$$

and the distribution of carbon in all m qualities at time $t = 0$ is given by the vector $\rho_{\mathbf{C}}(\mathbf{q}, 0)$; i.e., the initial state of the system

$$\rho_{\mathbf{C}}(\mathbf{q}, 0) = \begin{pmatrix} \rho_C(1,0) \\ \rho_C(2,0) \\ \vdots \\ \rho_C(m,0) \end{pmatrix}.$$

We can set values for all transition probabilities p_{ij} according to certain assumptions about the behavior of the system, with the only requirement that $\sum_i p_{ij} = 1$. Transitions from time-step n to $n+1$ can be obtained by the product $\mathbf{P}\,\rho_{\mathbf{C}}$, but we need to represent the dynamic behavior of the system first.

We will continue using the approach of representing quality in m different classes, but now instead of using m analytical solutions we will find m numerical approximations to the system of differential equations for each time step n, with l representing the size of each time increment. This approach will allow us to introduce the transition scheme at each time step. The state of the system at some time $n+1$ will be represented by $\mathbf{U}^{n+1}$, which is the result of the update of the system by the transition matrix $\mathbf{P}$ and an r-order finite difference approximation $D_r f'(\mathbf{U}^n)$ to the system of differential equations for C and N, so

$$\mathbf{U}^{n+1} = \mathbf{P}(\mathbf{U}^n + l\, D_r f'(\mathbf{U}^n)). \tag{4.22}$$

which is equivalent to

$$\mathbf{U}^{n+1} = \mathbf{P}\left[\begin{pmatrix} \rho_{C,q_1}(n) & \rho_{N,q_1}(n) \\ \rho_{C,q_1}(n) & \rho_{N,q_1}(n) \\ \vdots & \vdots \\ \rho_{C,q_m}(n) & \rho_{N,q_m}(n) \end{pmatrix} + l \begin{pmatrix} D_r f'(\rho_{C,q_1}) & D_r f'(\rho_{N,q_1}) \\ D_r f'(\rho_{C,q_2}) & D_r f'(\rho_{N,q_2}) \\ \vdots & \vdots \\ D_r f'(\rho_{C,q_m})t & D_r f'(\rho_{N,q_m}) \end{pmatrix}\right], \tag{4.23}$$

where for each $q \in \{q_1, \ldots, q_m\}$ the system of differential equations is given by

$$f'(\rho_{C,q}) = \frac{d\rho_{C,q}}{dt} = -k_q \rho_{C,q} \tag{4.24}$$

$$f'(\rho_{N,q}) = \frac{d\rho_{N,q}}{dt} = \frac{-f_C u_q}{e_q}\rho_{N,q} + f_N u_q \rho_{C,q}. \tag{4.25}$$

The finite difference approximation chosen to find solutions for the m systems in (4.23) was the fourth-order Runge-Kutta method, which in general provides solutions with high accuracy; that is $E = O(l^4)$ (LeVeque 2007).

4.3.9 Stabilization and destabilization of organic matter

Since we already have relationships to obtain values of u_q and e_q for each quality class, we only need to specify $\mathbf{P}$ to solve equation (4.22). Although the Markovian structure of (4.22) provides opportunities for representing complex transitions in the quality domain, we will take a very simple approach here to test two different assumptions about sequential transformations of quality. First, we assume that at each time step a portion of the carbon is transferred to the immediately adjacent quality class in the direction towards lower quality. There are no transitions to better quality classes. This is equivalent to assuming no destabilization mechanisms, or that stabilization outweighs any destabilization process.

Assuming that at each time step the amount of carbon that is transferred to the adjacent quality class is 50% of the current amount, then

$$\mathbf{P_1} = \begin{pmatrix} 1 & 0.5 & 0 & \cdots & 0 \\ 0 & 0.5 & 0.5 & \cdots & 0 \\ \vdots & 0 & 0.5 & \cdots & \vdots \\ \vdots & \vdots & \vdots & \ddots & 0.5 \\ 0 & 0 & 0 & \cdots & 0.5 \end{pmatrix}.$$

Notice that the first element implies that once a certain amount of carbon is transferred to the lowest quality class, it remains confined there indefinitely. In other words, once certain amount of carbon is transformed to a stable compound it cannot be transformed into a substrate of better quality.

The second assumption considered includes destabilization processes for each quality class. At each time step we assumed that 50% of the substrate stays in the same class while 25% is transferred to the adjacent higher quality class and 25% gets transferred to the adjacent lower quality class. For the lowest quality class we assumed that 25%

of the material is destabilized at each time step, so the transition matrix for our second assumption is defined as

$$\mathbf{P_2} = \begin{pmatrix} 0.75 & 0.25 & 0 & \cdots & 0 \\ 0.25 & 0.5 & 0.25 & \cdots & 0 \\ 0 & 0.25 & 0.5 & \cdots & \vdots \\ \vdots & \vdots & \vdots & \ddots & 0.5 \\ 0 & 0 & 0 & \cdots & 0.5 \end{pmatrix}.$$

We incorporated this Markovian approach in the decomposition model for the two different assumptions $\mathbf{P_1}$ and $\mathbf{P_2}$ also assuming that the initial amount of carbon was normally distributed, and $m = 200$.

The model successfully represented the gradual change in the overall quality of the substrate over time as well as a reduction in the total amount of carbon and nitrogen as an effect of decomposer activity (Figure 4.8). Over time, for the stabilization assumption ($\mathbf{P_1}$), an increasing amount of carbon accumulates in the lowest quality class because the decomposition rate there is zero and the material does not transition to other quality classes. However, when the decomposition rate is constant for all quality classes, including the lowest quality class, carbon and nitrogen is lost continually from the system (Figure 4.8a and 4.10a). At the end of the simulation, all the carbon remaining is stored in the lowest quality class, with the total amount depending on the functional relationship between k and q (Figure D-9). For the assumption of simultaneous stabilization and destabilization, the final amount of carbon was stored in a wider range of quality classes, mainly of lower quality, with the exception of the constant functional shape (Figure D-10).

Decomposition proceeded faster when the relationship between k and q was represented with a concave function and slower when represented with a convex one (Figure 4.8c, d and 4.10). Although this was already observed in previous simulations, it can be

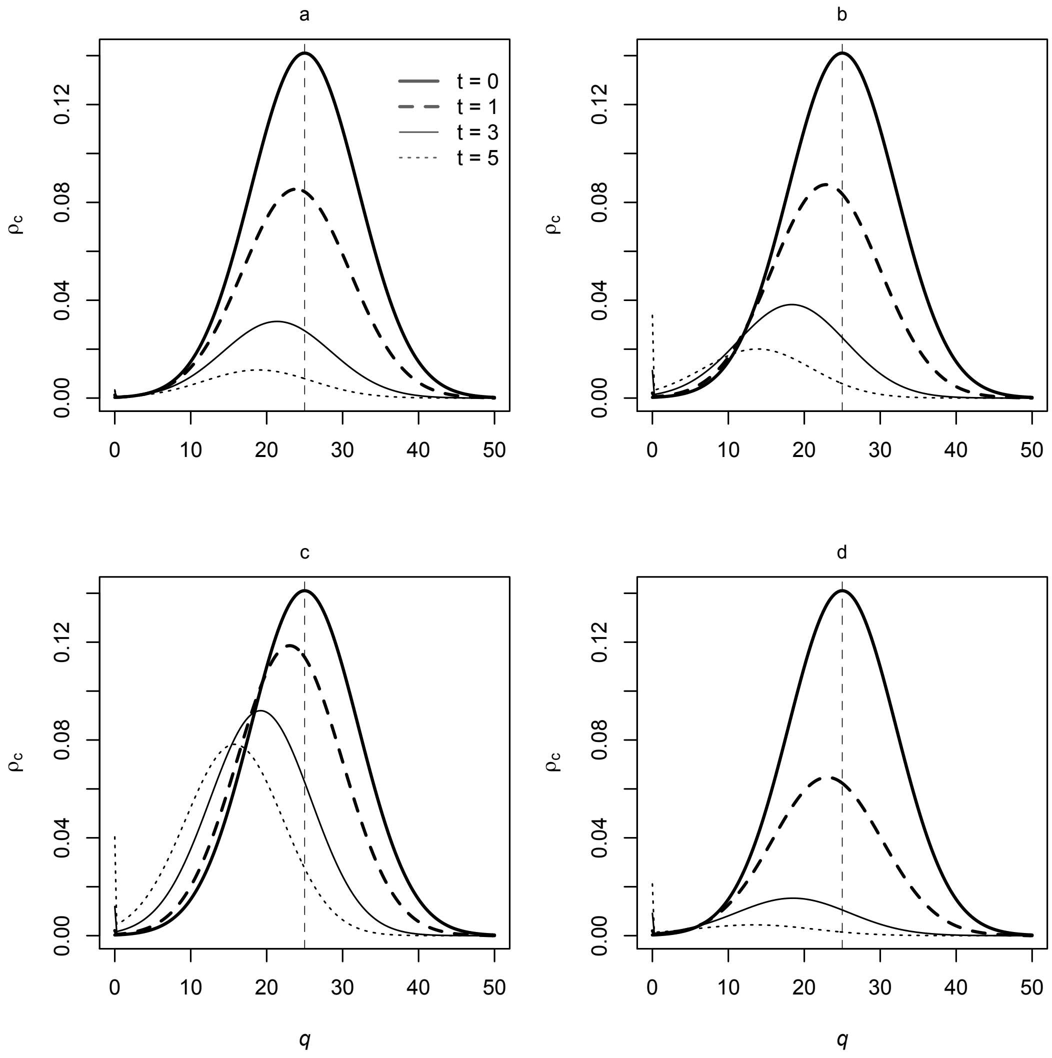

FIGURE 4.8 – Distributions of the density of carbon in the quality continuum at different time steps t assuming only stabilization processes ($\mathbf{P_1}$). Each panel depicts different assumptions about the relationship between k and q: a) constant, b) linear, c) convex, and d) concave.

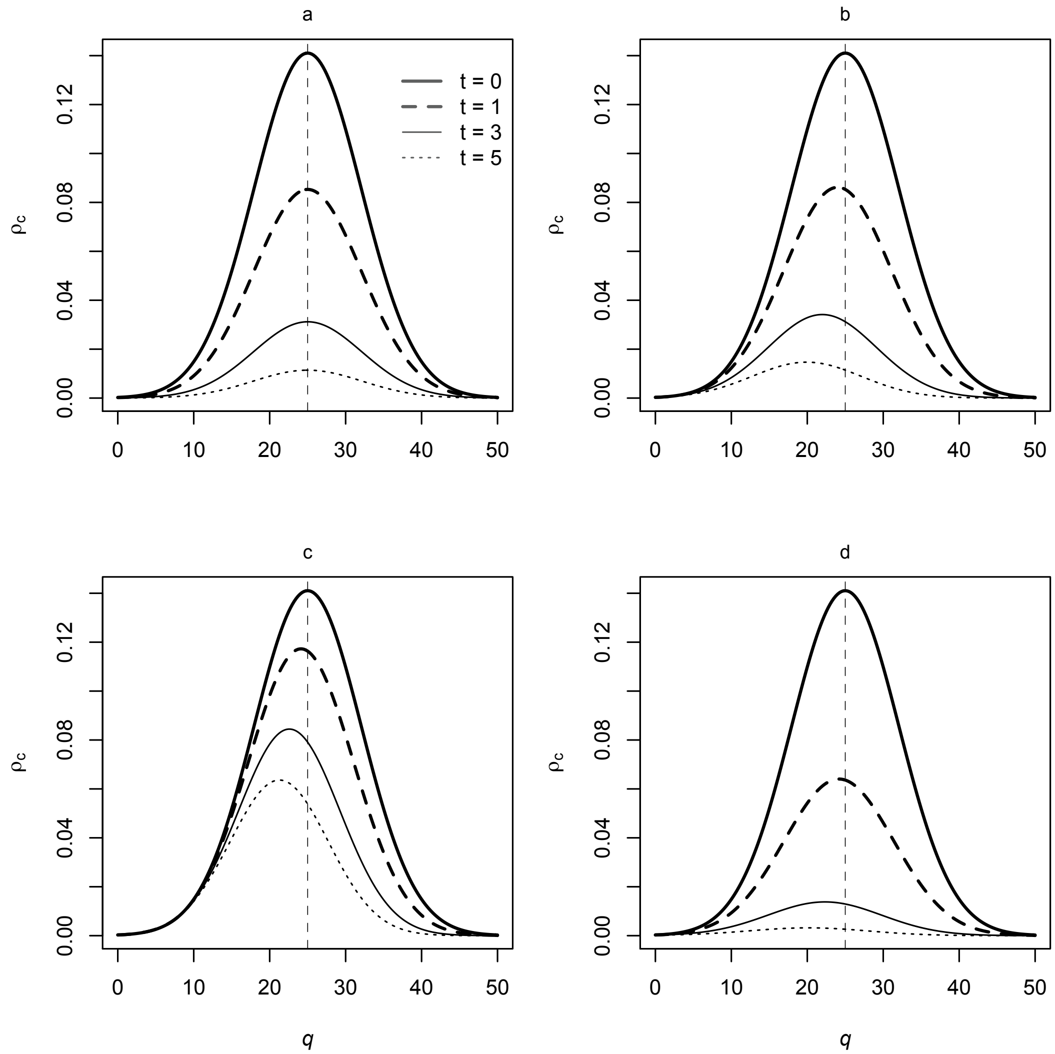

FIGURE 4.9 – Distributions of the density of carbon in the quality continuum at different time steps t assuming simultaneous stabilization and destabilization processes ($\mathbf{P_2}$). Each panel depicts different assumptions about the relationship between k and q: a) constant, b) linear, c) convex, and d) concave.

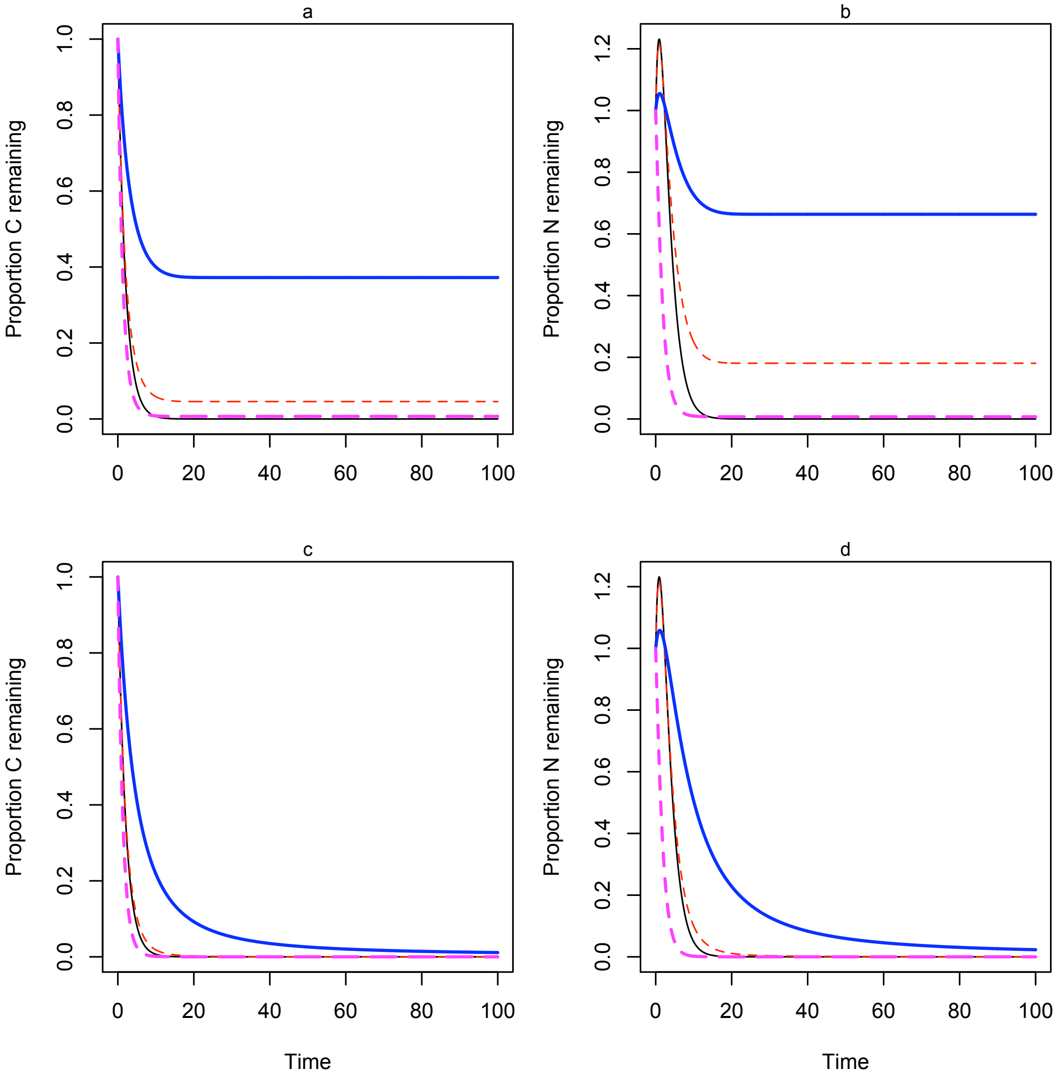

FIGURE 4.10 – Temporal behavior of the remaining amounts of carbon and nitrogen for the different assumptions of the relationship between k and q: constant: thin black, linear: thin-dashed red, convex: thick blue, concave: thick-dashed purple. Panels a and b for the assumption of stabilization only ($\mathbf{P_1}$), and panels c and d for the assumption of simultaneous stabilization and destabilization ($\mathbf{P_2}$).

seen in Figures (4.8c and d) that the convex shape leads to higher accumulation of stable undecomposable substrate. Since lower quality substrate decomposes faster in the concave functional form, decomposition proceeds faster and less material accumulates in the more stable fractions.

When both stabilization and destabilization were considered in the transition matrix, very small amounts of stable substrate remained at the end of the simulation period (Figures 4.10c and d). With the exception of a constant decomposition for all qualities, most of the remaining substrate was accumulated in the lower quality classes, decreasing exponentially to higher classes (Figure D-10). This is a more realistic distribution than when destabilization was not included in the transition matrix (Figure D-9). The assumption of constant decomposition leads to a final material similar in quality to the initial distribution of the substrate.

Similarly as carbon, the amount of nitrogen decreases over time and accumulates in the lower quality classes (Figure D-11). Although the amount of carbon and nitrogen is proportionally constant for the initial substrate; i.e., constant C:N ratio, the relative proportion of these elements in the substrate changes over time with a tendency to accumulate substrate of the same C:N ratio in the lower qualities.

4.4. Environmental variability

Until this point we have considered the process of decomposition for a single cohort occurring without perturbations of the external environment. We now will explore potential interactions of environmental variables on the decomposition process. However, before that we will introduce another important component to this model, which is the recurrent addition of multiple cohorts of substrate to the soil.

4.4.1 Litter inputs and their heterogeneity

Litter from aboveground plant parts and roots is by far the dominant input of organic matter to the soil. This litter enters the soil in a variety of amounts and qualities that depend on the dominant vegetation, its phenology, and the climate, among other factors. Litter quality for different pools is often defined by the chemical characteristics of the material such as the contents of nitrogen and carbon as well as the relative proportions of compounds such as lignin, cellulose, polyphenols, etc.

In this analysis we used a qualitative description of the distribution of carbon in different qualities for a small set of plant parts. Leaves, fine roots, branches, wood, bark and coarse roots were the different pools considered, and we defined hypothetical shapes of their carbon distribution in the quality continuum (Figure 4.11).

The distribution of carbon and nitrogen entering the soil at each time step n is given by

$$\mathbf{L}^n = \mathbf{L_{lv}}^n + \mathbf{L_{fr}}^n + \mathbf{L_{br}}^n + \mathbf{L_{wd}}^n + \mathbf{L_{bk}}^n + \mathbf{L_{cr}}^n \tag{4.26}$$

where $\mathbf{L}$ is a m-by-2 matrix that represents the distribution of carbon and nitrogen of incoming litter for each quality class. The subscripts represent different plant parts: lv: leaves, fr: fine roots, br: branches, wd: wood, bk: bark, cr: coarse roots. These distributions were produced using Beta probability distribution functions with arbitrary parameters selected to reproduce hypothetical shapes for each pool (see Figure 4.11).

The system of equations for representing organic matter decomposition can now be expressed to include litter inputs by simply adding the $\mathbf{L}^n$ term to (4.22),

$$\mathbf{U}^{n+1} = \mathbf{P}(\mathbf{U}^n + l\,D_r f'(\mathbf{U}^n)) + \mathbf{L}^n, \tag{4.27}$$

so now the system includes both inputs and losses to and from the soil. To include

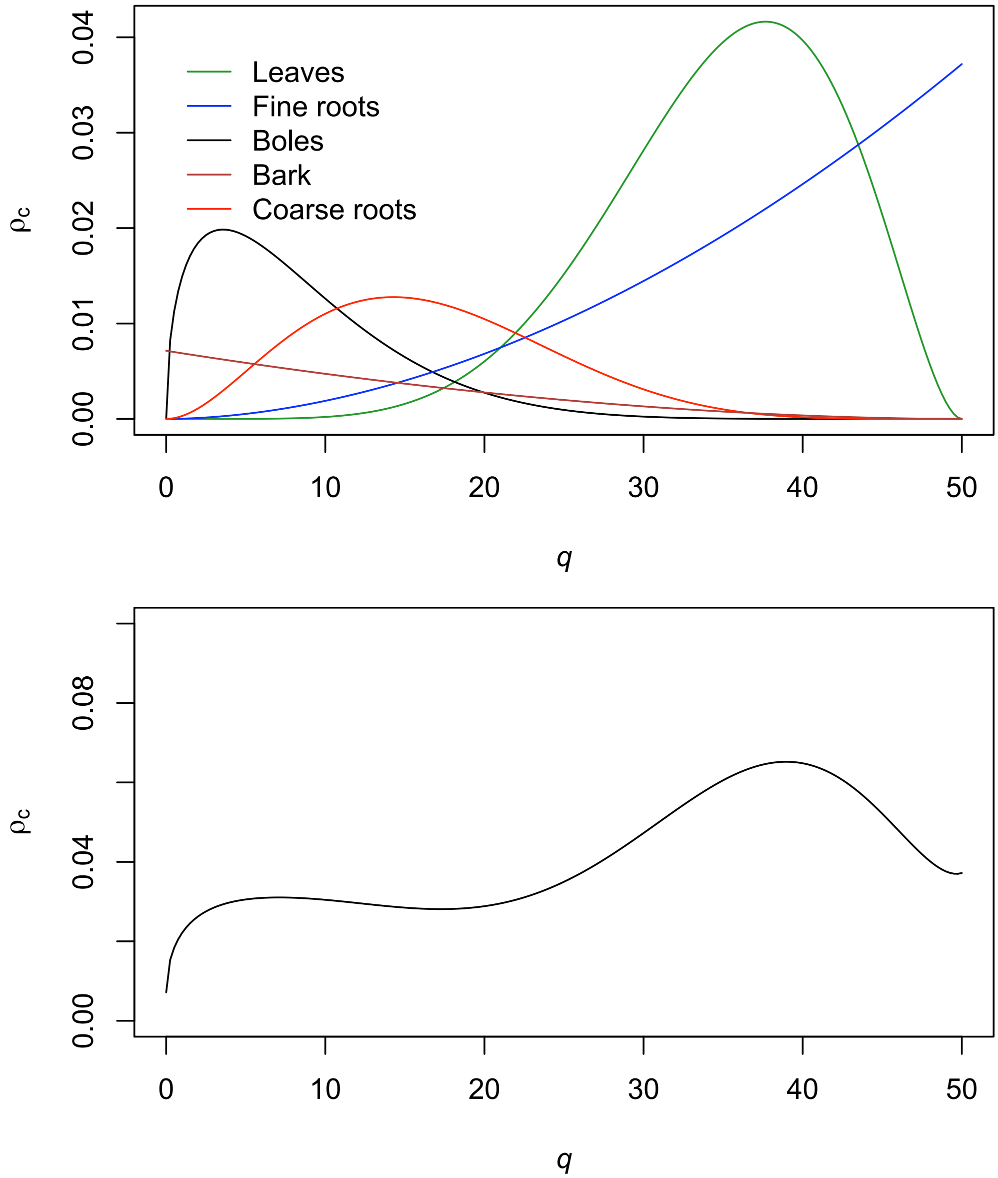

FIGURE 4.11 – Hypothetical distributions of carbon for different litter pools in the quality continuum. The upper panel shows the distribution of carbon for each individual pool and the lower panel the total amounts.

variability in the inputs of litter, we selected random amounts of carbon from a normally distributed average amount of inputs for each pool.

4.4.2 Accumulation of carbon and nitrogen over time

If only stabilization is included in the transition matrix, carbon and nitrogen accumulates linearly over time (Figures 4.12a and c). However, when decomposition is constant for all quality classes, the system quickly reaches steady state. In contrast, when stabilization and destabilization are both included in the transition matrix, the total amounts of carbon and nitrogen accumulate asymptotically (Figures 4.12b and d).

The final distribution of carbon tends to accumulate most of the substrate in the lower quality classes, with the exception of the constant functional shape, which presents a distribution of carbon similar to the distribution of the incoming litter (Figure 4.13). For the concave shape, which decomposes the substrate faster and reaches equilibrium faster than the other shapes, the amount of carbon in higher qualities is relatively high. This reflects the relative importance of the incoming material once the system has reached equilibrium.

A similar pattern was observed for nitrogen (Figure 4.14). The assumption of constant decomposition rates produces a distribution of nitrogen similar to the distribution in the incoming litter. For the other functional shapes, nitrogen tends to accumulate in the lower quality classes, but with a significant amount in higher qualities representing the incoming litter.

These results suggest that the substrate that accumulates over time tends to be of similar quality, with an important fraction accumulated in the lower qualities and a fraction accumulated in higher qualities representing the fresh litter. This distribution of substrate in different quality classes depends on the shape of the relationship between q and k. The concave shape, which decomposes lower quality faster than the other shapes, tends to accumulate significantly higher proportions of carbon in high quality classes.

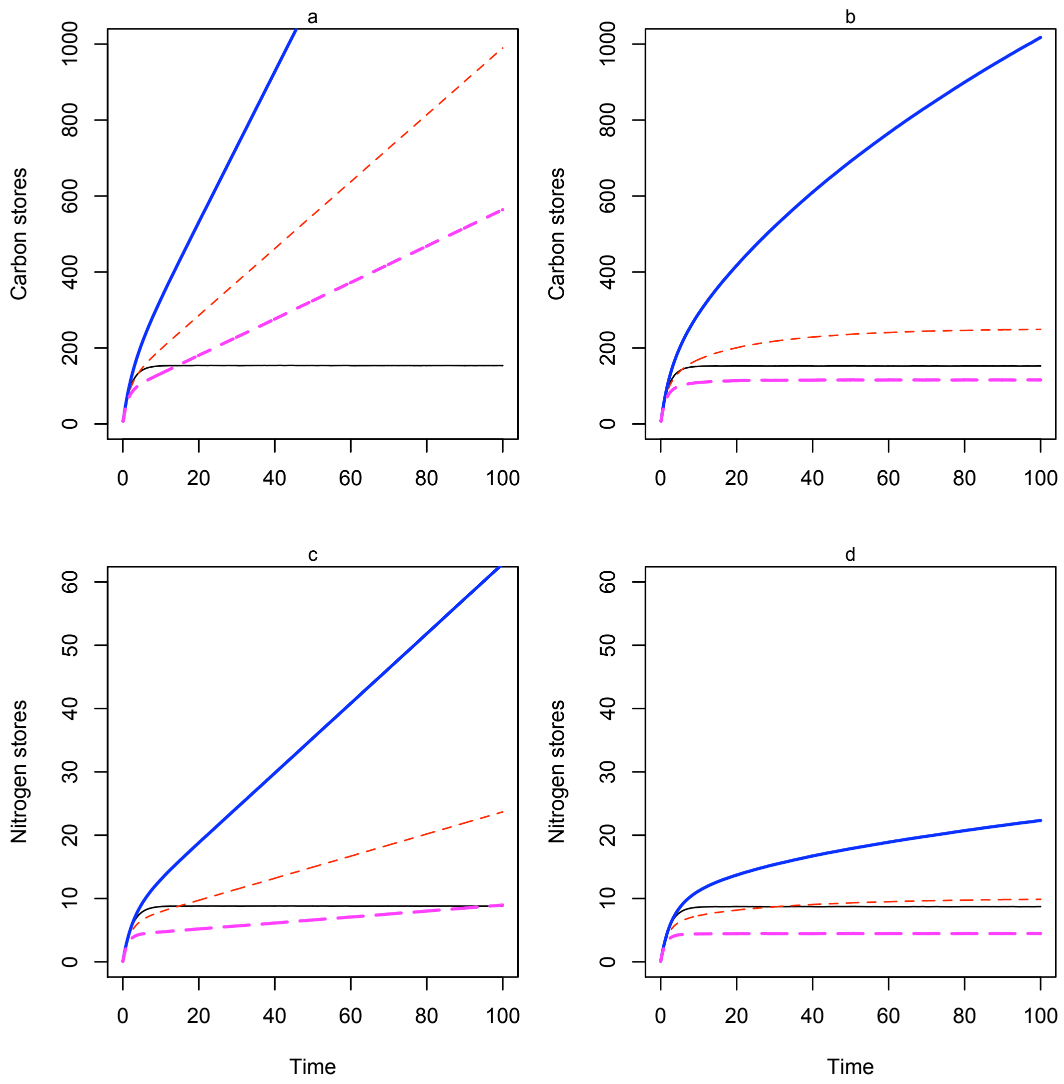

FIGURE 4.12 – Carbon and nitrogen stores over time for the assumption of stabilization only ($\mathbf{P_1}$) (panels a and c), and for the assumption of simultaneous stabilization and destabilization ($\mathbf{P_2}$) (panels b and d). Line colors represent the different functional shapes of the relationship between k and q. constant: thin black, linear: thin-dashed red, convex: thick blue, concave: thick-dashed purple.

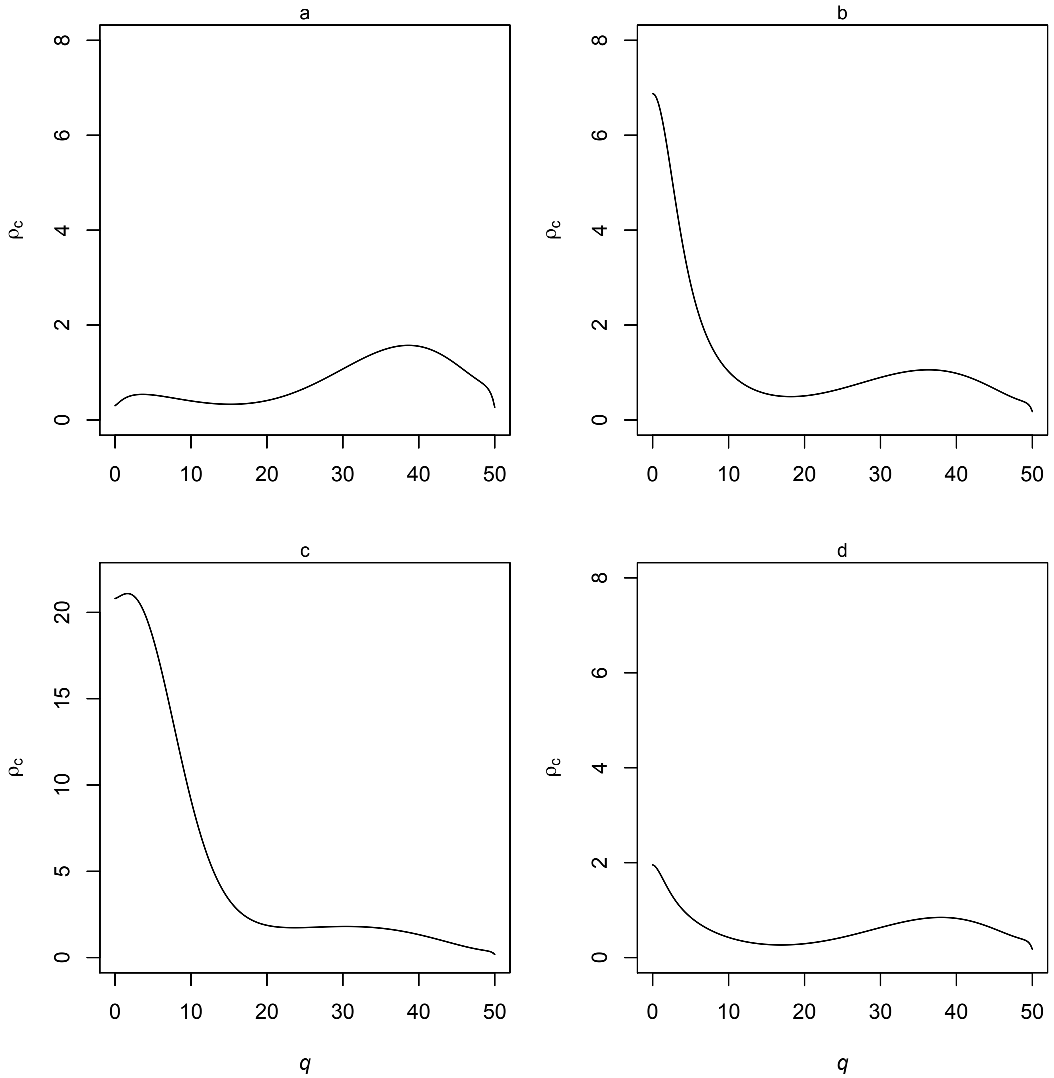

FIGURE 4.13 – Distribution of carbon at the final time step when both stabilization and destabilization are included in the transition matrix $\mathbf{P_2}$. Each panel represent different assumptions about the relationship between decomposition rate and quality, a) constant, b) linear, c) convex, and d) concave.

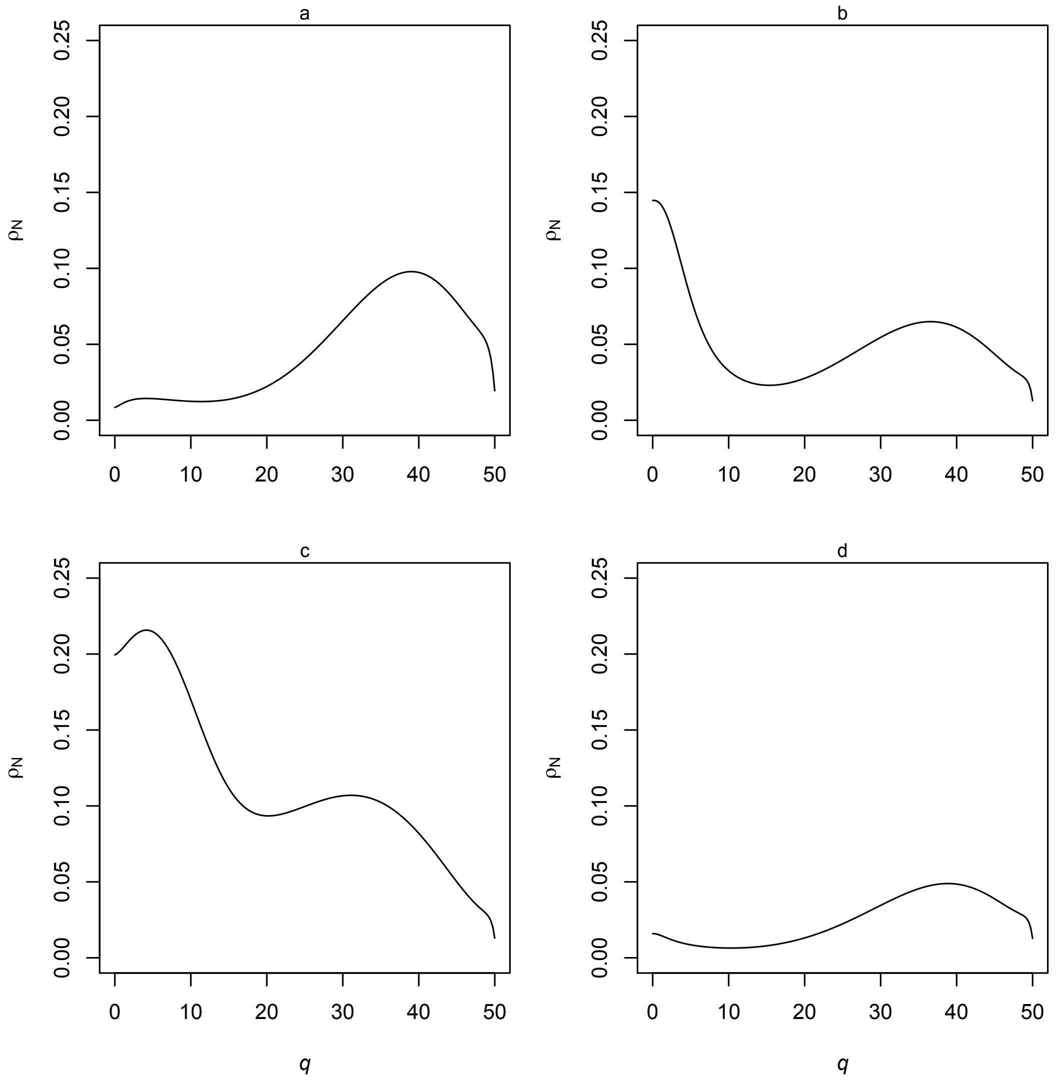

FIGURE 4.14 – Distribution of nitrogen at the final time step when both stabilization and destabilization are included in the transition matrix $\mathbf{P_2}$. Each panel represent different assumptions about the relationship between decomposition rate and quality, a) constant, b) linear, c) convex, and d) concave.

4.4.3 Temperature effects on decomposer growth rates

The rate at which decomposers grow and mineralize carbon and nutrients is highly dependent on temperature (Price & Sowers 2004, Davidson & Janssens 2006). The temperature dependance of microbial growth rates fit remarkably well the exponential models proposed by Arrhenius and Van't Hoff in the late 19th century (see Chapter 3). These exponential models can also be derived from thermodynamic concepts, which Bosatta & Ågren (1999) used to propose an equation for decomposer growth rates as a function of quality and temperature:

$$u(q, T) = u_0 e^{-E_a/\Re T q}, \tag{4.28}$$

where E_a is the activation energy, $\Re$ is the universal gas constant, T is the absolute temperature in Kelvin and u_0 a reference growth rate. In this equation the growth rate of the decomposers responds exponentially to changes in quality, which does not conform to the theoretical framework we have developed in this manuscript. An alternative representation can be given by

$$u(q, T) = (u_0 q^\beta) e^{-E_a/\Re T} \tag{4.29}$$

Equation (4.29) takes as a reference growth rate what would be predicted by each quality at a reference temperature and adjusts it by the sensitivity to temperature. Alternatively, the modified Van't Hoff model (Chapter 3) can be used to represent the temperature sensitivity of microbial growth using the Q_{10} parameter and a reference temperature T_{ref} as

$$u(q, T) = (u_0 q^\beta) Q_{10}^{\frac{(T - T_{ref})}{10}}. \tag{4.30}$$

With this representation we obtain a temperature response of microbial growth for each quality class, with less increase in decomposer growth for the lower than for the higher qualities (Figures D-12, D-13, and D-14).

We ran this model for a hypothetical average temperature of 12°C over 10 years and increased it gradually to 16°C over 5 years and observed the behavior of the system for an additional decade. As expected the model predicted a reduction of carbon after the temperature increase, but also provided some insights about which pools were losing more or less carbon (Figure 4.15). In all cases there were no reductions of carbon in the higher quality classes. This can be explained by the fact that carbon in these classes decays fast inherently so increases in temperature cannot further affect this high quality substrate. When decomposition is assumed to be constant for all quality classes, carbon is reduced in proportion to where it is most abundant, so the losses of carbon occur proportionally to the quality of the incoming litter. In all other cases, carbon is lost primarily from the most stable pools even though increases in temperature for these pools do not increase microbial growth as much as for higher qualities (Figures D-12, D-13, and D-14). The larger amounts of carbon released in low quality classes are due to a considerable amount of carbon stored there.

4.4.4 Interactions between substrate heterogeneity and temperature variability

In the previous chapter we found that due to the convexity of the relationship between temperature and soil respiration, increases in temperature variance amplify the amount of respiration whereas decreases in variance reduce it. In theory, the results from the previous chapter should apply also to the overall process of decomposition. However, in that analysis we assumed an homogeneous soil layer. To test whether or not the predictions of changes in variance would also apply to heterogeneous substrates, we ran our decomposition model for the different assumptions of heterogeneity, increasing and decreasing temperature variance by a factor of 2.

After running the model with different variances, we found that predictions of the previous chapter only applied to the assumption of constant decomposition for all qualities; i.e., only for homogeneous substrates. An increase in variance increased the carbon losses

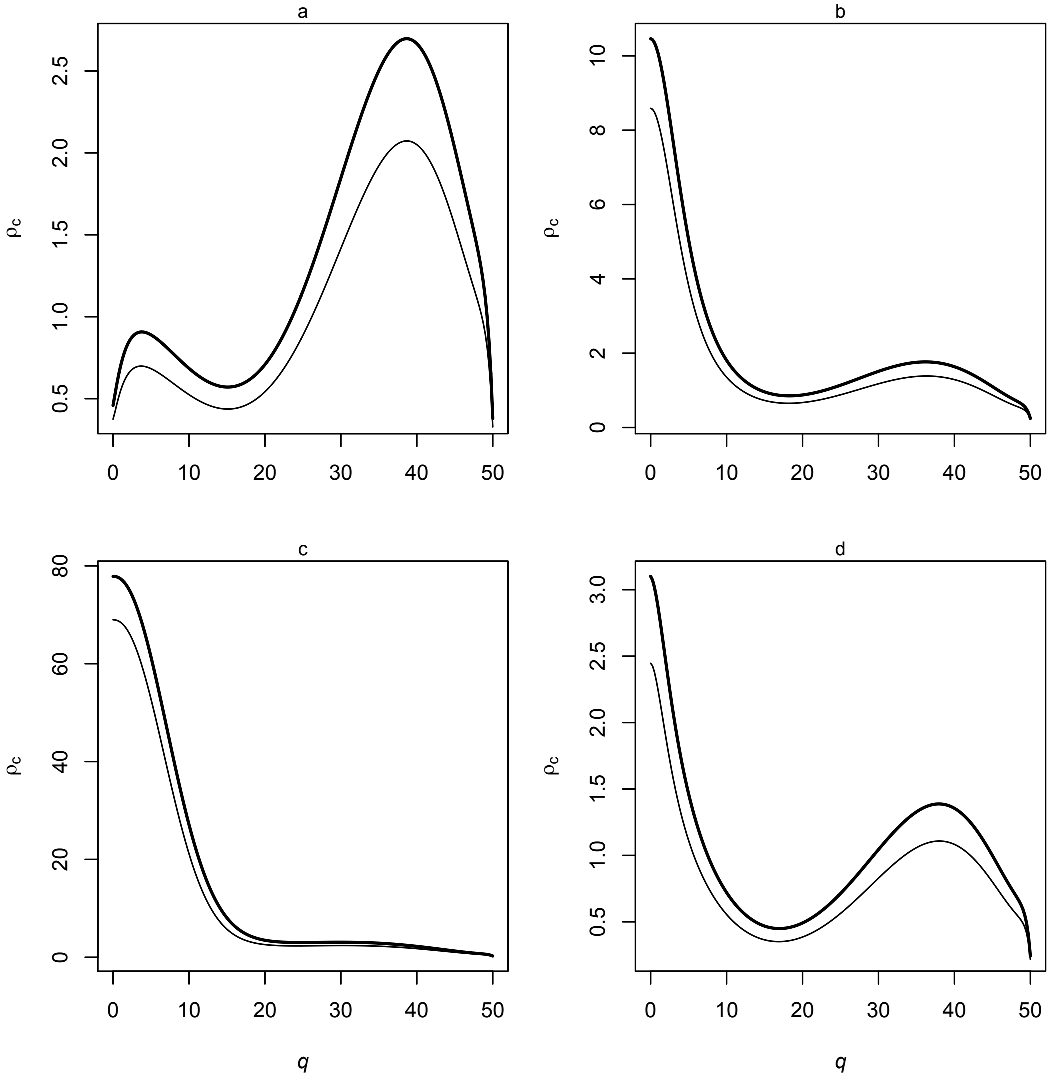

FIGURE 4.15 – Changes in the distribution of carbon due to an increase in the average temperature of 4°C. The thick line represents the distribution of carbon at 12°C and the thin line the distribution at 16°C. a) Constant, b) linear, c) convex, and d) concave.

which resulted in a decrease in soil carbon stores under this assumption (Figure 4.16a). Similarly, a decrease in variance resulted in an increase in carbon stores relative to a scenario with no changes in variance. However, complex behaviors emerged for the other functional shapes. When the decomposition rate increase linearly with quality, a decrease in variance did not result in an increase in carbon stores as expected: both the increase and decrease in variance resulted in a decrease in carbon stores relative to a scenario with no changes in variance (Figure 4.16b). The complete opposite result was obtained when the relationship between quality and decomposition rate was concave (Figure 4.16d). In contrast, for the convex relationship, the results were relatively similar to the assumption of a constant decomposition rate, but the changes in variance produced a larger effect (notice difference in scale in Figure 4.16c).

For nitrogen the results were similar to those of carbon (Figure 4.17), which suggests that changes in variances can also affect the mineralization and storage of nitrogen in soils. These changes in variance most likely will have a larger effect on substrate of higher quality, that is, in relatively fresh litters, but can also affect the storage in more stable pools if the relationship between decomposition and quality is convex (Figure 4.17c).

4.5. Discussion

The results obtained in this analysis provide support for the hypothesis initially posed: the inclusion of substrate heterogeneity in modeling decomposition introduces properties and behaviors that cannot be obtained by representing homogeneous substrates. Heterogeneous substrates are characterized by having different proportions of material with different susceptibilities for decomposition. In general, the behavior of the system over time in terms of carbon and nitrogen mineralization would reflect this arrangement of the substrate in different quality classes. In addition, variability of the environment can

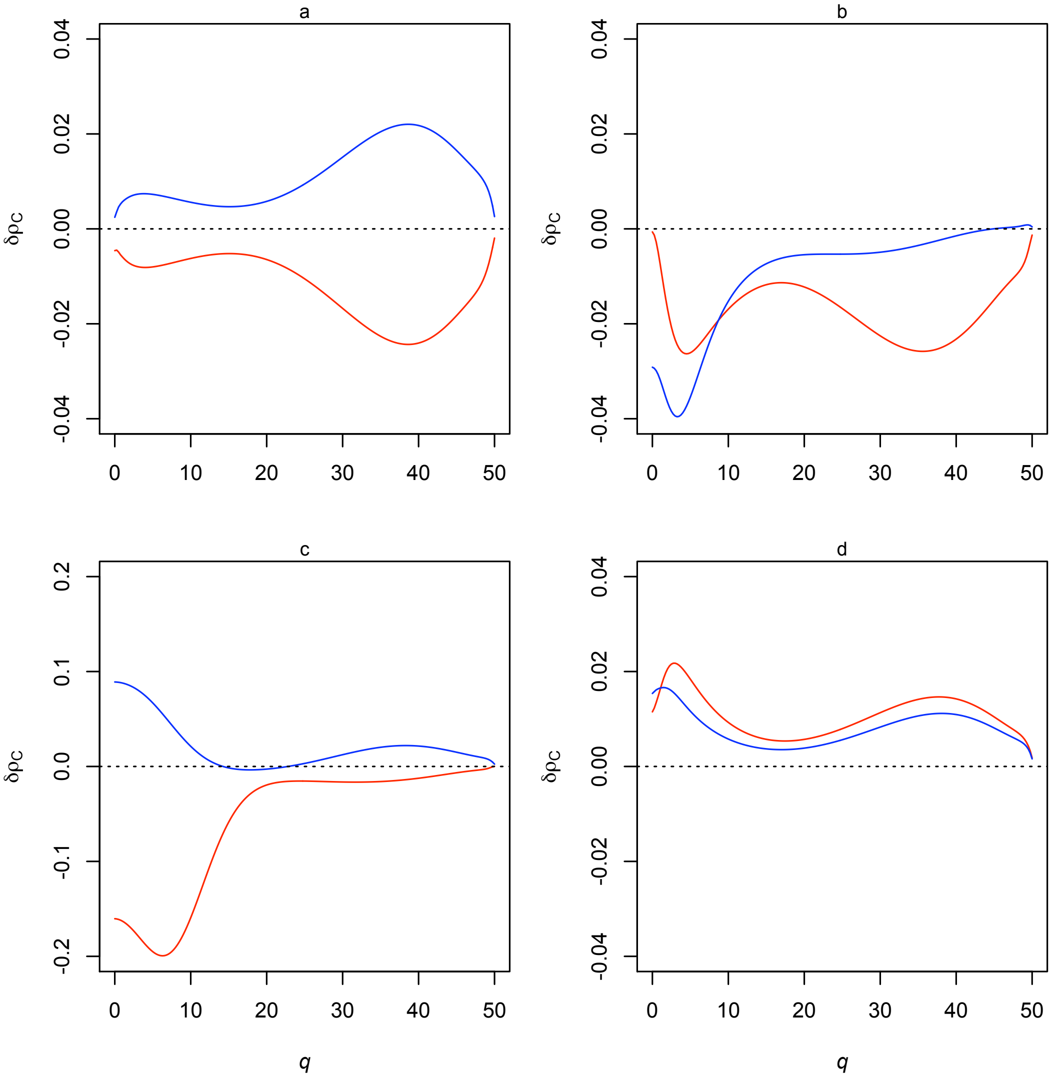

FIGURE 4.16 – Effect of changes in temperature variance in the final distribution of carbon ($\delta\rho_C$) after increasing the average temperature by 4°C. Red lines represent the effect of increasing the variance by 2 and the blue line the effect of reducing variance by half. a) Constant, b) linear, c) convex, and d) concave.

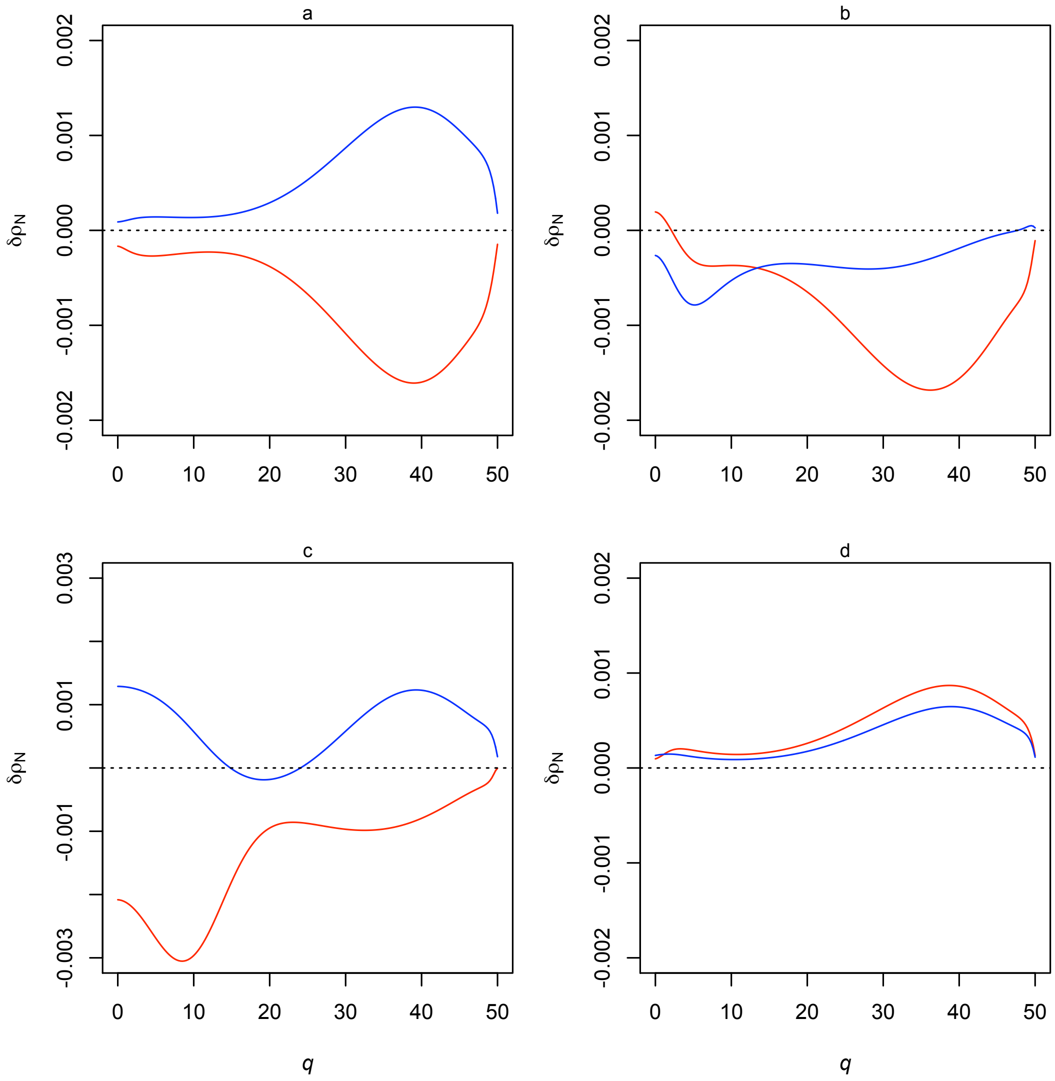

FIGURE 4.17 – Effect of changes in temperature variance in the final distribution of nitrogen ($\delta\rho_N$) after increasing the average temperature by 4°C. Red lines represent the effect of increasing the variance by 2 and the blue line the effect of reducing variance by half. a) Constant, b) linear, c) convex, and d) concave.

further modify the rates of carbon and nitrogen mineralization of heterogeneous substrates.

Despite the realism of representing the quality of organic matter as a continuous variable, most models have traditionally used a compartmentalization approach. From more than 200 decomposition models reviewed by Manzoni & Poroporato (2009), only three represent quality as a continuous variable; a very surprising number given the conceptual generality and flexibility of the continuous approach. The concept of continuous quality was first proposed almost three decades ago (Carpenter 1981), and it has been treated exclusively in theoretical models with analytical solutions. This might explain its lack of attractiveness among modelers. However, as shown here, quality as a continuous variable can be easily implemented in numerical models. One of the main advantages of this approach is that the number of parameters needed to represent decomposition rates for different pools is reduced to just one or two parameters describing a functional relationship between quality and decomposition rate.

Finding parameters and functions to describe growth rate and efficiency of decomposers with quality may be challenging though. There are a number of laboratory techniques that seem to be promising for providing representations of substrate quality in a continuous fashion. Bruun et al. (2009) reviewed a large number of methods with potential application for describing substrates in a continuum of qualities. The methods can be grouped in physical, chemical, and biological fractionations, as well as spectroscopy methods. Although there is not much research on applications of these methods for modeling decomposition in the continuous quality framework, there are enormous research opportunities. Many laboratory methods are currently used for parameterizing compartment models but it is still an open question if the operationally defined partitioning of chemical or physical fractions correspond to the assignment of quality compartments in models. The continuous approach in this case may actually help to solve this dilemma since the compartmentalization is not necessary when quality is treated continuously.

4.5.1 Overall rates of carbon and nitrogen mineralization

Traditionally, it has been assumed that the overall rate of carbon mineralization can be described by a single decomposition rate (e.g., Olson 1963). As the results from this analysis showed, this assumption is only valid when the substrate subject to decomposition has homogeneous properties and its quality does not change over time. The overall decomposition rate of a substrate is the result of a combination of decomposition rates for different qualities weighted proportionally to the amount of carbon in those qualities. If more carbon is stored in lower than in higher qualities the overall rate of carbon release would be slower than if a higher proportion is stored in higher qualities. Therefore, decomposition rates by themselves only provide part of the information needed to determine how fast decomposition proceeds for a given substrate. The same can be said for nitrogen, but in this case the amount and the timing of immobilization would depend on this proportional localization of substrate in the quality range.

The behavior of decomposers' growth and efficiency in lower quality ranges is also a significant factor determining the overall rates of mineralization. As the substrate becomes less accessible, decomposers might decrease their activity drastically or more moderately, which results in convex or concave shapes of their activity on the quality axis, respectively. This marginal response can produce dramatic differences in the overall rates of carbon and nitrogen mineralization in addition to the relative proportions of substrates in different qualities.

Moreover, the continuous redistribution of organic matter to different qualities results in a gradual accumulation of material of lower qualities. On the whole, this process tends to reduce the overall rates of mineralization. When we considered simultaneous stabilization and destabilization process in our model the proportions of material passing to low and high qualities were equal for most of the quality range. However, since the material at lower qualities has lower decomposition rates more carbon accumulates in lower quality classes, which eventually results in a decrease of the overall mineralization rate.

The continuous transformation of organic matter results in a relatively similar distribution of substrate regardless of the incoming litter. This behavior in our model is consistent with observations of ^{13}C nuclear magnetic resonance (NMR), which show that the proportions of complex molecular structures such as alkyls, *O*-alkyls, aromatics, and carbonyls are remarkably similar in soils worldwide independent of land use, climate, and management (Mahieu et al. 1999). Results from long-term large-scale decomposition studies suggest that litter tends to reach a phase of slow decomposition in the long-term (Harmon et al. 2009), which could be explained by the accumulation of low quality substrate. This accumulation of substrate in lower qualities is also consistent with the concept of *convergence* of the decomposition process (Swift et al. 1979), by which the branching of substrate degradation through different food webs converges to final products of similar characteristics. Since under certain mathematical conditions Markov chains converge to stationary distributions regardless of the initial conditions (Bharucha-Reid 1960), they appear to provide useful representations of transformations of soil organic matter quality.

4.5.2 Temperature sensitivity of organic matter pools

The response of organic matter to temperature change is a topic that has recently received a great deal of attention (Trumbore 1997, Liski et al. 1999, Ågren 2000, Giardina & Ryan 2000, Knorr et al. 2005, Reichstein et al. 2005, Davidson & Janssens 2006). An important part of this discussion has centered on the question of what carbon pools will be more sensitive to mineralization under higher temperatures. A topic of contention has been whether or not recalcitrant-stable pools are more sensitive to decomposition with climate change. Unfortunately, the arguments supporting or rejecting the hypothesis of higher sensitivity for recalcitrant pools have been based on analyses of compartment models with one or two pools (however see Bosatta & Ågren 1999). The results from the analysis presented here provide some information that may enrich the debate on the temperature sensitivity of organic matter pools.

We found that the overall release of carbon is a combination of the temperature sensitivity and the amount of carbon available for decomposition at each quality class. Low quality substrate may require high activation energies and therefore have low sensitivity to temperature changes, but if large amounts of carbon are stored in low quality classes the overall release of carbon can still be significant. If in contrast, the sensitivity of low quality pools is higher for low qualities (Bosatta & Ågren 1999, Ågren 2000) a drastic release of carbon can be expected from warmer soils because most organic matter tends to be accumulated in low quality classes (Mahieu et al. 1999).

In addition to the response of increases in the average temperature, soil organic matter responds to changes in the variance of temperature. This response to variability tends to amplify or dampen the change in decomposition generated by changes in the average temperature, but differs by quality classes. The response of different quality classes to variability is highly dependent on the nonlinearity of the system, primarily the response of decomposers to temperature change along the quality domain. A better understanding of the functional relations of decomposer growth rates with temperature in the quality continuum would greatly improve predictions of the possible effects of climate change on carbon release from ecosystems. The different responses observed in this analysis could produce drastically different projections of carbon release with different consequences for projections of future climate.

4.6. Summary and conclusions

Although some of the limitations of using one or a few homogenous pools to describe soil organic matter have been discussed previously, this is, to our knowledge, one of the few systematic analysis that report the consequences of excluding heterogeneity from modeling organic matter decomposition. This analysis confirmed the hypothesis that substrate heterogeneity introduces behaviors in the decomposition of organic matter that cannot be predicted when homogeneous substrates are assumed. Our main findings were: i) dissecting organic matter into relatively few compartments introduces representation error in both the distribution of carbon in the different pools and the decomposition rates assigned to each class. The total approximation error is proportional to the size of the compartments and the functions that best represent substrate heterogeneity. ii) The temporal behaviors in the mineralization of carbon and nitrogen are highly dependent on the functions that describe the efficiency and growth rate of decomposers with quality; i.e., the convexity of the relationship between decomposition rate and quality. The assumption of homogenous substrates imply equal efficiencies and growth rates for all different substrates present in the soil organic matter. This assumption can only provide realistic behaviors when the relationship between quality and decomposition rate is linear and the substrate is symmetrically distributed around an average value. In all other cases, the assumption of homogeneous substrates produces different amounts and rates of mineralization for carbon and nitrogen. iii) The continuous transformations of organic matter in the soil tend to accumulate carbon in organic matter of low qualities independent of the quality of the incoming litter. This can only be represented by stabilization and destabilization mechanisms operating simultaneously. Without destabilization processes, carbon will accumulate indefinitely in soils. iv) The additional amounts of carbon that can be mineralized as an effect of increases in temperature depend largely on the amounts of substrate available for decomposition. Even though low quality substrate may not be very sensitive to temperature, its abundance in most soils can provide large amounts of material to be utilized by microbes with the additional energy provided by higher temperatures. v) Substrate heterogeneity and temperature variability produce complex behaviors in the mineralization of carbon and nitrogen. Temperature variability can either amplify or dampen the response of the system to increases in the average temperature, but this response depends on the degree of nonlinearities within the system.

4.7. References

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5. CONCLUSIONS

The different tests and analyses performed throughout this dissertation provided a variety of theoretical evidence that suggests that variability and heterogeneity introduce behaviors in ecosystem models that cannot be predicted by simpler models. Since ecosystem models are mathematical conceptualizations of natural systems, it is possible to use mathematical tools for synthesis and generalizing patterns. In this chapter I present some generalizations that emerged from explicit treatments of environmental variability and system heterogeneity. Specific conclusions pertaining each chapter are also presented.

5.1. Generalizations from explicit treatments of environmental variability

Climate variability is an integral part of the natural environment of ecosystems. Although the average climatic conditions for a region gives important information that can be used for predicting ecosystem properties, climate variability gives a greater amount of information that can substantially change predictions based on average conditions alone. Throughout this dissertation we examined variability of climate and its effects on the total amounts of carbon and nitrogen stored in an ecosystem. Effects of changes in variability were contrasted with the effects predicted by changes in average conditions alone. We found that variability introduces important behaviors in the mineralization of carbon and nitrogen, which are likely dependent on the degree of nonlinearity of the system, so changes in environmental variability become highly relevant for nonlinear systems.

It is therefore important to look at the concept of nonlinearity more carefully. There are two main interpretations of this term in the ecological literature. One interpretation, also a synonym of complex systems, is that nonlinear systems are those whose behavior cannot be expressed as the sum of the behaviors of the individual parts. Another interpretation is that nonlinear systems are those whose response is not proportional to a forcing variable; with the implication that small changes in the forcing can push the system across a threshold. In mathematics, nonlinear functions are defined as those who do not satisfy additivity

$$f(x_1 + x_2) \neq f(x_1) + f(x_2), \tag{5.1}$$

or homogeneity

$$f(\alpha y) \neq \alpha f(y). \tag{5.2}$$

These two equations correspond exactly to the interpretations of nonlinearity for ecological systems given above.

The non-additivity characteristic of nonlinear systems has always focused on the internal elements of ecosystems. However, the results of this dissertation suggest that this property also applies to the temporal dimension when the environment is constantly changing. If x_1 and x_2 are considered periods of time with different but relatively homogeneous climatic characteristics, then we can infer that *the behavior of a nonlinear system over a given period of time cannot be expressed as the sum of the behaviors of the system in shorter time intervals.* This property is scale dependent; i.e., depends on how homogeneity in climatic conditions is defined.

In its simplest form, nonlinearity can be characterized as the convexity of the relationships between independent and response variables. For convex relationships we can constrain the initial predictions of equation (5.1) using Jensen's inequality. If for example a strictly convex system experiences climatic conditions X, we can predict that the average response is always larger than the response of the system under average conditions, that is

$$f(E(X)) < E(f(X)). \tag{5.3}$$

The importance of this inequality is that it goes beyond stating that the responses are different; it gives a qualitative ranking of the values that these responses can take.

Now, we can make a further generalization if we assume two variables X and Y symmetrically distributed around the same mean value, but with different variances, so $\mathrm{Var}(X) < \mathrm{Var}(Y)$. An extension of Jensen's inequality derived in this dissertation is that

$$E(f(X)) < E(f(Y)). \tag{5.4}$$

This inequality implies that increases in variance of the forcing result in an increase of the average response of the system, in the convex case. For concave systems the response decreases. A consequence of this inequality is that changes in the variance of climate alone can produce changes in the average behavior of nonlinear systems.

Another generalization, which can be deduced from the numerical results of Chapter 3, is that changes in variance amplify or dampen the effects of changes in average conditions. If the average forcing (average climatic conditions) increase in proportion to a quantity $\alpha > 1$, then

$$\alpha E(f(X)) < E(f(\alpha X)) < E(f(\alpha Y)). \tag{5.5}$$

The left hand side inequality is a special case of the non-homogeneity property of nonlinear systems (equation 5.2). It implies that the average behavior of the system due to a proportional increase in the climatic conditions is higher that the same proportional increase of the system under average conditions. The right hand side of (5.5) implies that the average response of the system is higher if the variance of the climatic conditions increases. The sign of the inequality is reversed if the system is concave or the variance of X is lower than the variance of Y. A possible consequence of this inequality is that small pushes of the system by a slight increase in the frequency of rare events can bring the system across a threshold.

5.2. Generalizations from explicit treatments of system heterogeneity

The results from Chapter 4 showed that the behavior of a system for which all parts are assumed to be homogeneous is different than the behavior of a system for which the parts are assumed heterogeneous. This corresponds to the principle of non-additivity of nonlinear systems presented above (equation 5.1), but differs somewhat from the generalizations presented for climatic variability.

The heterogeneity of a system can be characterized by the relative frequency of different elements comprising the system. If a higher frequency of elements with relative similar characteristics compose the system, then the average behavior will be largely influenced by the response of this set of frequent elements.

Taking as example equations (4.11 and 4.12),

$$C(t) = \int_0^\infty \rho_C(q,0)\exp(-k(q)t)dq, \tag{5.6}$$

we can make some generalizations about the overall behavior of an heterogeneous system Y represented by a function $f(X,t)$ that depends on a property X with a continuous density function $g(X)$,

$$Y(t) = \int g(X)f(X,t)dX. \tag{5.7}$$

In the case the property X is broken in a discrete number of qualities x_i with probabilities $p(x_i)$,

$$Y(t) = \sum p(x_i)f(x_i,t). \tag{5.8}$$

In both cases (equations 5.7 and 5.8), $Y(t)$ matches the definition of the expected value of a function, $E(f(X,t)) = Y(t)$.

Equations (5.7) and (5.8) show that the behavior of the system depends on two of its properties, one is the density function or relative frequency of heterogeneous elements, and the other is the functional relationships between driving and response variables. The simulation results from Chapter 4 showed that for linear systems with homogeneous distributions or symmetric distribution around an average value

$$E(f(X,t)) = f(E(X,t)). \tag{5.9}$$

That is, the behavior of the system at each time can be predicted by the average element of the system. In all other cases

$$E(f(X,t)) \neq f(E(X,t)). \tag{5.10}$$

More specific generalizations about the sign of possible inequalities in (5.10) depend on both the symmetry of the density functions and the linearity of the system. Even for linear systems, the asymmetry of the distribution of elements produce behaviors inconsistent with the behavior of the average element or the behavior of an homogeneous system. A diversity of responses can be obtained by the different combinations of nonlinearity and asymmetry.

5.3. Philosophical implications

Nonlinear behavior is ubiquitous throughout ecological systems; indeed, it is much more difficult to find examples of linear than nonlinear systems in nature. Similarly, there are hardly any examples of systems in which the elements are homogeneous or symmetrically distributed around an average value. In contrast, examples of terrestrial biogeochemistry models assuming linearities, homogeneity, or symmetry abound. This discrepancy implies that our models cannot predict important properties and behaviors of natural systems. Ignoring variability and heterogeneity reduces the domain of possible responses of ecosystems to environmental changes.

A first step to advance in our understanding of natural systems and how we are changing them is recognizing the inherent variability and heterogeneity of natural systems. A second step is implementing models that explicitly treat complex nonlinear systems using tools from probability and statistics. The current generation of computers are powerful enough to deal with large probabilistic models, and even bigger more powerful ones are on the assembly line.

5.4. General conclusions

My working hypothesis was confirmed throughout the multiple analyses presented in this dissertation: environmental variability and system heterogeneity introduce behaviors in terrestrial biogeochemical models that cannot be predicted in simpler models that ignore these properties. Along the way other important conclusions were obtained:

1. Interannual variability of ecosystem carbon fluxes can be explained by both climate and intrinsic forest dynamics. As a result, forests at steady-state and under relatively constant environmental conditions can behave either as a source or sink of carbon for short periods of time. Therefore, the concept of dynamic equilibrium in a carbon balance should be thought as a range of variation around an average carbon flux of zero.

2. Variation of annual carbon fluxes poses an important challenge in our ability to determine whether an ecosystem is a source, sink, or neutral in regard to CO_2 at longer time scales. Simulations that included climatic variation and stand dynamics (system heterogeneity) showed that the probability of incurring in Type I and II error

is above 10% for time series shorter than 10 years. In some cases the probability of error does not drop below 10-20% given the natural variation of climate and the heterogeneity of the system.

3. The concepts of stability, steady-state, or resilience can be quantified explicitly using probability distributions of the net carbon flux in forest ecosystems. This approach helps to interpret field observations and calculate the probabilities of possible changes of system behavior.

4. Changes in the variance of temperature alone can potentially increase the amount of respiration from terrestrial ecosystems over decadal time scales. Furthermore, simultaneous changes in the average and variance of temperature can either amplify or dampen the net effect of mean temperature increase, depending on whether the change in variance is positive or negative, or the respiration function is concave or convex.

5. This implies that the increase in mean and decrease in variance expected for high latitude regions would result in lower amounts of respiration than the estimated by change in mean temperature alone.

6. Separating organic matter into few compartments introduces approximation error in both the distribution of carbon in the different pools and the decay rates assigned to each class. The total approximation error is proportional to the size of the compartments and the functions that best represent substrate heterogeneity.

7. The temporal behaviors associated with the mineralization of carbon and nitrogen are highly dependent on the rate of change of the efficiency and growth rate of decomposers with quality; i.e., the convexity of the relationship between decomposition rate and quality. The assumption of homogenous substrates implies equal efficiencies and growth rates for all substrates present in the soil organic matter.

This assumption can only provide realistic behaviors when the relationship between quality and decomposition rate is linear and the substrate quality is symmetrically distributed around an average value. In all other cases, the assumption of homogeneous substrates produces different amounts and rates of mineralization for carbon and nitrogen.

8. The continuous transformations of organic matter in the soil tend to accumulate carbon in organic matter of low qualities independent of the quality of the incoming litter. This only occurs when stabilization and destabilization mechanisms are operating simultaneously. Without destabilization processes, carbon will accumulate indefinitely in soils.

9. The additional amounts of carbon mineralized as an effect of temperature increases depend largely on the amounts of substrate available for decomposition. Even when low quality substrate is not highly sensitive to temperature increases it can provide large amounts of material to be respired by microbes.

10. Substrate heterogeneity and temperature variability produce complex behaviors in the mineralization of carbon and nitrogen. Temperature variability can either amplify or dampen the response of the system to increases in the average temperature, but this response depends on the degree and nature of nonlinearities within the system.

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APPENDICES

A APPENDIX STANDCARB Model description

Tree mortality is calculated one of two ways depending on the time an upper tree has occupied a cell. In the case of the lower trees, mortality occurs each year of the simulation. In the case of upper trees, however, the layer may either represent a population or a single individual depending on the amount of time it has occupied the upper tree layer. For a given cell, upper tree mortality occurs each year that the time a species has occupied the upper canopy layer is less than the age required for a single tree to occupy a cell. There are two rates of mortality. One is a fraction of the value determined by the maximum age, and the other is that value set by the maximum age. A major assumption used to calculate mortality rates is that as the amount of light absorbed by the stand increases, the mortality rate for trees increases.

STANDCARB contains 11 major modules that perform specific functions. The following section describes each module as well as modifications relative to version 1.0 of the model (Harmon and Marks 2002).

A1 PLANT AND DIEOUT Modules

The PLANT and the DIEOUT modules determine the "birth" and "death", respectively of plant layers and are the most analogous to those found in a typical gap model. The PLANT module determines when herb, shrub, upper tree layer or lower tree layers establish in a cell and determines which tree species will establish in a cell depending upon the local abundance of species as well as the light, temperature, and moisture conditions present as predicted by the NEIGHBOR and CLIMATE modules. The DIEOUT module determines when the upper tree layer is replaced given that trees have a finite lifespan. Trees are represented by a cohort of multiple individuals until they reach an age when self-thinning would leave a single tree and tree crowns reach their maximum horizontal extent. Tree mortality at this point means that the upper tree layer has to be replaced by the PLANT module. In version 2.0 the time a cell reaches a single upper tree is determined stochastically once the minimum age has been reached.

A2 NEIGHBOR Module

This module simulates the interaction among the cells arranged on the rectangular grid work regarding light. Diffuse radiation can be blocked in eight directions (every 45 degrees), whereas direct radiation is only blocked on the east, southeast, south, southwest, and west facing directions. The degree of shading is determined by the relative heights of trees in cells and the distance among cells. The height is estimated from the age of the upper tree layer in each cell and a Chapman-Richards equation that specifies the maximum height of a species and the age that maximum was reached. Boundary effects, a problem in all spatially explicit models, are addressed by assuming the surrounding forest height was the same as average of the simulated forest. In version 2.0 the maximum tree height is a function of site index.

A3 GROWTH Module

This module calculates the mass of the seven live parts or C pools and is divided into nine functions which perform specific calculations including the absorption of light and foliage growth; the allocation of production to fine roots and woody plant parts; respiration from living parts; heartwood and heart-rot formation; losses from mortality, litterfall, and pruning; calculation of live stores; and conversion of bole mass to wood volume. Each of these functions is invoked for each plant layer present in a cell. Parameters controlling these functions are specific to plant layers and in the case of trees, are specific to species.

The growth of each layer is a function of the amount of foliage present in a layer that is, in turn, dependent on the amount of light absorbed by them. Light is expressed as a percentage of full sunlight and we assume that if taller layers are present they will absorb light before underlying layers. The light coming into a cell can be reduced by shading from surrounding cells (see NEIGHBOR module); although in version 2.0 a small proportion of direct light is allowed to pass through neighboring cells to account for the sun flecks passing through minor openings. Layers are able to increase their foliage mass until the light compensation point for that layer or species of tree is reached. The amount of light remaining below the foliage of each layer is a function of the mass of foliage of that layer as defined by a Beers-Lambert equation.

The photosynthate produced by foliage is allocated to the sapwood, branches, fine roots and coarse roots by assuming that rates of allocation are fixed. In version 2.0 the production of the trees changes with age, so that as trees reach their maximum height their production declines by an amount set by the user. This was done to account for the fact that production in older forests appears to be limited relative to younger forests (Acker et al 2000, Acker et al 2002). While there is some dispute about the exact cause of this phenomenon, there is little doubt it occurs in many types of forests (Ryan et al 1997). Allocation rates are set to give the proportions of a typical tree ¿50 cm diameter at breast height as solved by allometric biomass equations (Means et al. 1994). We used this diameter range because the proportions of tree parts become relatively stable at this size.

Losses to live parts occur as respiration, mortality, and formation of new materials (e.g., sapwood forms heartwood). Respiration losses are deducted from the allocation added to woody plant parts. Respiration of all plant parts except heartwood is estimated from their mass and a respiration rate that is a $Q_1$0 function of mean annual temperature (Ryan 1990). The mass transferred from sapwood to heartwood for each tree layer is determined by the rate of heartwood formation and the mass of sapwood. The rate of heartwood formation is parameterized so that the proportion of boles in sapwood matches the values in mature trees of the various tree species (Lassen and Okkonee 1969). In version 2.0 heart-rot is formed from heartwood after trees reach a minimum age, although the year heart-rot begins to form in a particular cell is stochastic. Losses for parts occur as tree mortality or in the case of non-bole parts via pruning (i.e., branches and coarse roots) or normal turnover (i.e., litterfall or fine root death). Losses can also occur due to timber harvest (see HARVEST module) and fire (see BURNKILL module).

A4 MORTALITY Module

This module determines the mortality rate of foliage, fine roots, branches, and coarse roots when entire trees die and/or when parts are pruned. Sapwood and heartwood are only transferred to dead pools when entire trees die. Foliage, branches, fine roots, and coarse roots are transferred to dead pools when both entire trees die and when these parts are self pruned. The turnover of foliage and fine roots are constants based on the longevity of these parts. It is assumed that as the amount of light absorbed by the stand increases, pruning of branches and coarse roots as well as the mortality rate for entire trees increases. However, mortality of upper trees also depends upon the time a species has occupied a cell. When a single tree is in the upper tree layer, then mortality is a function of tree longevity and becomes independent of light.

A5 DECOMPOSE Module

This module simulates the input, decomposition, and storage of C in dead and stable pools. The functions contained in this module calculate the total amount of input from the various layers and parts, the effect of substrate quality on decomposition, the rate of decomposition, change in detritus stores, the transfer to and loss from stable pools. All detritus pools are named after the corresponding live plant parts with the prefix Dead added with the exception that heart-rot contributes to dead heartwood. In version 2.0 dead sapwood and dead heartwood are separated into standing and downed material to account for the different microclimates of these two positions. Another change in version 2.0 was made to account for the fact a period of decomposition is required before stable materials are formed, dead pools are tracked using a cohort structure for each years input for a cell. Once a lag time modified by climatic conditions has been exceeded a dead pool cohort is stochastically transferred to the appropriate stable pool. Another change in version 2.0 is that there are three stable pools. Dead foliage is transferred to stable foliage (i.e., the organic horizon), aboveground dead wood pools to stable wood, and dead fine and coarse roots to stable soil.

The balance for each detritus pool is the inputs minus the losses from decomposition, consumption by fire, salvage harvest of dead wood, and transfers to the stable pools. For any given year, input can come from several sources: 1) litterfall, pruning, and mortality, 2) the dying out of the upper tree layer, 3) thinning and harvesting, and 4) fire killed plants. The decomposition rate of each dead pool cohort is dependent on the weighted average substrate quality of the inputs to that pool. The overall decomposition rate is calculated from the substrate quality effect and the effects of the abiotic factors as calculated in the CLIMATE module. Losses from harvest and fire are calculated by the HARVEST and SITEPREP modules.

Changes in a stable pool C is determined by the balance of C transferred from the dead pools minus the losses from decomposition as a function of the particular stable pool in question and the effects of temperature and moisture calculated by the CLIMATE module. It is assumed that stable foliage decomposes faster than stable wood, which in turn decomposes faster than stable soil.

A6 SOIL TEXTURE Module

The maximum amount of water storage in a soil is based upon the soil texture, depth, and fraction of soil free of coarse particles ($<$ 2 mm diameter). The fraction of the soil volume that can store water between field capacity and the wilting point is based on soil texture and the fraction of the soil profile with soil particles.

A7 CLIMATE Module

This module estimates the effect of temperature, precipitation, and solar radiation on the establishment of tree species, growth of plants, autotrophic respiration, and decomposition. The processes of water interception, evapotranspiration, and water stores, as well as the effects of climate on decomposition and growth are calculated each month on each cell, whereas for plant respiration effects are calculated annually. The effect of temperature on plant part respiration is modeled as a Q10 relationship. For the dead pools we assumed there is an optimum temperature for decomposition.

To estimate the amount of water available for plant growth and decomposition, the interception by the canopy, woody detritus, and forest floor is calculated. Monthly total potential evapotranspiration of the site is calculated using a modification of the Priestly-Taylor method (Bonan 1989, Jensen 1973, Campbell 1977). Total potential evapotranspiration for a month is assumed to be proportional to the estimated solar irradiance, the monthly mean air temperature, and number of days in a month. The constants used to solve the Priestly-Taylor method are empirically derived after Jensen and Haise (1963) and Jensen (1973) from elevation and the mean minimum and mean maximum daily temperatures for the warmest month of the year. To estimate the potential amount of transpiration by plants, the total potential evapotranspiration is reduced to account for the evaporation portion of the water loss. The actual transpiration losses each month are controlled by the soil water stores and a linear function of foliage mass. The effect of soil moisture on transpiration is calculated from a modification of the relationship developed by Emmingham and Waring (1977). Volumetric moisture content is converted to water potential using a reciprocal function similar to Running and Coughlan (1988)

The moisture content of six detritus pools and the mineral soil is calculated monthly and represents the balance of inputs through precipitation/throughfall and outputs via evapotranspiration. The loss of water from the mineral soil is controlled solely by the transpiration from plants. The rate that water is lost from detritus pools is calculated from the monthly evaporative demand (a function of radiation received and temperature) multiplied by a pool-specific drying constant. Decomposition is limited by moisture when either it is too low (i.e., a matric effect) or too high water (i.e., a limitation of oxygen diffusion).

A8 HARVEST, BURNKILL, AND SITEPREP Modules

The HARVEST, BURNKILL, and SITEPREP modules determine if a cell is to be disturbed by silvicultural treatments, timber harvest, or fire and the degree to which these disturbances reallocate the C in the living and dead pools.

If a harvest activity occurs in a given simulation year, then the HARVEST module determines which type and spatial pattern of activity is to occur. Activities include cutting and harvesting of trees (cut trees can be left onsite), salvage of dead wood, and site preparation fires. Cutting and removal may be performed on either the upper or lower tree layer or for certain target species on all or a subset of cells.

The BURNKILL module determines the timing and amount of live vegetation killed by natural- or management-caused fire reducing the amount of live C in the GROWTH module and transferring some to the DECOMPOSE module as fire-killed detritus inputs. Not all the live vegetation killed by fire is necessarily transferred to detritus; some is consumed by the fire itself. The fraction of plant material killed and consumed by fire also increases with fire severity. Above- and below-ground plant parts are consumed by fire to different degrees, with below-ground parts having less material consumed for a given fire severity.

When a natural- or management-caused fire occurs the SITEPREP module determines the degree that dead pools are reduced. The degree that the dead pools are reduced is determined by the user; we have assumed that as fire severity increases from low to high the fraction of each of the above-ground detritus pools removed by fire increases. It is assumed that the stable soil pool does not decrease when there is a fire.

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B APPENDIX A probabilistic argument to explain less carbon storage under the variable climate scenario

In general, STANDCARB models the effect of temperature T on autotrophic and heterotrophic respiration using a Q_{10} factor and an equation of the form:

$$f(T) = R = R_{10} Q_{10}^{(T-10)/10} \tag{B.1}$$

Where R represents the respiration rate of a given carbon pool, and R_{10} the respiration rate of that pool at 10°C. Equation (B.1) is a convex function with respect to temperature. Because we are interested in obtaining a measure of central tendency using equation (B.1), we can calculate either the expected value of the function, i.e. $E[f(T)]$, or evaluate the function at the expected value of the random variable, i.e., $f(E[T])$. These two cases correspond to the variable and constant climate scenarios used in our simulations, respectively. $f(T)$ can be expanded using a Taylors series about $\mu = E[T]$,

$$f(T) = f(\mu) + f'(\mu)(T-\mu) + \frac{f''(\xi)(T-\mu)^2}{2} \tag{B.2}$$

where ξ is a value between T and μ. Since $f''(\xi) \geq 0$,

$$f(T) \geq f(\mu) + f'(\mu)(T-\mu). \tag{B.3}$$

Taking expectations at both sides gives

$$\begin{aligned} &E[f(T)] \geq f(\mu) + f'(\mu)E[T-\mu] = f(\mu) \\ &E[f(T)] \geq f(E[T]) \end{aligned} \tag{B.4}$$

Equation (B.4) is commonly known as Jensens inequality in probability theory.

From this equation we can infer that the average respiration rate will always be higher under the variable climate scenario than the respiration rate of the average temperature. This respiration function will also produce larger respiration fluxes with small but finite probabilities because the resultant probability distribution for respiration is skewed to larger values.

C APPENDIX Derivation of geometric inequality

The point $\bar{x}$ can be defined as the average value of both $[a, b]$ and $[c, d]$, so $\bar{x} = \lambda a + (1-\lambda)b = \lambda c + (1-\lambda)d$. Applying the definition of convexity (equation 3.13) we can see that

$$f(\bar{x}) = f(\lambda a + (1-\lambda)b) \leq \lambda f(a) + (1-\lambda)f(b). \tag{C.1}$$

Now, the points a and b can be expressed as a linear combination of c and d

$$a = \alpha c + (1-\alpha)d, \tag{C.2}$$

$$b = (1-\beta)c + \beta d. \tag{C.3}$$

Given that $\alpha = \beta = \lambda$ and $\lambda + (1-\lambda) = 1$, λ and $(1-\lambda)$ can be expressed in terms of α and β as

$$\lambda = \lambda\alpha + (1-\lambda)\beta, \tag{C.4}$$

$$(1-\lambda) = \lambda(1-\alpha) + (1-\lambda)(1-\beta). \tag{C.5}$$

We can now express the right-hand side of (C.1) in terms of c and d as

$$\begin{aligned}
&\lambda f(\alpha c + (1-\alpha)d) + (1-\lambda)f(\beta c + (1-\beta)d) \\
&\qquad \leq \lambda\alpha f(c) + (1-\alpha)f(d) + (1-\lambda)\beta f(c) + (1-\beta)f(d) \\
&\qquad \leq f(c)[\lambda\alpha + (1-\lambda)\beta] + f(d)[(1-\alpha) + (1-\beta)(1-\lambda)] \\
&\qquad \leq \lambda f(c) + (1-\lambda)f(d).
\end{aligned} \tag{C.6}$$

Therefore,

$$f(\bar{x}) \leq \lambda f(a) + (1-\lambda)f(b) \leq \lambda f(c) + (1-\lambda)f(d). \tag{C.7}$$

D APPENDIX Additional figures

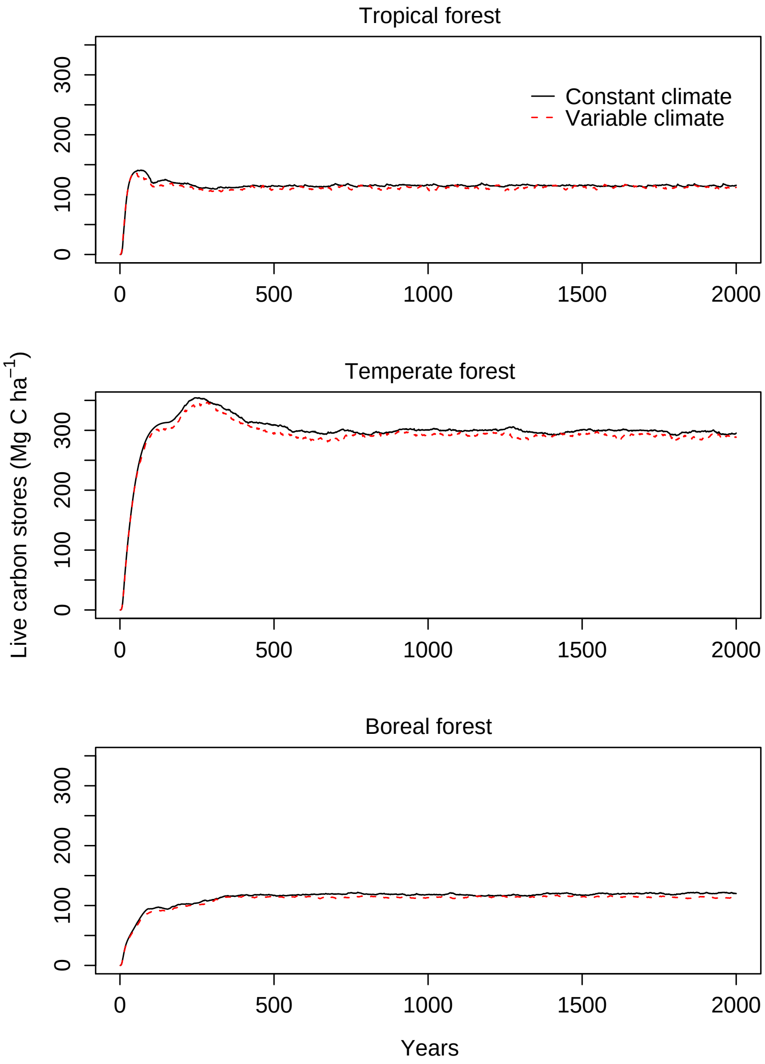

FIGURE D-1 – Live biomass for a tropical (upper panel), temperate (middle panel), and a boreal (lower panel) under the constant climate (black continuous line) and the variable climate scenarios (red dotted line).

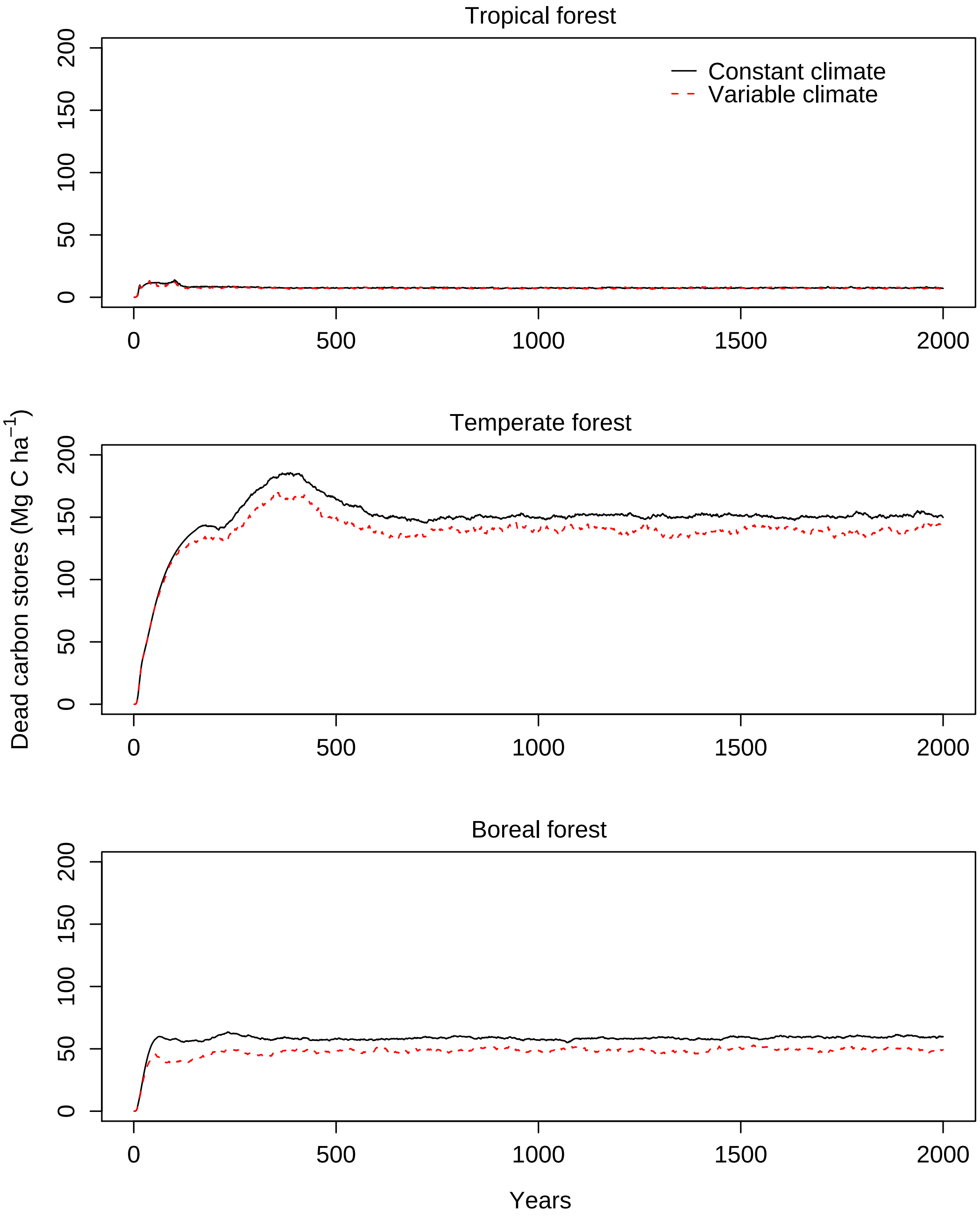

FIGURE D-2 – Dead biomass for a tropical (upper panel), temperate (middle panel), and a boreal (lower panel) under the constant climate (black continuous line) and the variable climate scenarios (red dotted line).

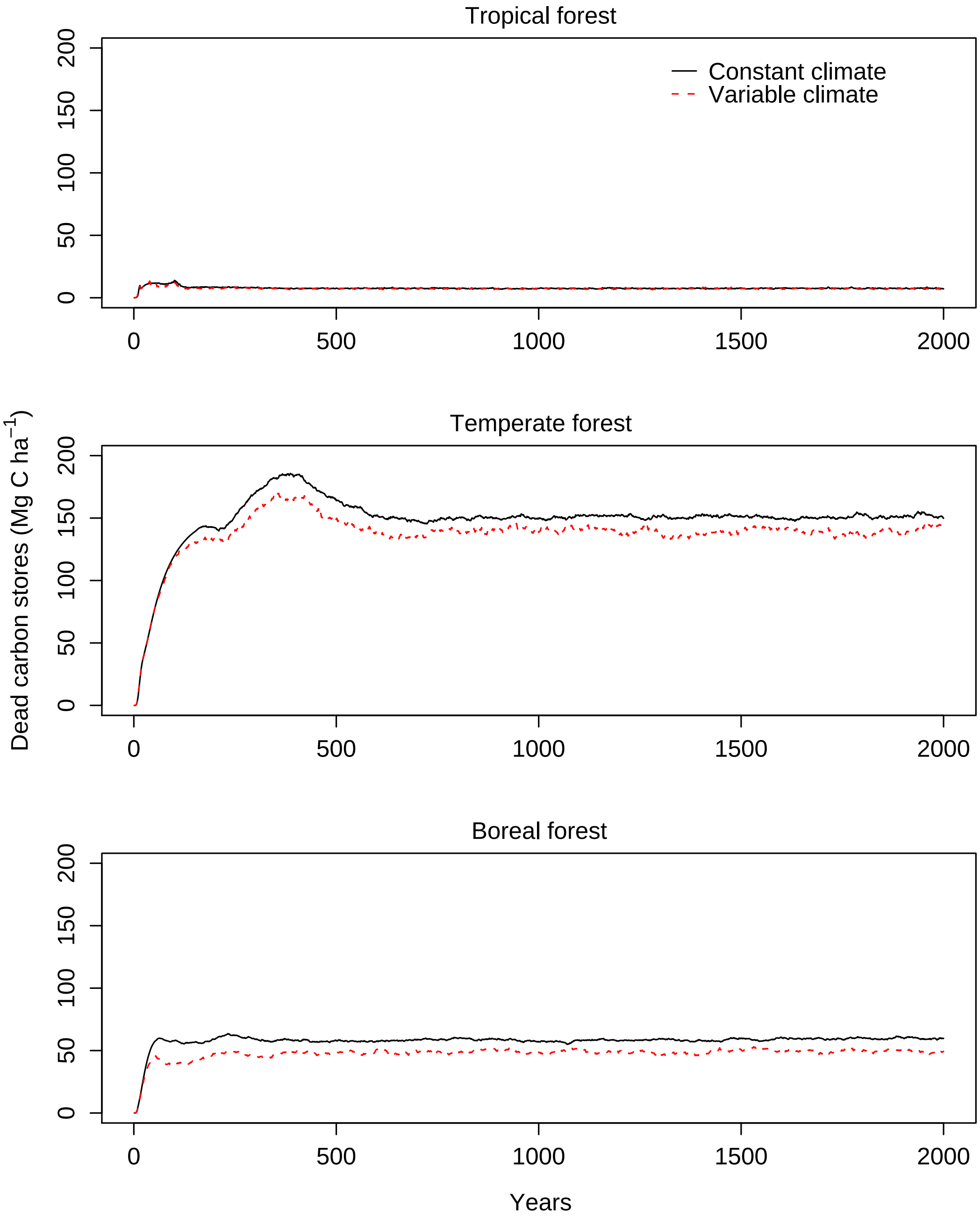

FIGURE D-3 – Soil organic matter for a tropical (upper panel), temperate (middle panel), and a boreal (lower panel) under the constant climate (black continuous line) and the variable climate scenarios (red dotted line).

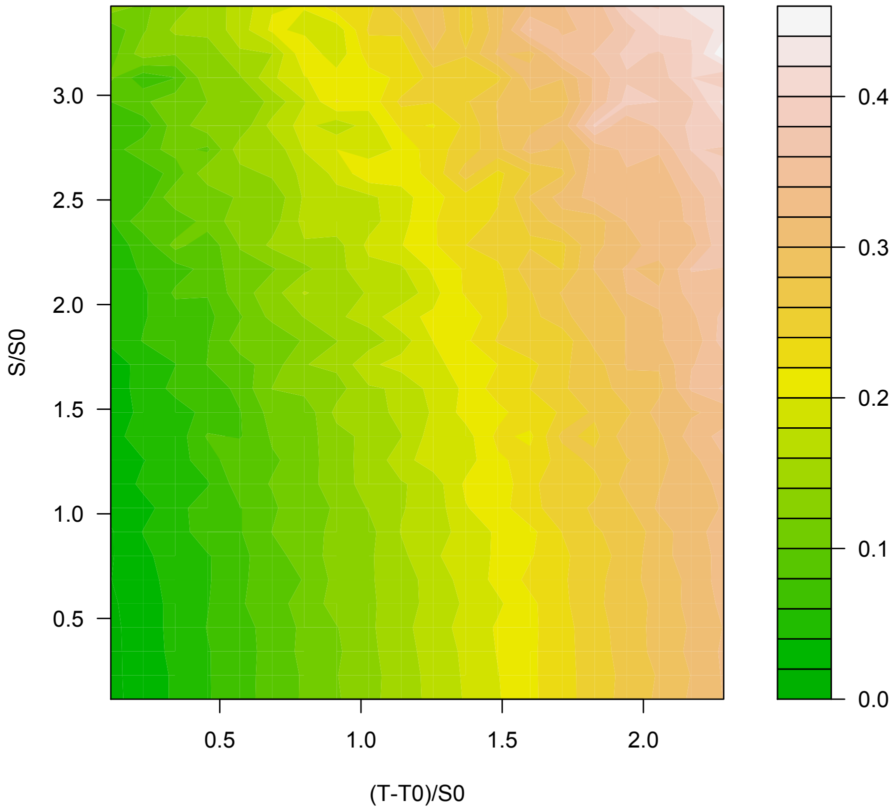

FIGURE D-4 – MSC plot for H.J. Andrews in the months of December, January and February using the modified Van't Hoff equation with $Q_{10} = 4$. Colors represent values of δR.

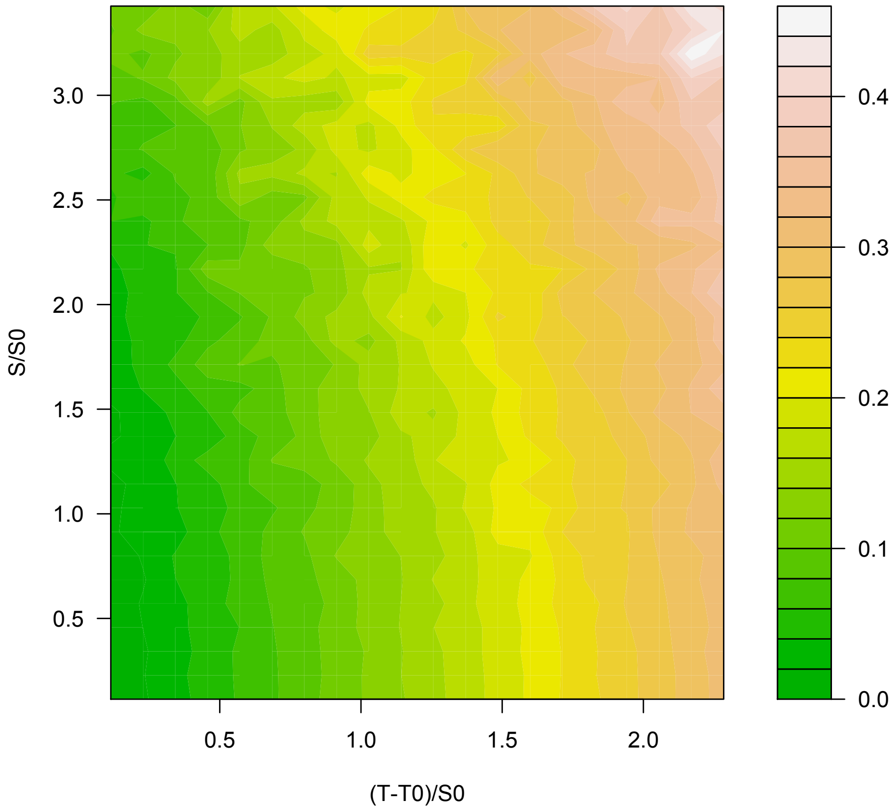

FIGURE D-5 – MSC plot for H.J. Andrews in the months of March, April and May using the modified Van't Hoff equation with $Q_{10} = 4$. Colors represent values of δR.

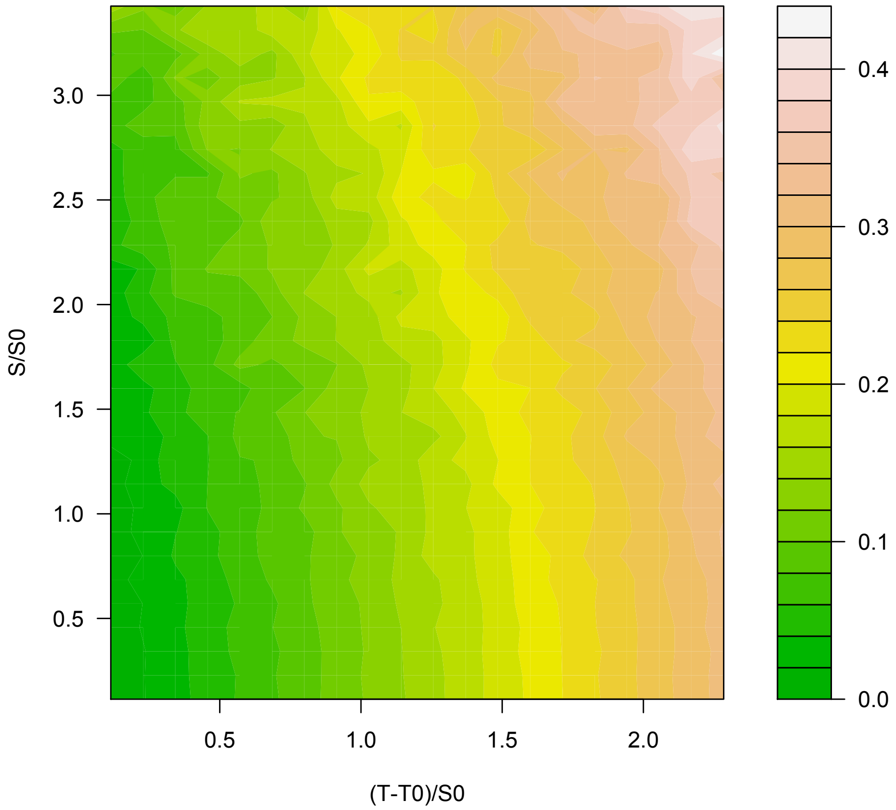

FIGURE D-6 – MSC plot for H.J. Andrews in the months of June, July and August using the modified Van't Hoff equation with $Q_{10} = 4$. Colors represent values of δR.

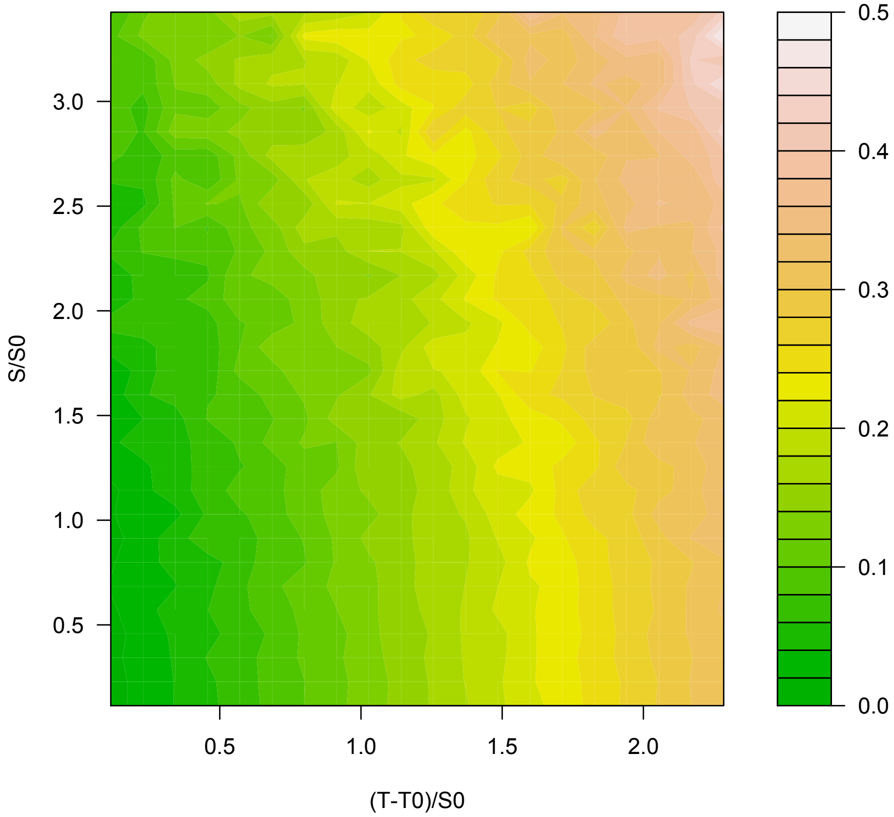

FIGURE D-7 – MSC plot for H.J. Andrews in the months of September, October and November using the modified Van't Hoff equation with $Q_{10} = 4$. Colors represent values of δR.

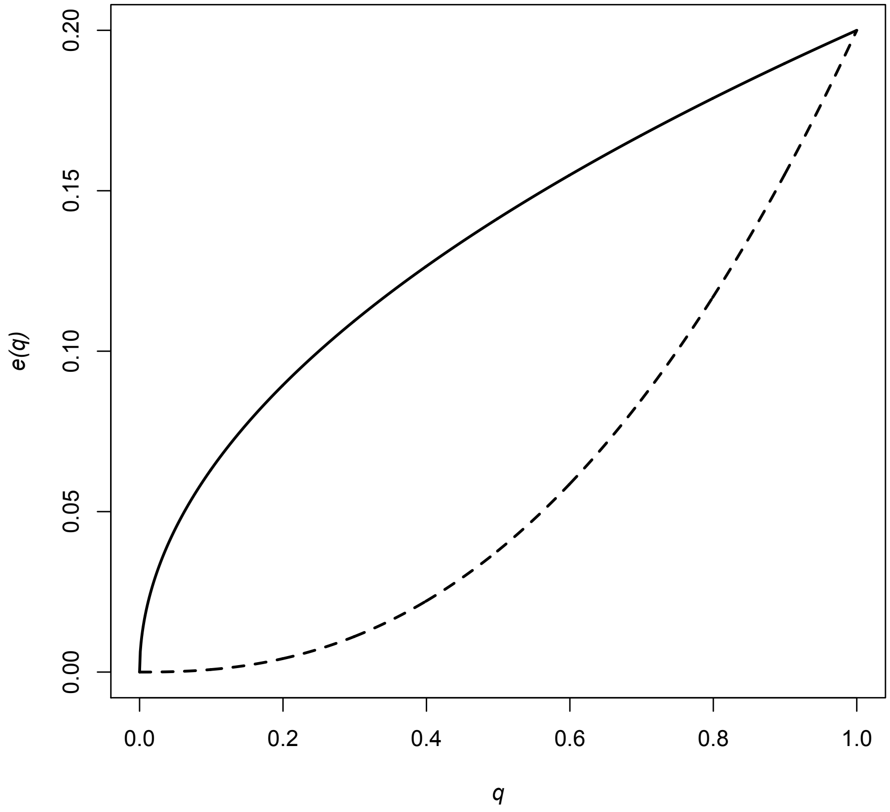

FIGURE D-8 – Functional relationships between quality q and decomposer efficiency $e(q)$ for the constant and linear scenarios. Continuos line: $e(q) = 0.2q^{0.5}$; dashed line: $e(q) = 0.2q^{2.4}$.

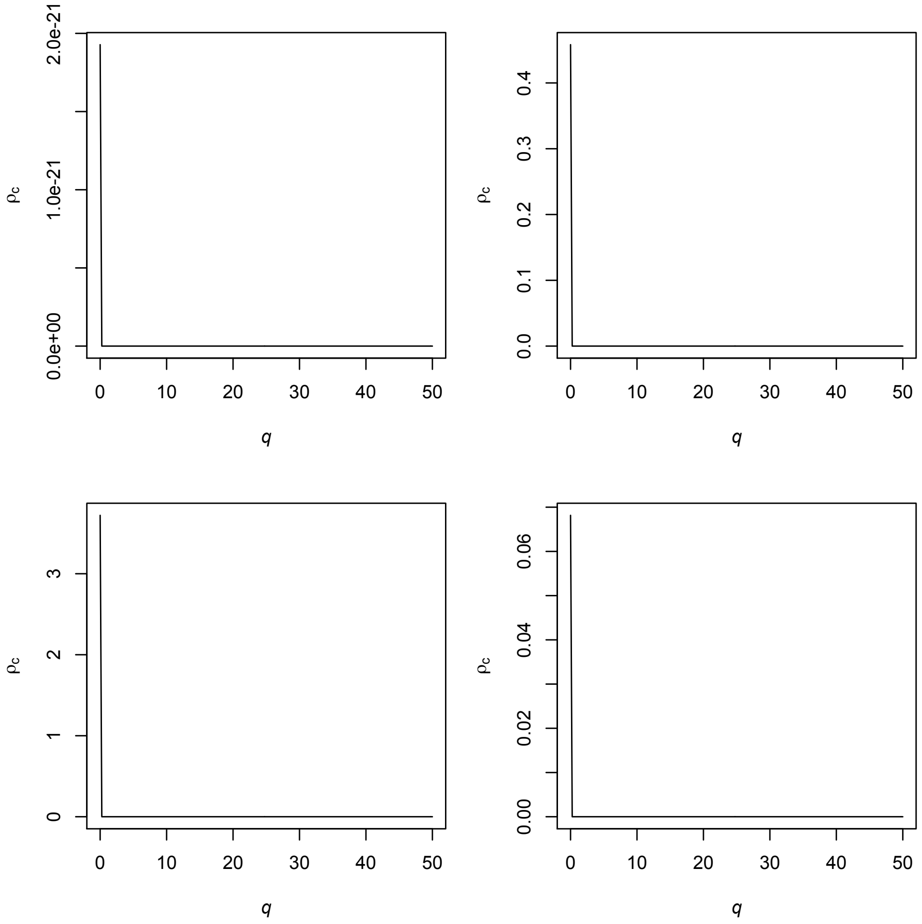

FIGURE D-9 – Final distribution of carbon after 100 years of decomposition for the four functional shapes considered and assuming stabilization processes only ($\mathbf{P_1}$). Upper left: constant, upper right: linear, lower left: convex, and lower right: concave.

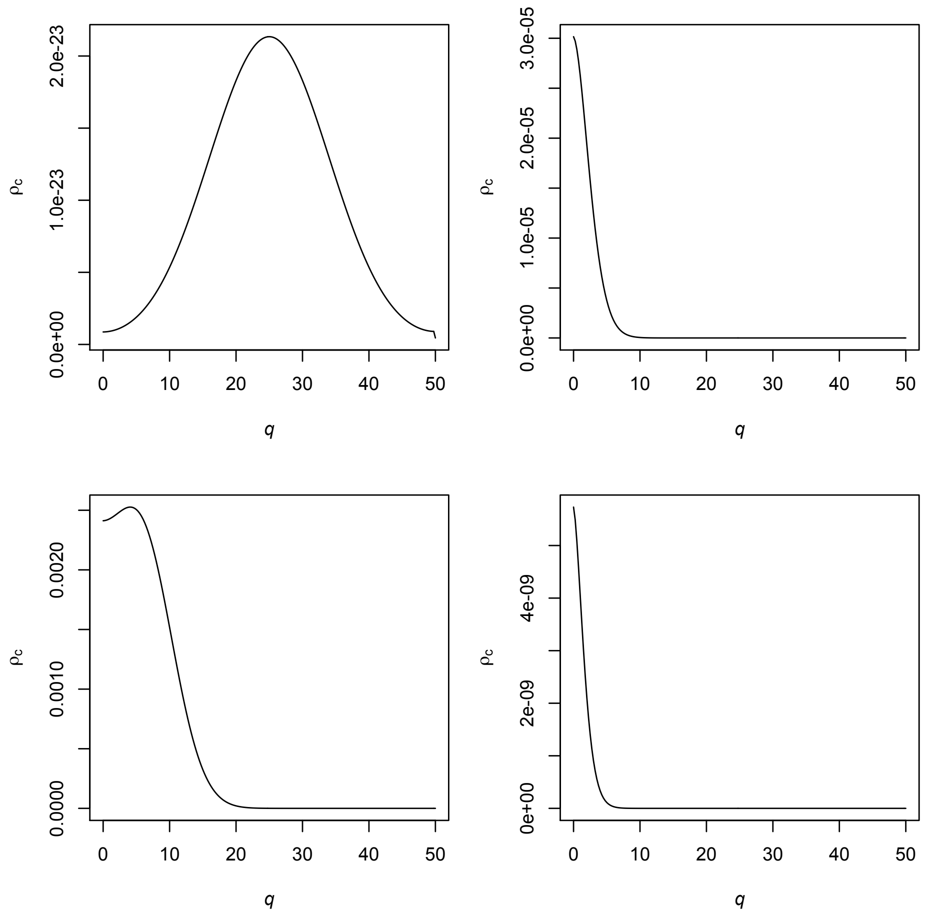

FIGURE D-10 – Final distribution of carbon after 100 years of decomposition for the four functional shapes considered and assuming simultaneous stabilization and destabilization processes ($\mathbf{P_2}$). Upper left: constant, upper right: linear, lower left: convex, and lower right: concave.

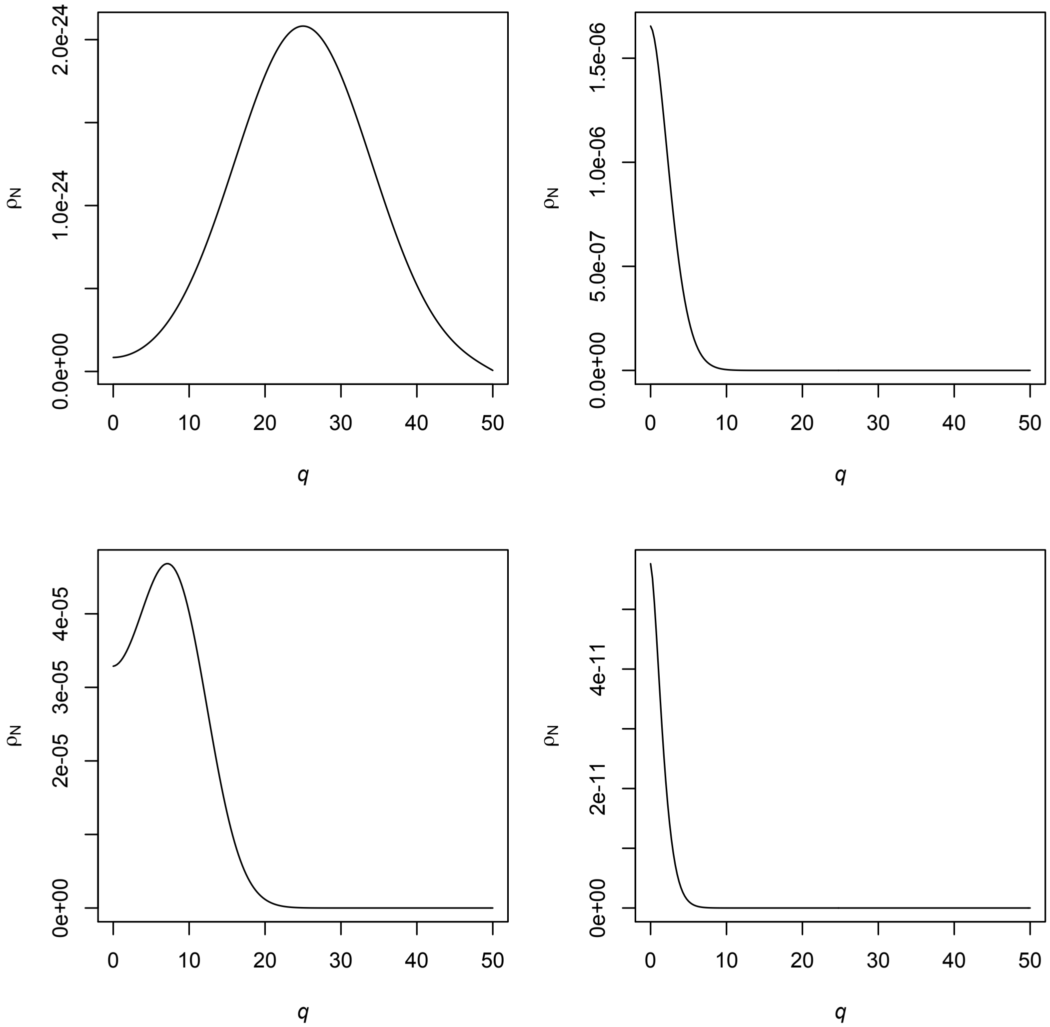

FIGURE D-11 – Final distribution of nitrogen after 100 years of decomposition for the four functional shapes considered and assuming simultaneous stabilization and destabilization processes ($\mathbf{P_2}$). Upper left: constant, upper right: linear, lower left: convex, and lower right: concave.

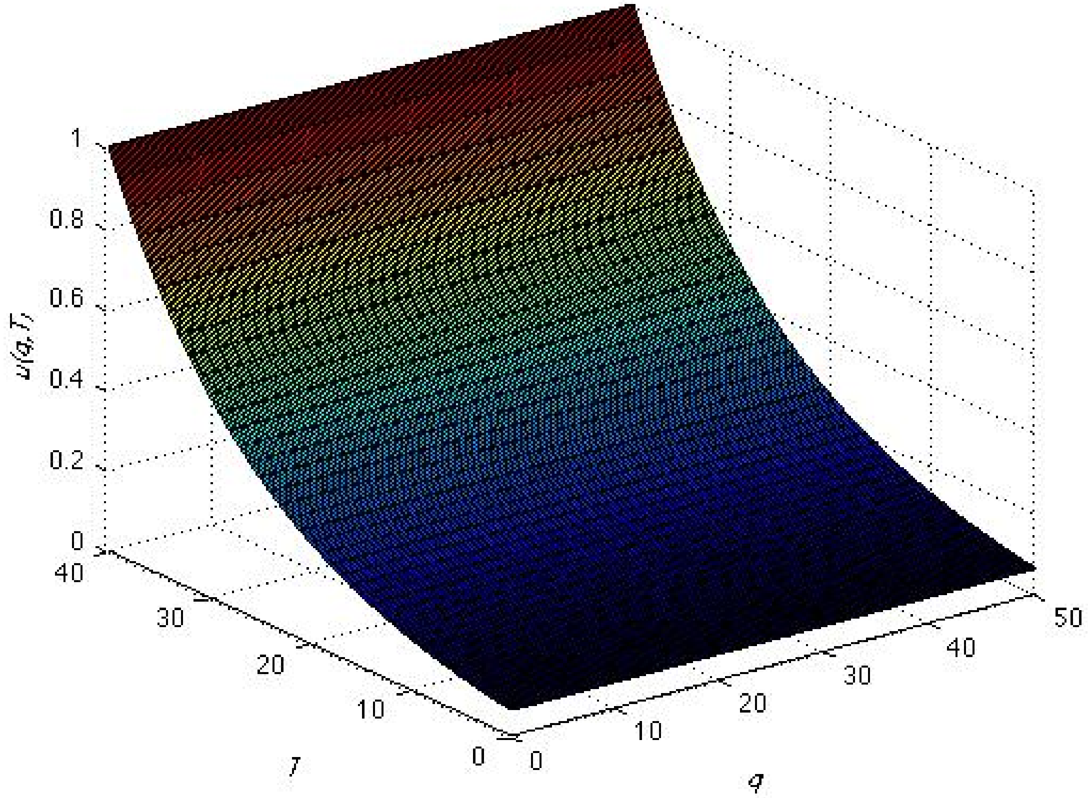

FIGURE D-12 – Surface plane for decomposer growth rates $u(q,T)$ as a function of substrate quality q and temperature T when $\beta = 0$.

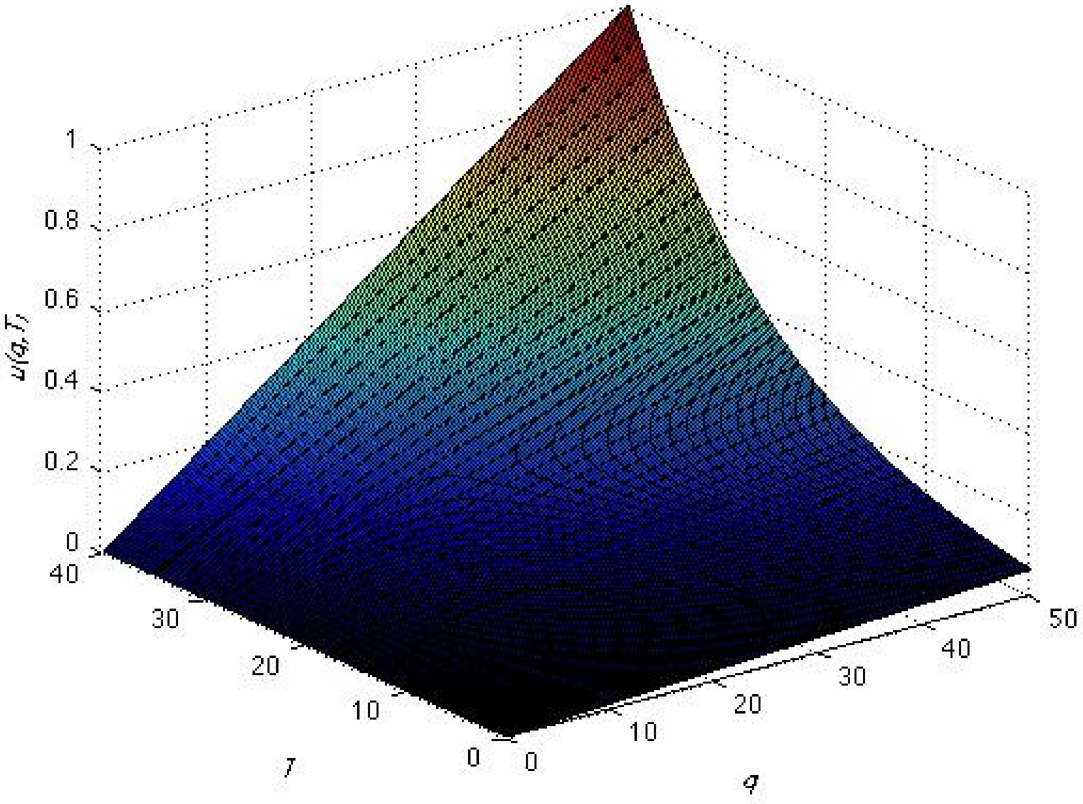

FIGURE D-13 – Surface plane for decomposer growth rates $u(q, T)$ as a function of substrate quality q and temperature T when $\beta = 1$.

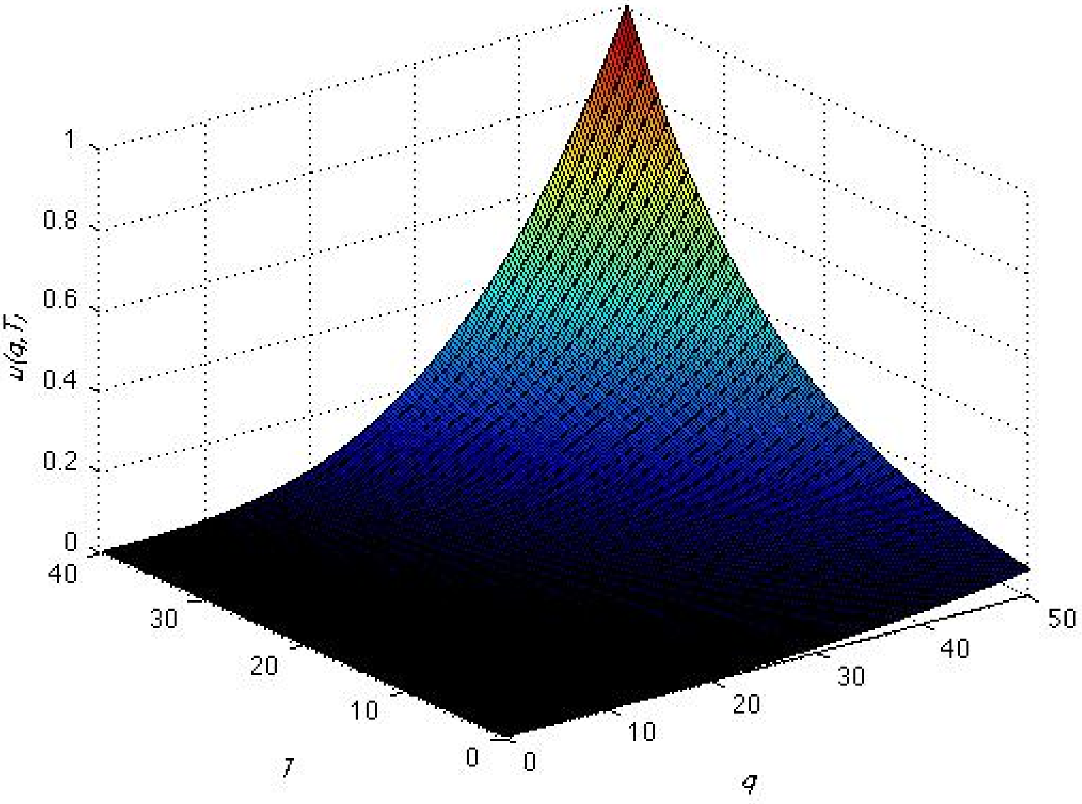

FIGURE D-14 – Surface plane for decomposer growth rates $u(q, T)$ as a function of substrate quality q and temperature T when $\beta = 3$.