



Towards a Classification of Landscape-Fire-Succession Models

Fire is a ubiquitous disturbance in many terrestrial ecosystems and serves as a primary driver of change in population structure and community composition. Fire can also induce major modifications of biogeochemical cycles, including the carbon cycle, as well as exert strong effects on biophysical properties of land surfaces that influence land-atmosphere interactions (Figure 1). Wildland fire is predicted to increase globally under forecasted future climatic warming (Overpeck et al., 1990). Predicting the broad-scale occurrence and effects of wildland fire is an important challenge for scientists and resource managers (McKenzie et al., 2000). Computer simulation models of

explicit models are needed to account for the heterogeneity of fire patterns and effects, even within large regions. A large number of LFSMs have been published in the recent years, corresponding to a wide range of objectives, approaches, and scales (Gardner et al. 1999). In order to design fire simulation approaches that can predict fire effects over multiple spatial and temporal scales relevant to a global perspective, we need a generic understanding of the processes included in different models and of their corresponding input and output data constraints. The aim of GCTE Task 2.2.2 is to develop such a framework, which will be applied to the prediction of future fire patterns and



Figure 1: Wildfire in Ontario, Canada [Courtesy: Brian Stocks]

ecosystem dynamics that incorporate fire behavior and fire effects provide researchers a tool for understanding how ecosystems and disturbance regimes will respond to climatic and land use change.

Landscape-fire-succession models (LFSMs) are those computer programs that simulate the processes of fire and succession in a spatial domain, with resolutions of 10-1000 m and extents of 1-100s km. It is argued that such spatially

effects at the landscape scale, as well as for the design of a strategy for incorporating fire into coarse scale Dynamic Global Vegetation Models (DGVMs). Investigation and comparison of the various approaches for modeling fire and successional processes will provide insight for identifying critical processes for coarse scale applications, and will allow evaluation of the tradeoffs as a consequence of implementing different approaches into an optimal modeling design. As a first step of this work we developed a prototype

classification of LFSMs, with support from the National Center for Ecological Analysis and Synthesis (NCEAS) to the 'Global change impacts on landscape fires' working group.

The classification attempts to group models by the approach or strategy used to design the component algorithms and functions, not by potential application, inherent realism, or accuracy. The classification was divided into three elements representing the three primary processes of: (1) vegetation succession, (2) fire ignition, and (3) fire spread. Each model was classified with respect to each of these elements. Within each element, we have attempted to classify models along a gradient of inherent complexity in modeling design. Therefore, we

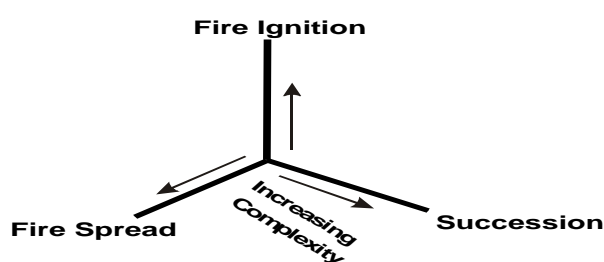


Figure 2: Classification space for Landscape-Fire-Succession Models (LFSMs).

defined the 'classification space' by assigning each element a dimension and increasing complexity along the corresponding axis (Figure 2). The goal of the GCTE model evaluation is not to compare all LFSMs, but rather to evaluate a representative subset that captures the majority of this 'classification space'. Such an exercise places the emphasis on identifying the range of available conceptual models rather than on specific algorithms. This perspective also recognizes the more and more common possibility that actual models often can combine elements from different conceptual classes, as has for example been outlined in the case of gap models (Task 2.1.1; Bugmann et al., In Press).

An overview of the three classification elements and a brief description of the categories and subcategories defined within each element are discussed below. It should be noted that this classification scheme is arbitrary and not completely exclusive. In many cases LFSMs represent a hybridization of approaches making it difficult to develop an exclusive classification scheme. Therefore, the classification outlined here acknowledges these limitations, but also recognizes the utility of developing an organizational framework that improves our ability to compare fundamentally different approaches.

1. Succession Drivers have been categorized into a wide variety of groups based on simulation design, spatial application, simulated entity, or level of complexity

(Botkin and Schenk, 1996; Shugart 1999). Our classification, however, stresses the link between fire and succession in category design. We recognized three major categories of succession drivers, and within each major category we have designated subcategories representing the type of processes considered.

1.1. Pathway Models (PATH) represent successional development in terms of the transition from one broad cover type and/or structural stage to another. They are referred to as pathway models because successional development normally occurs along pathways of successional community types that ultimately end in a climax or stable community type. Individual plants are not recognized, but different cover types may represent individual species. There are two subcategories of PATH models:

1.1.1. Markov (MARKOV) – This group of pathway models stochastically simulate successional development using Markov chains or some other probabilistic approach. Transition from one state (i.e., category or community type) to another is modeled from a probability distribution quantified from field data or expert knowledge.

1.1.2. Deterministic (DET) – This group of models transition from one state to another deterministically and therefore are repeatable. These pathway models can be composed of one or multiple pathways. Pathways are assigned to a biophysical setting or biome type across the landscape. Transition times are usually quantified from actual field data, model simulations from more detailed stand or individual-based models (see below), or expert knowledge.

1.2. Stand Models (STAND) do not simulate individual plant dynamics but rather simulate the successional development of one or more stand-level parameters. They differ from pathway models in that the modeled entity is a stand characteristic other than cover type and/or structural stage. For example, instead of simulating individual tree growth, a stand model would simulate the accumulation of aboveground biomass per unit area. There are two major subgroups of stand models:

1.2.1. Empirical Models (EMPIRICAL) – This group of stand models rely on extensive field data analyzed over time using various statistical approaches. Empirical models usually track a continuous variable that serves as a surrogate for succession such as fuel loading, stand height, or total biomass. Those models that simulate successional development only from age class are also included in this subcategory.

1.2.2. Biogeochemical Cycle Models (BGCC) – Biogeochemical stand models simulate the physical processes that influence ecosystems at the stand-level. These models are often called “Big-Leaf” models because the photosynthetic surface area is represented by leaf area, which can be visualized, as a single, large leaf.

1.3. Individual Plant Models (PLANT) are those that explicitly simulate the life cycle (regeneration, growth, reproduction, and mortality) of individual plants within some homogeneous simulation area. The major subcategory of models included in this group is the gap-phase models, which were built primarily to simulate stand development from individual trees based on canopy gap dynamics. The inherent simulation complexity of plant life cycles serves to identify the three subcategories:

1.3.1. Statistical models (STAT) – This subcategory is composed of individual plant models that use empirically derived relationships to drive growth, regeneration and mortality processes. Some of the most common statistical models are those designed to predict stand growth and yield for silvicultural applications.

1.3.2. Gap-phase (GAP) – This subcategory includes all gap models that simulate the effect of environmental variables on plant life cycles using algorithms to represent complex physiological and demographic processes. All JABOWA and FORET derived models are included in this class because tree growth and regeneration are simulated as a reduction of maximum based on factors that abstractly describe the effect of environment on tree dynamics.

1.3.3. Biophysical Gap Models (BGAP) – This subcategory includes those models that use an ecophysiological approach to model mechanistic processes that fundamentally govern plant growth, reproduction, and/or mortality. These models generally simulate biogeochemical cycles to drive photosynthesis, respiration, and evapotranspiration at an individual plant level.

2. Fire Ignition is defined as the start of a fire event, and it follows that a fire is only started if it spreads to at least one neighboring cell. Following fire ignition, the spread component immediately begins for the simulation of fire growth. In this classification, spotting is considered a spread process within the original fire. Fire ignition is dependent on many vegetation, environmental, and climatic characteristics that interact across time and space scales. For example, fire ignition from lightning strikes is dependent on thunderstorm tracking, topographic complexity, vegetation structure, and fuel moisture at the strike location. This inherent complexity has caused modelers to take a stochastic approach to simulating fire starts. However, we created a category in the classification

for models that attempt to simulate ignition by explicit representation of the depended physical processes across relevant temporal and spatial scales.

2.1. Stochastic Fire Ignition Models (STOCH) simulate ignition as either a random process or as a process dependent on one or more ecosystem characteristics. In the random subcategory fire starts are simulated as random events with no explicit inclusion of environmental influences. In contrast, the empirical subcategory includes the influence of biophysical variables on fire initiation. Often, environmental parameters such as weather (wind, temperature, humidity), topography (elevation, slope, aspect), fuel moisture, and/or vegetation characteristics are included as independent variables.

2.2. Deterministic Fire Ignition Models (DET) simulate ignition by explicit representation of deterministic functions. An empirical subcategory would use statistical relationships to represent the influence of biophysical variables on fire initiation. In contrast, physically based fire ignition models attempt to mechanistically simulate the physical processes that drive fire initiation from driving variables of weather, fuel moisture, and lightning simulation. This is an extremely difficult process that is fraught with scale, data, and knowledge limitations.

3. Mechanisms of Fire Spread across the landscape after a fire has been ignited are considered within the fire-spread element. We have aggregated the process of fire extinguishment into this element because it is often highly dependent on the spread algorithms. Many approaches have been used to simulate the growth of fire but none seem superior in all categories. The most accurate fire spread algorithms often require copious computer resources that prohibit millennia-scale simulations, while the simplest approaches often produce unrealistic fire perimeters. We have recognized three categories of fire spread approaches. In each category we have designated the same three subcategories, which will be defined in the first category below.

3.1. Cellular Automata (CELL) models simulate the spread of fire from one pixel to another in a raster spatial domain. Lattice and percolation cell-based spatial spread models are designated within this class of models. These are the most common types of models at the landscape scale.

3.1.1. Probabilistic (PROB) – The functions that govern the spread of fire use probabilities to determine the effect of environmental (and vegetation) variables on fire spread.

3.1.2. Empirical (EMP) – These models use empirical-

based functions to drive the spread of fire. These functions utilize statistical relationships to represent the influence of biophysical variables on fire spread. The McArthur (1967) equations are an example of such an empirical-based approach.

- 3.1.3. Physical (PHY)** – These models use algorithms that provide a mechanistic simulation of the physical processes that drive fire growth in determining which pixels burn. Often, this subclass of models uses the Rothermel (1972) equations to compute the spread of fire across the landscape.
- 3.2. Vector (VECTOR)** models are similar to cellular automata models except that the spatial simulation uses a vector rather than a raster approach. Often, these models use raster layers for model input, but the actual spread of the fire is simulated using vectors. The same subcategories apply to vector models as cellular automata models.
- 3.3. Shape (SHAPE)** models simulate the growth of fire by a “cookie cutter” approach where all land area within a predetermined fire perimeter (often a truncated ellipse of varied size) are considered to be burned. Wind, slope, and vegetation can influence fire shapes. Fires in this class of models are never actually “spread” across the landscape, but rather the fire pattern is superimposed onto the vegetation without the incorporation of spatial relationships. Again, the same subcategories apply to shape models as cellular automata and vector models.

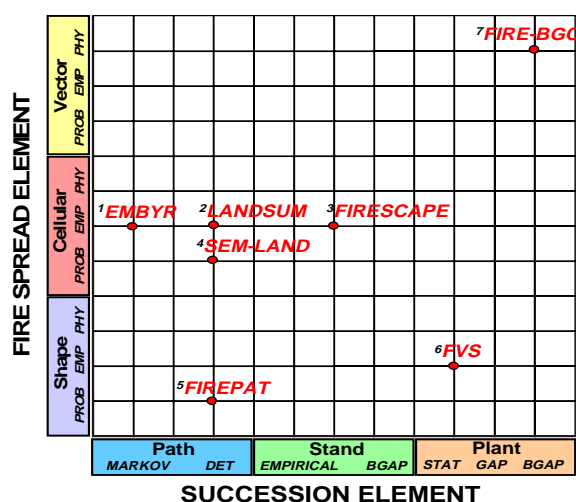


Figure 3 : A small group of landscape fire succession models arranged in two-dimensional classification space of the succession and fire spread elements. Refer to references for description of individual models (¹Gardner et al., 1996; ¹Hargrove et al., In Press; ²Keane et al., 1997; ²Keane and Parsons, In Press; ³Cary, 1998; ³Cary and Banks, 1999; ⁴Li, 2000; ⁵Keane and Long, 1998; ⁶Wykoff et al., 1982; ⁷Keane et al., 1996).

This classification exercise will provide a future information framework for researchers and land managers interested in the theory and application of LFSMs. Application of LFSMs at coarse scales demands an inventory of current modeling efforts so that the best components of each modeling approach can be used in developing DGVMs that predict realistic vegetation complexes. For example, figure 3 illustrates the arrangement of a few LFSMs in a two-dimensional classification space of the succession and fire spread elements. This classification scheme will allow us to efficiently compare LFSM process modules in order to better understand the linkages between landscape fire, vegetation and weather/climate at a variety of spatial and temporal scales. Additionally, this classification system could be used as a starting point for the development of a decision matrix for land managers who would like to know which LFSMs are appropriate to use to achieve a specific objective (e.g., habitat restoration, fuel load reduction, stand conversion, etc.).

The classification scheme for LFSMs is ongoing and will culminate in a peer reviewed journal article, which will provide a detailed description of the component elements and a review of relevant LFSMs. Therefore, the authors invite the broader scientific community to comment on the prototype classification scheme presented here.

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A particular model in LAMOS will then consist in the combination of: one succession method, one or several disturbance types with associated spread methods, one dispersal method for each FT, and the water flow method. Any of the modules can be switched off to exclude one particular process.

An example: feedbacks between dispersal and fire disturbance patterns in Mediterranean landscapes

Landscapes of the northern Mediterranean Basin are presently subjected to an interesting dynamics where, in areas that were formally intensively managed by agriculture and grazing, land is now mostly under natural succession. Humans are however still present, and are in particular the most frequent source of ignition of fires. These fires can now propagate relatively easily across landscapes where flammable fuel is accumulating as a result of the recolonization by woody species. Questions of interest are: 1) to what extent does landscape initial configuration (e.g. distribution of seed sources for woody species) affect future fire regimes and vegetation patterns? 2) How is it influenced by the capacity of species to disperse through the landscape?

To explore this questions we developed with LAMOS a model combining:

- Vital Attributes succession; vegetation of the Montpellier region (France) was described using six FTs, including herbs, clonal grasses, resprouter shrubs, one seeder tree (pines) and two resprouting trees (evergreen and

deciduous oaks).

- A single disturbance, fire, with contagious spread
- Seed dispersal with continuous kernels for all FTs
- No lateral flows (for this exercise we assumed a flat landscape)

Simulations were then run for a period of 1000 years with a variety of initial patterns of distribution of woody vegetation in the landscape. In an experiment designed to assess the role of dispersal in the development of fire regimes and vegetation patterns we compared two dispersal scenarios: kernel dispersal (the 'normal' scenario), and dispersal restricted to local seed set. This experiment was designed to demonstrate the feedbacks between two landscape processes, disturbance and dispersal (Figure 2). When dispersal is restricted to pixels with existing adults, successional development is considerably slowed down by the lack of seed exchange across the landscape and the vegetation remains grassy. This in turn results in small and relatively infrequent fires. In the opposite case, when species disperse seeds around existing stands, the encroachment of woody species into the landscape is rapid, and fires are bigger and more frequent. Experiments like this one are useful in helping us understand the consequences of basic processes of landscape dynamics. They also draw our attention about how the loss of a dispersing vector for key structural species can affect landscape patterns and disturbance regimes.

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Simulations for Mediterranean garrigue vegetation starting from a landscape where agricultural activities are stopped and trees (*Quercus ilex*) are only present as a small strip of adults (red) fringed by seedlings (yellow) (Fig. 2a). The landscape matrix is formed by a degraded rangeland with herbaceous vegetation (not shown) and juvenile shrubs. When seeds can be dispersed outside of existing stands (fig. 2b) the landscape is rapidly covered by woody vegetation, and fires are large (on average 50% of the landscape is burned for each fire year). When on the other hand dispersal is restricted to stands where seeds originate body species do not manage to gain much of the landscape. Fires are smaller (on average 20% of the map burned per fire year) and the landscape is more heterogenous.

Fig. 2: Effects of dispersal on landscape vegetation and fire.

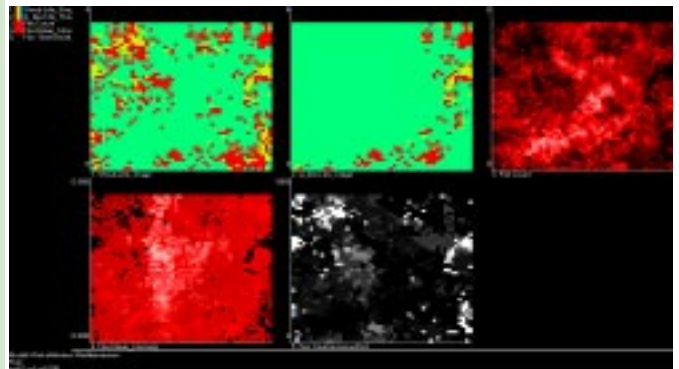


Figure 2a

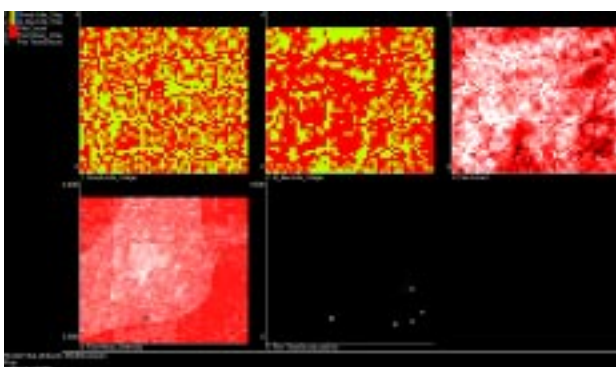


Figure 2b

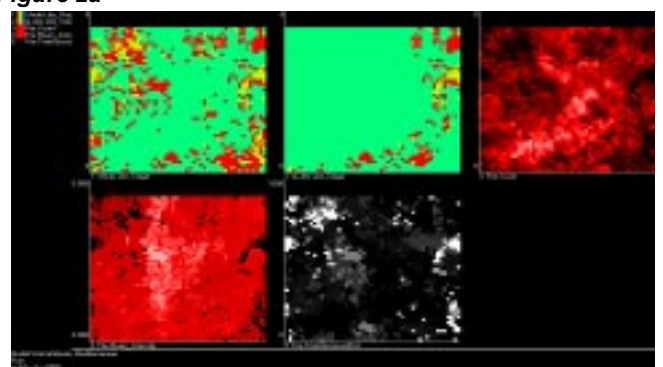


Figure 2c

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Crop Production in Asia under a CO₂-rich Atmosphere

China-FACE

A group of Chinese and Japanese scientists is working together to set up a Free Air Carbon dioxide Enrichment (FACE) project in Wuxi, near Shanghai, China. The FACE site is located in rice-winter wheat growing region near the Taihu Lake. This project is designed to address the questions of how rising atmospheric CO₂ affects crop productivity, nutrient cycling, and other ecosystem processes. In particular, the project will have five objectives: (1) to understand mechanisms of crop (rice and wheat) responses to elevated CO₂, (2) to quantify CO₂ effects on crop yield and quality, (3) to estimate changes in nutrient and water use efficiencies under elevated CO₂, (4) to contribute to model development for C and N uptake, transfer, and cycling in the agro-ecosystem, and (5) to evaluate potential effects of elevated CO₂ on exchanges of greenhouse gases in the agro-ecosystems with the atmosphere.

This project is scheduled to finish infrastructure construction and be operational in June 2001. The experiment will have three control plots with ambient CO₂ and three FACE rings with ambient + 200 ppm CO₂. Each ring is 12.5m in diameter with pure CO₂ injection adopting the Japanese design. The first experimental period will be from June to October 2001, which is the growing season for rice in that region. The CO₂ fumigation system is expected to fully operate for 365 days a year from 2002 to 2005.

Since China is one of the largest rice and wheat production countries, the project has the potential to evaluate the impacts of global environmental change on food supply and feedbacks of agro-ecosystems to climatic changes through the greenhouse gas exchanges.

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Crop responses to rising atmospheric CO₂ in India

The fast rise in atmospheric CO₂ concentration is a unique challenge for agricultural scientists in India because of its implications on crop productivity and food security for a population over a billion. The Government of India and Indian Council of Agriculture Research started an impact assessment analysis through studies on "Effect of rising atmospheric CO₂ on photosynthesis and productivity of crop plants under



Figure 1: Open-top chambers in India

moisture stress conditions", in the Indian Agricultural Research Institute, New Delhi. Efforts were made to develop experimental techniques to keep high CO₂ concentrations around growing crops, and open top chambers were designed specifically to suit the needs of experimentation in the South Asian region (Figure 1)) (Upreti et al 1995).

Results from such studies show that increased CO₂ concentration mitigates some of the negative effects of water deficit. Other studies focused on the differential response of C₃ (mungbean) versus C₄ (maize), crops changes in C:N dynamics, chemical composition of grains, photosynthetic performance, nitrogen cycling, and changes in leaf anatomy in Brassica species. See references: Upreti et al. 1996, 1997, 2000, 2001, Rabha & Upreti 1998, Upreti & Mahalaxmi 2000, Upreti & Rabha, 1999, Upreti 1998 [contact Dr. Upreti for full list of references].



More recently, and thanks to a grant from the Asian Pacific Network (APN) and the support of START and GCTE, a new Free Air Carbon dioxide Enrichment (FACE) system has been established in India (Figure 2 above).

A Mid-FACE facility was developed at IARI in collaboration with Italian and NPL scientists. It has good portability and the cost of operation is low. It consumes approximately 400 litres of CO₂ per day (12 hours) for an 8m-diameter octagon shaped ring (Figure 2). CO₂ is injected at the input blower for pre-mixing and CO₂ concentration is measured at the center of the ring at 10 to 15 cm above the crop canopy level to monitor and control CO₂ gradients. This technology has been established for the first time in a South Asian country and the experiment is now in progress.

The expected outcomes of this research are:

1. To understand basic mechanisms that control elevated CO₂ responses of different crop plants.
2. To design strategies for choosing suitable crop species and identifying management practices for changing atmospheric composition.
3. To develop and validate crop models that can predict future productivity under global change.
4. To act as a research center with facilities available to other scientists in the South Asian region.
5. To provide relevant information to policy formulation on food security and crop productivity in this region.

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(Please see <http://www.gcte.org/news.htm> for references)

Stable isotope measurements and biosphere-atmosphere exchange

Improving estimates of the magnitude and regional distribution of the terrestrial carbon sink remains a key research priority for many global change researchers, as well as for GCTE Focus 1. During the 1980's the net sink, including emissions from deforestation, was on the order of 1.9 Gt C/yr, while preliminary analyses of the 1990's indicate that the sink may be even larger (Watson et al. 2000). Proposed mechanisms underlying a net uptake of CO₂ by terrestrial ecosystems include CO₂ fertilization, nitrogen deposition, and forest regrowth on abandoned agricultural lands (Schimel et al. 2000). Different factors are likely to dominate in different biomes and regions; for instance, forest regrowth has been proposed as an important and perhaps dominating mechanism for net carbon uptake in the eastern United States (Houghton et al. 1999). However, estimates of regional carbon sinks are highly variable and often inconsistent among "bottom-up" approaches that scale-up from biomass or productivity estimates, and "top-down" approaches that rely on atmospheric CO₂ measurements. Stable isotope measurements of terrestrial ecosystems and the atmosphere can be an important component of both approaches, and offer a great of potential for refining and constraining carbon balance estimates.

The top-down or inverse-modeling method of estimating net carbon fluxes relies on measured atmospheric gradients of CO₂ and atmospheric transport models to determine sources and sinks of carbon. CO₂ measurements alone yield net carbon sources globally and for large regions, but do not distinguish between oceanic and terrestrial sinks. Partitioning the carbon sink into its component parts requires additional atmospheric information, including measurements of the isotopic composition of atmospheric CO₂, that is, the ratio of ¹³C/¹²C and ¹⁸O/¹⁶O. Terrestrial ecosystem processes strongly discriminate against the heavy isotopes ¹³C and ¹⁸O in CO₂ and impart an isotopic signature to the atmosphere that is distinguishable from oceanic effects. As a result, inverse models

incorporate estimates of terrestrial ecosystem isotope discrimination in order to determine the magnitude of the terrestrial carbon sink.

The biochemical and physical basis for isotopic discrimination by photosynthesis has been well established (Flanagan and Ehleringer, 1998). For carbon, both diffusion to site of carboxylation, as well fixation by RuBP carboxylase (Rubisco), discriminate against ¹³C. Oxygen isotopes in CO₂ are also subject to diffusional effects, but once inside the leaf oxygen in CO₂ rapidly exchanges with oxygen in water, which becomes heavily influenced by the isotopic signature of leaf water. These leaf-level processes have been quantified and used to predict the isotopic composition of plant biomass. Because studies suggest that there is no isotopic fractionation of carbon during respiration, many models rely on leaf-level photosynthetic equations to predict net terrestrial ecosystem discrimination. To determine the isotopic signature of ecosystem respiration, a disequilibrium term is included to account for the lag between fixation and respiration. However, the isotopic composition of respiration is complex, as is it

composed of materials fixed at many different times which may contribute to total ecosystem respiration in varying proportions depending on environmental conditions.

The isotopic composition of soil or ecosystem respiration can be directly determined with a method developed by Keeling (1961). By plotting the isotope ratio of the CO₂ in an air sample against the inverse of its concentration, a highly linear relationship is obtained (Figure 1). The intercept of the resulting linear equation is the isotopic composition of respired CO₂. Spatial variability in the "Keeling plot" intercept has long been observed, particularly between ecosystems comprised of C₃ vs. C₄ plants. Because of their unique anatomy, C₄ plants do not discriminate against heavy isotopes to a very large degree. This effect is readily discernible in the Keeling plot intercepts of mixed C₃-C₄ ecosystems (Figure 1). Because the C₄ isotopic signature is much closer to the oceanic effect than the C₃ signal, it is important to correctly estimate the proportional contribution of C₃ and C₄ plants to global photosynthesis for carbon cycle calculations. In addition, there is geographic variation even within

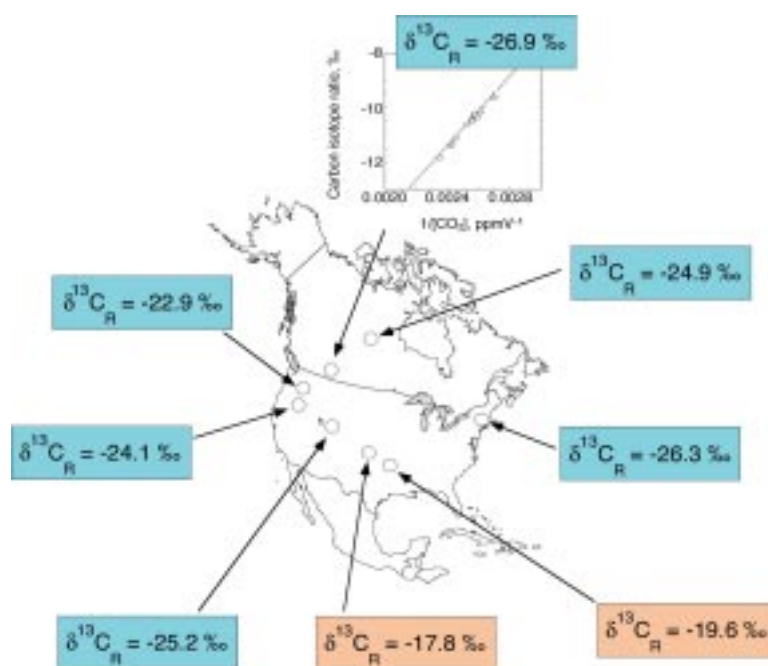


Figure 1: Spatial variability in the isotopic composition of ecosystem respiration, or "Keeling plot" intercept (see text for explanation). A representative Keeling plot is shown at the top of the figure. Values highlighted in blue were obtained from C₃ ecosystems, values in orange from mixed C₃-C₄ grasslands.

C₃ ecosystems that could result in errors in carbon sink calculations if one assumes that discrimination is constant (Figure 1).

The GCTE Focus 1 Biosphere-Atmosphere Stable Isotope Network (BASIN) is a consortium of studies of the isotopic composition of ecosystems and their exchange of trace gases with the atmosphere. BASIN researchers determine the isotopic composition of respiration, organic material, components of evapotranspiration, and other trace gases in order to improve our understanding of ecosystem processes controlling biosphere-atmosphere exchange. A major goal of BASIN is to determine the processes underlying spatial variation in ecosystem discrimination and improve our ability to predict the isotopic composition of ecosystems for top-down carbon sink estimates.

There is growing evidence from a number of BASIN sites to suggest that the components of ecosystem respiration are dynamic and show a great degree of temporal variation. In fact, within C₃ ecosystems the magnitude of interannual variability in the isotopic composition of ecosystem respiration can be greater than the spatial variation (Figure 2). As interannual variability in carbon sinks has been shown to be of primary importance in the global carbon cycle, it is essential to determine the mechanisms underlying annual fluctuations in isotopic discrimination. Studies of the underlying cause of changes in ecosystem isotope effects on the atmosphere may reveal important information about the

controls of biosphere-atmosphere exchange. Even more directly, assuming a terrestrial biosphere with a dynamic versus fixed isotopic signal will necessarily influence the magnitude of any regional terrestrial carbon sink (Fung et al., 1997).

It is known that climate affects leaf level discrimination through variations in photosynthesis and stomatal conductance with temperature, drought, and rainfall. The net effect of these changes on autotrophic and heterotrophic respiration is contained in the isotopic signal in ecosystem respiration. BASIN researchers have correlated interannual variability in the isotope ratio of respiration with extreme climatic events, such as El Niño (Figure 2), and variability in monthly and annual rainfall. This effect is likely to be at least partially driven by drought stress-induced stomatal closure, although there may be additional effects on heterotrophic respiration due to changes in soil moisture. The isotopic composition of soil respiration has been directly measured in a number of studies, including a coniferous forest in northern Sweden that showed a surprising coupling between atmospheric conditions and the isotope ratio of soil CO₂ flux. By correlating the carbon isotope ratio of soil respiration with humidity measured 3-4 days before the soil CO₂ flux, Ekblad and Högborg (2001) showed that recently produced photosynthate comprised a large proportion of belowground respiration within a relatively short period. Their results illustrate how isotopic measurements can improve our understanding of ecosystem function. This type of information may greatly refine

process-level models of biosphere-atmosphere exchange and carbon balance.

FLUXNET, the international network of studies measuring Net Ecosystem Exchange (NEE) of CO₂ and water vapor currently coordinates a comprehensive program of ecological measurements associated with ecosystem carbon metabolism. Combining NEE and associated FLUXNET measurements with isotopic sampling offers the most promising approach to advancing our understanding of the terrestrial component of the carbon cycle. For this reason, BASIN was created in partnership with FLUXNET, and in fact a large proportion of BASIN studies are ongoing at FLUXNET sites. Over the next several years, combined analyses and model comparisons of FLUXNET results and the growing BASIN isotopic database will provide a more comprehensive understanding of the factors controlling NEE and its components and in the present, and in the future under changing environmental conditions.

For more information, please visit the BASIN webpage at <http://gcte-focus1.org/basin.html>.

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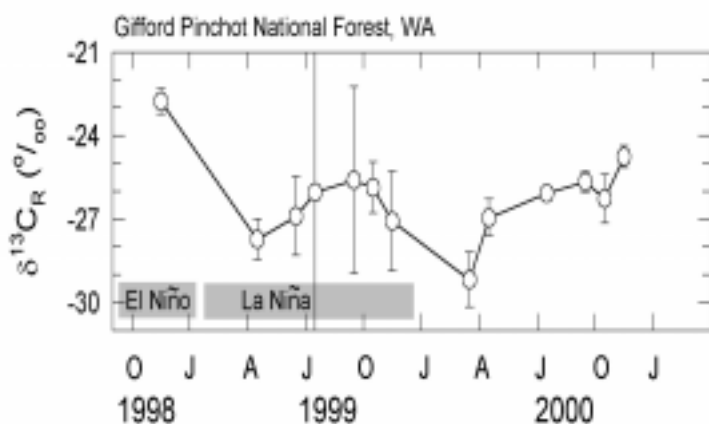


Figure 2: Temporal variability in the isotopic composition of ecosystem respiration at the Wind River Canopy Crane site in Washington, USA. From Fessenden et al. in review.

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Biodiversity and ecosystem functioning: an overview of findings and of recent controversies

Humans have significantly altered the Earth after Industrial Revolution: we have transformed 40-50% of its ice-free land surface, fossil fuel combustion has led to a 15% increase in the atmospheric concentration of CO₂ over the last 40 years, and the fixation of nitrogen from agro-industrial sources more than doubles all natural inputs combined. These changes in the chemical composition of the atmosphere, the extension and geographic distribution of natural habitats and the global climate are having an important effect on biogeochemical cycles that provide the energy and materials necessary to sustain human life. In addition, these changes, and notably the changes of land use, have led to both a decrease of the number of species and their geographic distribution at various spatial scales ranging from regions to continents.

The functioning of ecosystems involve the movement and transformation by the biota of millions of tons of material per year between organic and inorganic pools through the processes of decomposition, nutrient mineralization, assimilation and production.

There is a growing concern that changes in the number and spatial distribution of species can have a important effect on ecosystem functioning, whereby species-poor ecosystems may perform differently or less efficiently than the more species-rich systems from which they are derived. From a functional point of view, it is not that all species matter per se for the integrity or the functioning of ecosystems. Rather, the potentially critical consequence of species losses is that their disappearance can lead to the loss of individual traits that are essential for the production of organic matter and the functioning of biogeochemical cycles.

Albeit at a small scale, ecologists have started constructing and manipulating experimentally entire ecosystems in the field, explicitly asking aspects whether ecosystem functioning may be changed, disrupted, de-stabilized or made unreliable by the loss of biodiversity. These ambitious field and laboratory controlled experiments have essentially tested the short-term effects that changes in species

diversity can have on various aspects of ecosystem functioning. However, the results of these short-term experiments have not always been consistent across ecosystem types and processes, and the analysis and interpretation of these results have been the subject of an intense debate. We (Michel Loreau, Shahid Naeem and Pablo Inchausti, of GCTE Focus 4) recently organised an international conference in Paris

with the aim of synthesizing the results of experiments and theories across ecosystem types, and of reaching a consensus on the main issues of the debate between the relation of biodiversity and ecosystem functioning.

Some conclusions emerging from this experimental and theoretical work presented and debated in this conference include:

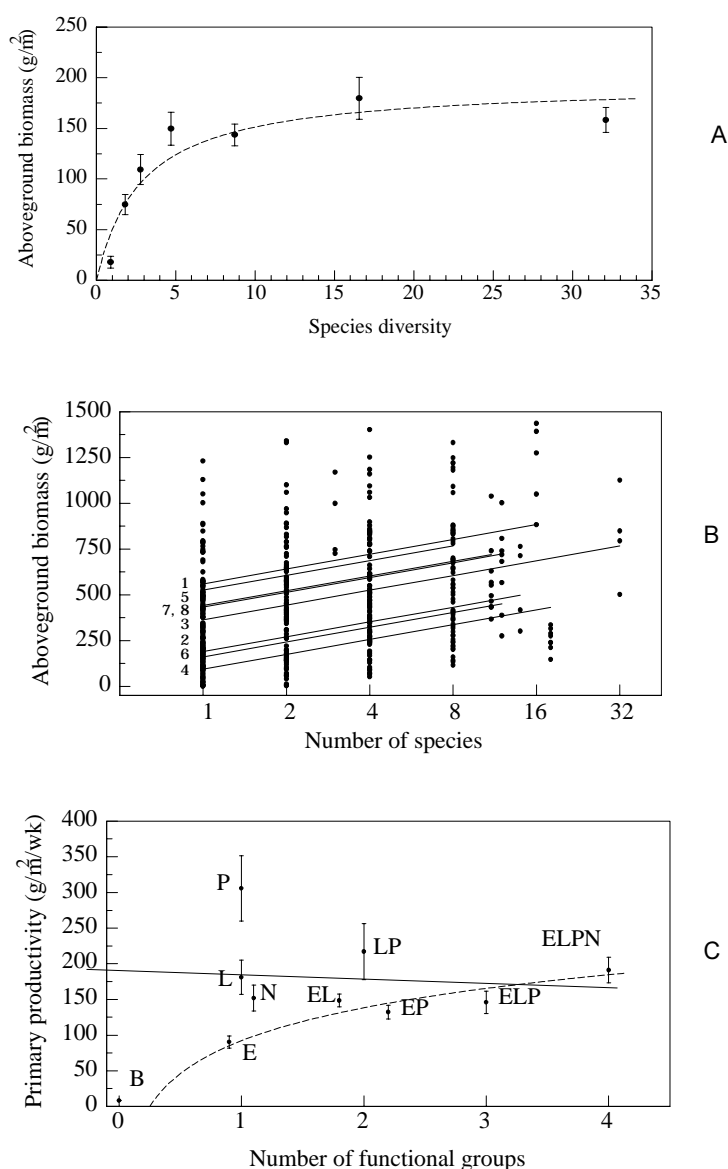


Figure 1: Response of (A,B) aboveground plant biomass in Minnesota and European grasslands and (C) net primary productivity in a Californian serpentine grassland as a function of species diversity (A,B) or of functional group diversity (C) in each grassland community. Sources of data are (A) Tilman et al (1997 p.277), (B) Hector et al. (1999 p.***) and (C) Hooper and Vitousek (1997, p. 1304).

- There is evidence to suggest that small, critical changes in biodiversity may have an adverse effect on the average rates of ecosystem processes such as primary production, and nutrient retention (Figure 1) in some natural ecosystems such as temperate grasslands. These few studies often failed to detect significant effects of biodiversity on belowground decomposition processes, raising the question to what extent their results can be generalized to other processes and ecosystems. When present, there is a positive saturating relationship between species richness and variables describing ecosystem processes such as primary production and nutrient retention. The levelling-off of this relationship tends to occur at relatively low species richness.
- Two non-mutually excluding mechanisms have been proposed to explain of these findings. First, the coexistence of species in diverse mixtures is likely to involve differences along one or more niche axes that would allow a better collective use of resources, thus leading to an enhanced functioning of more diverse ecosystems (complementarity mechanisms). One common form of

complementarity in plant communities (which involves both resource partitioning and facilitation) comes between nitrogen-fixing legumes and other plants that utilize soil nitrogen. The second type (selection mechanisms) involve two phenomena: a sampling effect, whereby more diverse plant mixtures assembled from a pool of species have a higher chance of containing particular species, and a selection effect, by which each community becomes dominated by that species which is most productive when grown alone. Selection occurs when processes, such as interspecific competition or intrinsic growth differences, cause dominance of species with particular traits.

- Species whose loss is thought to have large functional consequences are those that modify the availability of limiting resources, that affect the disturbance regime, or that alter the trophic structure of the impacted ecosystem. There is an on-going effort to identify suite of physiological and life history traits that would allow classifying those species whose loss is likely to have consequences for ecosystem functioning into functional groups.
- Over longer times, modeling results indicate that high species diversity might allow the reliable functioning

of ecosystem by buffering the impact of species losses and of the extreme environmental fluctuations brought about by global changes ("the insurance hypothesis"). According to this hypothesis, species that are functionally redundant for an ecosystem process at a given time may no longer be redundant through time. Although a small number of empirical and experimental studies have provided results consistent with this hypothesis (Figure 2), there is a critical need to verify and extend these results.

We believe that an important challenge for the next decade is to scale up the relationship between ecosystem processes and biodiversity from the small patch, where most empirical and theoretical studies apply, to the landscape level where most management issues are dealt with. There is also a critical need to extend research efforts to encompass full ecosystems (multi-trophic levels), habitats other than temperate grasslands, and to extend the research to ecosystem processes other than primary production.

It has become apparent that although changes in biodiversity (as measured by the number of species) may not necessarily be the main driver of ecosystem processes, they can importantly modify the effects that factors such as changes in land use, atmospheric composition and climate have on ecosystem functioning. The effects that these fast and drastic changes in the chemical composition of the atmosphere, the geographic distribution of biomes and climate will be controlled or altered by the effect of biota on the global biogeochemical cycles. Biodiversity can no longer be considered only the "passive" result of composing static abiotic constraints with the dynamics of biotic interactions. While it remains an open empirical question to determine what species have a critical functional role for which processes in what ecosystems, it is indisputable in our view that the Earth biota and its astonishing diversity plays a critical and active role in modulating, regulating and largely controlling the results of human actions on the planet.

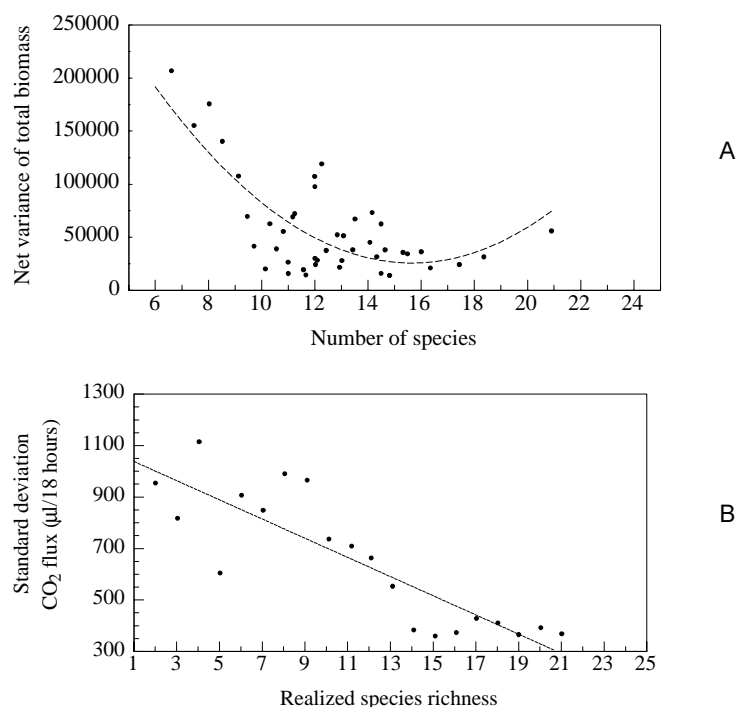


Figure 2: Relationship between temporal variability of ecosystem processes and the number of species. (A) Net variance in the total aboveground biomass in Cedar Creek, USA; data from Tilman 1999 p.1463). (B) Standard deviation of CO₂ flux over 18 h in a microbial microcosm; data from McGrady-Steel et al. 1997 p. 163).

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Upcoming Meetings

26-28 March, Beijing, China
XII GCTE-SSC meeting. Contact: Pep Canadell, E-mail: pep.canadell@gcte.org

29-30 March, Beijing, China
Chinese-GCTE Global Change Conference. Contact: Guangsheng Zhou, E-mail: zhousg@public2.bta.net.cn and Pep Canadell, E-mail: pep.canadell@gcte.org

28-30 March, Oslo, Norway
International symposium : Snowmelt erosion and related problems. Contact: Lillian Øygarden, E-mail: lillian.oygarden@jordforsk.no
For more information please visit <http://www.jordforsk.no/Avdmiljo/snowmelt.htm>

9-13 April, Montpellier, France
Estimating rare long-distance dispersal to predict plant persistence and migration. Contact: Steve Higgins, E-mail: higgins@nbict.nbi.ac.za

22-24 April, Albuquerque, New Mexico
Developing guidelines and strategies for scaling patterns and processes in heterogeneous landscapes: Applicability to current issues in ecology. (co-sponsored by LTER) Contact: Debra Peters, E-mail: debpeters@nmsu.edu

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26-27 April, Mexico
Tropical Cereals Modelling. Contact: John Ingram, Email: jsii@ceh.ac.uk

2-4 May, Beaufort, NC, USA
GCTE Focus 1 Workshop: Tracing carbon in elevated CO₂ experiments: a workshop on isotopic analyses of where the carbon is going. Contact: Diane Pataki, E-mail: pataki@biology.utah.edu

9-11 May, Valencia, Spain
Plant Functional Types in relation to Disturbance and Land Use: Synthesis and Challenges. Contacts: Juli Pausas, E-mail: juli@ceam.es

10-12 May, Santa Barbara, USA
GCTE/NCEAS working group meeting: Progressive nitrogen limitation of plant and ecosystem responses to elevated CO₂. Contacts: Yiqi Luo, Email: yluo@ou.edu and Chris Field, Email: chris@jasper.stanford.edu

TBA, Salt Lake City, Utah, USA
BASIN Steering Committee meeting: Contacts: Diane Pataki, pataki@biology.utah.edu, Jim Ehleringer: ehleringer@biology.utah.edu.

26-29 May, Duke University, Durham, North Carolina, USA
Nonlinear responses to Global Environmental Change: Critical Thresholds and Feedbacks. IGBP Nonlinear Initiative. Contact: Pep Canadell, E-mail: pep.canadell@gcte.org

26-30 May, Beijing, China
GCTE Soil Erosion and Land-use Change (as part of the 12th Conference of ISCO). Contact: John Ingram, Email: jsii@ceh.ac.uk

10-15 June, Berlin, Germany
An Integrated Assessment of the Ecological, Meteorological, and Human Dimensions of Global Desertification. Contact: James F. Reynolds, E-mail: james.f.reynolds@duke.edu.

19-23 June, Montpellier, France
Plant dispersal and migration modelling for global change. Contact: Steve Higgins, Email: Higgins@esa.ufz.de, Sandra Lavorel, Email: lavorel@cefe.cnrs.mop.fr and Lou Pitelka

19-21 July, Tune, Denmark
Production Systems open planning workshop. Contact: John Ingram, Email: jsii@ceh.ac.uk

N.H - Autumn, The Netherlands
Linking Models to Observations. Contact: Peter de Ruiter, E-mail: p.deruiter@frw.ruu.nl

September, Jena, Germany
Manipulating insect herbivory in biodiversity-ecosystem function experiments. Contact: Valerie Brown, Email: v.k.brown@reading.ac.uk

12-15 September, Glacier National Park, Montana, USA
Global Change and fire effects at landscape scales. Sponsored by US Forest Service. Contact: Bob Keane, Email: rkeane@fs.fed.us

19-22 September, Barcelona, Spain
Global analysis of base rates and impacts of biotic invasions. Contacts: Montserrat Villa, Email: vila@cc.uab.es Mark Lonsdale, Email: Mark.Lonsdale@ento.csiro.au and R.Mack.

12-16 November, Santa Barbara, CA, USA
Global Change and fire effects at landscape scales. Sponsored by NCEAS. Contact: Mike Flannigan, Email: mflannig@nrcan.gc.ca and Sandra Lavorel, Email: lavorel@cefe.cnrs.mop.fr

TBA, Nairobi, Kenya
Land use change and crop-associated biodiversity. Contact: Valerie Brown, E-mail: v.k.brown@reading.ac.uk

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