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# COMBINING PROCESS-BASED MODELS FOR FUTURE BIOMASS ASSESSMENT AT LANDSCAPE SCALE

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## Abstract

We need an integrated assessment of the bioenergy production at landscape scale for at least three main reasons: i) it is predictable that we will soon have landscapes dedicated to bioenergy productions; ii) a number of “win-win” solutions combining several dedicated energy crops has been suggested for a better use of local climate, soil mosaic and production systems; and iii) “well-to-wheels” analyses for the entire bioenergy production chain urges us to optimize the life cycle of bioenergies at large scales. In this context, we argue that the new generation of landscape models allow *in silico* experiments to estimate bioenergy distributions (in space and time) that are helpful for this integrated assessment of the bioenergy production. The main objective of this paper was to develop a detailed modelling methodology for this purpose. We aimed at illustrating and discussing the use of mechanistic models and their possible association to simulate future distributions of fuel biomass.

We applied two separated landscape models dedicated to human-driven agricultural and climate-driven forested neighbouring patches. These models were combined in the same theoretical (i.e. virtual) landscape for present as well as future scenarios, by associating realistic agricultural production scenarios and B2-IPCC climate scenarios depending on the bioenergy type (crop or forest) concerned in each landscape patch. We then estimated esthetical impacts of our simulations by using 3D visualizations and a quantitative “depth” index to rank them.

Results first showed that the transport cost at landscape scale was not correlated to the total biomass production, mainly due to landscape configuration constraints. Secondly, averaged index values of the four simulations were conditioned by agricultural practices, while temporal trends were conditioned by gradual climate changes. Thirdly, the most realistic simulated landscape combining intensive agricultural practices and climate change with atmospheric CO<sub>2</sub> concentration increase corresponded to the lowest and unwanted bioenergy conversion inefficiency (the biomass production ratio over hundred years divided by the averaged transport cost) and to the most open landscape. Managing land use and land cover changes at landscape scale is probably one of the most powerful way to mitigate negative (or magnify positive) effects of climate and human decisions on overall biomass productions.

**Keywords:** Formal grammar; landscape modelling; heterogeneity; agricultural production system; Tree-growth model; Mediterranean forests; evergreen oak; dendrochronology; CO<sub>2</sub> fertilization effect.

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## 1 Introduction

There exists a debate about the interest of bioenergy to enhance energy security, to reduce Green House Gas (GHG) emissions and to provide economical transport. No one is today able to predict the contribution of each bioenergy source to our needs (Connor and Minguez 2006). However, it is clear that the use of biomass to supplement and replace oil for liquid transportation fuel will happen as oil supplies decline and become every day more costly. In addition, a major challenge linked to bioenergy is to manage the natural environment to provide both fuel and food for a large and energy-demanding world population. We will need to provide both with the lowest impact on environment (Connor and Minguez 2006) and the lowest esthetical impact on our landscapes (Ervin 2001), among other criteria. In this paper, we aim at discussing this broad question by focusing on biomass assessment and highlighting the role of landscape-based studies and modelling.

To our opinion, three arguments justify an “integrated assessment” of bioenergy production at landscape scale. First, it is predictable that what has been proposed to extract energy from our existing landscapes will not satisfy the growing energy demand of the world population. Collecting agriculture or forestry wastes to extract cellulose-based energy or harvesting our meadows to produce C<sub>4</sub> grass bioenergy will not fill our needs. It is therefore obvious that we will soon need some territories dedicated to bioenergy production. Such landscapes would have to mitigate negative incomes such as fertilizers, to manage water supply and probably to use non-arable soils to leave them available for food production (Connor and Minguez 2006). By the way, if only parts of the landscapes would be covered by high grasses, hedgerows and forests for this purpose, their heights and densities would strongly “close” these landscapes (i.e. vanishing horizon and reducing depth). This point suggests simultaneously estimating esthetical impacts of landscapes managed for the bioenergy production. Esthetical assessment is even critical for the acceptance of bioenergy production by local populations (Sheppard 2005), as we have already observed it for wind-based energy production.

Secondly, we will rapidly need a wide range of mitigation actions to conserve global sustainability of such landscapes. We need well-thought bioenergy productions to manage conservation acreage for stabilizing soils, for providing wildlife communities, for reducing infestation and fire risks. We also have the objective to reduce the net GHG emissions by such bioenergy production because bioenergies recycle carbon dioxide that has been extracted from the atmosphere in producing biomass. Yet, it is certainly wrong to think that changing land covers from forests or savannahs to bioenergy crops will reduce the GHG sequestration by atmosphere (Fargione et al. 2008). Moreover, we received indications that mixing various bioenergies within the same energy-dedicated landscape would be a promising way for increasing its sustainability (Cormeau and Gosse 2008). Indeed, a number of “win-win” solutions combining several dedicated energy crops would allow a better use of local climate (mainly temperature), of resources (soil and water supply), and of production systems. To mix bioenergies also supposes to find the appropriate scale for minimizing the

possible threats (parasite and fire risks) that bioenergy production will have to face (Butler et al. 2007).

105           Thirdly, the broad cost-and-benefit analysis for the entire bioenergy production chain urges us to think this production at landscape scale. We need to quantify bioenergy impacts on ecosystems or territories, and on the world's economy. The global energy balance associated to each bioenergy production is the energy output / energy input ratio and depends on the energy types and origins. Furthermore, computing this efficiency ratio implies to quantify the input and output energies at the  
110 same scale and within equivalent (spatial and temporal) boundaries. This attempt is always difficult to achieve: we need a detailed "well-to-wheels" analysis to quantify all the bioenergy impacts on the basis of complete life-cycles (JRC Europe 2006). For example, we can no more consider the bioenergy crop to be produced in a field without location. Working in such spatially implicit scheme would hide local specificities of the field (soils, micro-climate conditions...) and would forget to take into account  
115 for the relative position of biorefinery associated to the field. We believe that the biorefinery location choices would benefit from an overall strategy at the appropriate scale, including transport costs and possible routes leading from the field to the biorefinery.

          In this context, we argue that it is now time to perform an integrated assessment of the  
120 bioenergy production. Furthermore, the new generation of landscape models allow *in silico* experiments to estimate bioenergy distributions (in space and time) that would have been difficult or even impossible for future assessments in real landscapes. The main objective of this paper was to develop a detailed methodology for achieving this integrated assessment objective at landscape scale. In a second objective, we aimed at illustrating and at discussing the use of mechanistic models and  
125 their possible association to simulate future distributions of fuel biomass.

          We illustrate the advantages of this modelling methodology by combining several models to simulate spatial distributions of fuel biomass within a chosen landscape. A major problem for this purpose concerned the high diversity of landscape drivers, either human decisions or natural forcing, which are responsible of the various bioenergy evolutions and their interactions in space. Landscape  
130 models are rarely exploring both human and natural drivers simultaneously (Monticino et al. 2007), while there exists today many process-based models to be coupled or simply combined. We intended to apply two landscape models dedicated to human-driven agricultural (DYPAL model (Gaucherel et al. 2006; Houet and Gaucherel 2005)) and climate-driven forested (MAIDEN model (Gaucherel et al. 2008a; Misson 2004)) neighbouring patches, after detailed calibration and validation stages. These  
135 models were then combined (not coupled) on the same theoretical (i.e. virtual) landscape, at different dates, to quantify the biomass fine scale distribution. The main hypothesis of this work was that scenarios having the highest economical benefits are not necessarily leading to the landscapes having the highest biomass. This assertion is partly due to the various biomass transport costs and to the

spatial distribution of the produced biomass, as biomass located nearby its biorefinery would save money compared to the same biomass amount located further.

This illustration was computed for present and future, by associating realistic agricultural land uses and B2-IPCC climate scenarios depending on the bioenergy type concerned in each patch (either crops, grasslands or forest-trees). First, landscape simulations consisted in maps and curves of the biomass annual variation per hectare and the associated transport cost per landscape unit. Second, some of the simulations were provided with 3D visualizations for helping “visual inference” and landscape managements useful to estimate esthetical impacts of our projections (Ervin 2001). Here, the working hypothesis was that various landscape changes may have a strong and possibly negative visual impact. Such impacts could be quantified by the use of a “closure index” to help identifying scenarios that mitigate these impacts. We assume that such an illustration may encourage combining and, even more, coupling complex process-based (mechanistic) landscape models to help managing bioenergy production.

## Methods

The methodology of this paper is detailed in the following four sections (Fig. 1). The idea was to combine models dedicated to various assessments to perform a more integrated estimation of the biomass dynamics within a landscape. The study area is theoretical but is based on a set of real conditions, namely landscapes where agriculture is very intensive and located in Brittany (north-western France), and forested sites located on calcareous soils in PACA region (southeast France). Quantitative assessments mainly depended on human-driven and climate-driven changes in landscapes, and were based on a careful choice of landscape scenarios. Qualitative assessments used an adapted visualizing explorer associated to an index to rank simulations according to their esthetical impacts.

### *Data and Scenarios*

For this theoretical study, agricultural simulations were made on an extended study site (13.9 km<sup>2</sup>, 1481 landscape units) located in France. We chose it to exhibit intensive agriculture, with a dense remaining hedgerow network with relatively small fields such as some observed in France (Houet and Gaucherel 2005; Houet and Hubert-Moy 2006). Land cover changes over 789 landscape agricultural units (or patches) come from agricultural practices such as crop successions. At a coarser scale, land cover changes depend on the spatial distribution of farms and their adaptation to economic constraints and policies (Thenail and Baudry 2004). The study site was composed by 23 farms made of four possible land covers (crop type one, crop type two, grasslands and forests), with proportions equal to 16.2, 14.5, 43.2 and 26.1 % respectively. In order to favour forests that are less productive than crops,

more than half of this site forests have been located along to hedgerows and roads, the other half belonging to forested patches.

For comparison requirements, two simulations have been run on this agricultural site: a first reference simulation (noted R) was performed with randomly chosen crop and grassland rotations (and no change on forest units). Second simulation (A) is based on a scenario aiming at forecasting plausible future for 2030-40. Scenario is based on agricultural trends and assumes that no major changes in land uses will occur. Farmers would pursue intensive dairy production and convert part of the cash crop production into bio-motor fuel production (corn and wheat for bio-ethanol). Thus, regional agriculture specialisation means that all farms of the study site would be characterized by the same land use and production system. This simplified system is characterized in term of mean land cover proportions annually observed at the farm scale (i.e. without forest areas): 55 % of hay (temporary grassland) and 30 % of crop type one (corn) completed by 15 % of crop type two (wheat). In addition, crop rotations were chosen so that the grassland presence frequency remained quite close to the one observed over 20 years in some French agricultural landscapes. Grasslands and part of the crop production are feeding cattle.

Forest simulations were made for Holm oak forests located in France. We used dendrochronological data from a Holm oak (*Quercus ilex*) stand for the second part of this theoretical study. An observed series have been used to calibrate some parameters of the tree growth model described below (Gaucherel et al. 2008a; Misson et al. 2004). Biological, ecological and topographical factors were also recorded at the concerned stand and used to help in calibrating several physiological processes. Observed daily temperatures and precipitation series serving as inputs of the ecophysiological model are obtained from a nearby Mediterranean (Météo-France) meteorological station.

Natural forcing is a symmetrical driver compared to agricultural human decisions. Climatic simulations for the 21<sup>th</sup> century were obtained from the global climate model ARPEGE-IFS (Gibelin and Deque 2003) driven by the IPCC-B2 scenario radiative forcing including greenhouse gases.

Doubling of atmospheric CO<sub>2</sub> concentration occurs towards the end of the 21<sup>st</sup> century with 610 ppm, while the 20<sup>th</sup> century concentrations are the observed values. The ARPEGE model, for which the time step is 30 minutes, provides daily maximum and minimum air temperatures as well as daily precipitations for the 1960-2000 and then 2000-2099 periods (Deque et al. 1994). The grid point used for regional extrapolation has a 0.5° × 0.5° cell size that we have interpolated as a function of latitude and longitude using a two-dimensional (2D) bi-cubic technique, then averaged over the 500 × 700 km<sup>2</sup> region. Two simulations have been run on these forests (Gaucherel et al. 2008b): a first climatic simulation was performed without any atmospheric CO<sub>2</sub> increase during the 21<sup>st</sup> century (simulations noted R and A). The second more realistic climatic simulation assumed a doubling of atmospheric CO<sub>2</sub> concentration towards the end of the 21<sup>st</sup> century growing gradually (R<sub>CO2</sub> and A<sub>CO2</sub>).

## Models



Concerning the agricultural model, we have implemented a formal grammar formalism (close to L-systems (Lindenmayer 1968; Prusinkiewicz 2004)) into the *LI* modelling platform (called DYPAL, for *Dynamic PATCHy Landscape*, in its most recent version) to mechanistically simulate landscape dynamics. The model used here is extensively described in (Gaucherel et al. 2006; Houet and Gaucherel 2005) and we only detail in this section the DYPAL management of landscape driving rules. DYPAL has been developed with a modular architecture and was designed around a kernel, which provides a stable organisational data structure (scenarios, time steps...) and a generic landscape description. The generic landscape is driven by *rules*, decomposed in many key processes, resulting from a set of single/elementary *actions* manipulating landscape units. These successive entities form a *template* which may be viewed as the main specificity of the DYPAL platform. The DYPAL model works with various scales and landscape types (field, farm, region...) and intends to simulate the unit dynamics of fields as well as dynamic linear networks such as hedgerows or roads. The main modelling difficulty appears when handling the set of rules and their action decomposition for each human decision and process, changing the neighbourhood graph and generating spatiotemporal conflict emergence (such as different land covers for the same unit at the same step).

This is one of the benefits from the L-systems framework to offer a friendly context to manipulate landscape driving rules (Prusinkiewicz 2004). The landscape driving rules are already handled by the use of various algorithms, while the corresponding formal grammar equations are not yet developed and are in progress. One of the main originalities of DYPAL is to allow attributive as well as geometrical actions (shape changes) of landscape units. Attributive modification only implies a change (or no change) of the main unit property, as in land use and land cover change (LUCC) models (Verburg et al. 2002), while geometrical modifications (absent in this study) refer to a limited number of unit deformations. When changing, each unit can dilate or erode, split into two or more distinct units, merge with one or more other units into a single unit, appear (with various forms) or disappear. Each action on units is developed within an independent function, gathering one or more algorithms. These functions can either be used in their original form, or be inherited (in an object-oriented scheme) and modified to take into account the unit context of real situations. In our realistic simulation A, to change the land cover of a grassland field depends on its age and its distance to the farmstead and needs specific algorithms (Fig. 2a).

Concerning the tree-growth model, we have used the process-based MAIDEN model extensively described in (Misson 2004; Misson et al. 2004). The model calculates processes such as photosynthesis, stomatal conductance, carbon allocation and forest development. The water balance is computed at the ecosystem level, including canopy water interception, transpiration, soil evaporation, soil water transfer, drainage and runoff. MAIDEN separates daily net primary production (NPP) between carbon pools (leaf, bole, root and storage) according to phenological phase-dependent rules. These phases are (1) winter: no activity, (2) spring: leaf and root expansion, (3) summer: bolewood production, (4) early falls: carbohydrate-reserve accumulation, (5) late fall: leaf and root senescence.



An original modelling procedure of carbon storage and mobilization was developed to reproduce the temporal autocorrelation structure of tree ring series (Guiot 1986). The annual increment of bole carbon pool at stand level is the modeled variable that will be compared with the observed dendrochronological tree-ring series. To be applied to a given species at a given site, the model needs several input variables such as altitude, latitude, maximum absolute Leaf Area Index (LAI), specific leaf area, initial bole biomass, soil thickness and soil textural classes, which can be obtained from site measurements. Moreover, it also needs eleven internal parameters that can be tuned to fit at best available ecophysiological and dendrochronological data, as explained in (Gaucherel et al. 2008a). Climatic driving variables are daily minimum and maximum temperature and precipitation.

### *Visualizations*

Such quantitative computations have been completed by a qualitative assessment of landscape simulations. In order to help perceiving simulations, we used the Seamless Landscape Explorer software (Griffon and Auclair 2009) to build 3D visual representations in year 2100 with the same point of view than a 2004 photograph (location: Lat.  $-5.56315^{\circ}$  / Long.  $48.39433^{\circ}$  (in decimal degrees); direction: WSW ( $255^{\circ}$ )). The representation of 3D landscape models requires a variety of components and corresponding spatial data types. These include terrain texture (ortho-imagery, raster maps), digital height models (DEM, DSM), land cover data (vector-based 2D geo-objects), 3D objects, and object textures. The spectrum of these components ranges from very large spatial objects to large numbers of complex and possibly dynamic 3D objects. These data types have very different characteristics and requirements in terms of management, visualisation and multi-scale representation. Technically, a dynamically optimized elevation mesh is computed and can be textured with the “texture splatting” technique (Bloom 2000; Tyrväinen and Tahvanainen 2000) or satellite imageries and thematic maps.

We also establish a fixed grid around the camera to manage the vegetation data for each layer of plants and other natural objects. Each grid cell contains all of the data to render its layer in the physical space it occupies. For each layer, we establish a distance from the camera that the layer needs to generate visuals; this determines the size of our virtual grid. This operation is done in real time and care must be taken to ensure that planting is a fast operation. Collecting polygons in a grid cell are done quickly by using an AABB tree or a similar data structure and it is also effective to queue up this task so that we spend only a relatively fixed amount of CPU on the task for each frame. The different layers of vegetation consist in trees, shrubs, small plants, rocks, and other debris to complete the illusion of natural complexity. We apply random transforms to vary their size and orientation as we pick our planting points. Some of these can be represented as textured planes (billboards) just as grass is, but the richness of the environment is enhanced when we mix in an assortment of geometric objects, as well.

### *Simulation methodology*

We chose to model biomass production on a virtual landscape as no exhaustive data set were available on the same site. We modelled the following simulations over the agricultural landscape described above with the oak forest located in its forested patches. To improve effect of land use on biomass we modelled agricultural land uses based on random (R) and realistic (A) simulations of crop successions. Similarly, to enhance influence of climate change on biomass production, we modelled landscape evolution over hundred years (2000 – 2100) based on two climate change hypotheses controlling tree growth even if agricultural land use changes remain plausible until 2030-2040. Four simulations (R, A, R<sub>CO2</sub> and A<sub>CO2</sub>) were run only one time as these mechanistic (and almost deterministic) simulations are robust and never exhibit in our tests more than 1 to 2 percent variation indices.

We computed two synthetic indices at each step of the four simulations: i) the total biomass production of the landscape ( $I_b$ , expressed in tons); ii) the averaged transport cost per landscape unit ( $I_c$ ) supposed to be proportional to the transported biomass and the distance (by road, with the same vehicle) of each landscape unit to the transformation industry (biorefinery); and iii) biomass production ratio / the averaged transport cost ( $r_i$ , in unit per m) to quantify the bioenergy conversion inefficiency of each landscape over hundred years. As farmers would usually seek minimizing transportation costs and maximizing biomass production, we expect high conversion inefficiency ratio to be preferred and be more relevant. For these computations spatial biomass distributions at each time step were available. The industry has been arbitrary located at the centre of the landscape (coordinates (267; 359) pixels of 8×8 m<sup>2</sup> each), in order to quantify the importance of landscape unit locations. We checked that results are qualitatively the same for other industry locations.

We chose the consensual bioenergy conversion that one ton equivalent petrol (tep) is equivalent to three tons of vegetal biomass, whatever is the vegetation concerned (Cormeau and Gosse 2008). We conservatively supposed the four land covers of our landscape to produce  $I_b = 6, 3, 2$  and 6 t/ha/year biomass for crop type 1, crop type 2, grassland and forest respectively. We chose exploitation ratio so that it corresponds to biomass production ratios effectively used at landscape scale equal to  $r = 0.2, 0.1, 0.066$  and 0.1 tep/ha/year for crop types 1 and 2, grassland and forest respectively. To work with comparable values, we considered indeed that one tenth of the crop production and one twentieth of the wood production is collected every year (i.e. corresponding to a 20-year forest management). This quite high forest production considered all tree-compartments for wood biomass production (Rambal et al. 2004) and should be calibrated according to real landscape observations.

The more qualitative assessment of esthetical impacts of simulations has been achieved on the basis of an index quantifying the “depth” ( $I_d$ ) of each image. We have developed a fragment program that run on GPU to compute for each pixel of the viewport the distance to the nearest object. The depth is defined as the distance between the photographer (the view-point) and the landscape element (a tree, a piece of soil...) composing the pixel, then normalized by the maximum distance displayed in the image. This index equals the average of the distances over the whole image, standardized between the

four simulations. Infinite distances (the sky) have previously been removed. This preliminary depth index aimed at capturing the broad idea that we have from “closed” or more open landscapes, and has been computed for the four simulations from the same view-point. In a first approximation, we expect lower depth index values to have higher esthetical qualities according to the French culture.

## Results

Results are threefold: first quantitative assessments of model specific landscape simulations; second, quantitative assessments of the combined model simulations; and third esthetical assessments of the visualization model.

### *Independent (crop and forest) simulations*

A first result was that randomly generated landscapes drastically differed from the rule-based landscapes (Fig. 2a). As simulations were made with landscape unit entities, a rule applied on a specific land cover modified its proportion and/or position (spatial distribution) in the landscape. While simulation R led to heterogeneous land uses (33 % of agricultural fields in average), simulation A increased the relative grassland surfaces (55 %), with specific positions in the landscape (Fig. 2b). The stabilization period due to a great number of compulsory rotations occurring onto all landscape units of the study site took several years only. Simulation A differed from simulation R (dominant frequency equals to  $\sim 0.33$ , Table 1) by adding some high frequencies (short term appearances): 0.7 and 0.95 (Fig. 2c). It corresponded to a grassland appearance every 3.05, 1.43 and 1.05 years respectively, estimations being averaged over the 789 agricultural landscape units.

#Table 1 approximately here#

The bole Carbon allocation was simulated to be around  $250 \pm 40 \text{ g/mm}^2$  for the oak species. This gives the C allocation per ground area unit, roughly corresponding to half the wood production. The oak MCMC calibration of MAIDEN model with dendrochronological series observed between years 1960 and 2000 showed a modal fit at  $r^2 = 0.50 \pm 0.06$  (Fig. 3a). Differences between the calibrated bole increment simulation and observations were quite homogeneous, showing the ability of the model to simulate a large variability of growth. The fact that the model was able to simulate the negative trend of the oak growth observed since the beginning of the year 70's may confirm its climatic origin because inputs into the model concerns meteorological data alone (without CO<sub>2</sub> effect). However, when including the direct effect of atmospheric CO<sub>2</sub> into the model (Fig. 3b), mean oak growth increased by about  $+ 24.1 \pm 5.6 \%$ . As highlighted by the twenty-year window moving average curve, the trend of regional oak growth with and without CO<sub>2</sub> direct effect (Fig. 3b) showed a progressive productivity increase throughout the 21<sup>st</sup> century with CO<sub>2</sub> direct effect versus a decrease with constant CO<sub>2</sub>. The gain due to CO<sub>2</sub> direct effect is optimum at low elevations (not shown). Tree

growth evolution for constant CO<sub>2</sub> concentration reached a maximum around year 2005 for the species which may be caused by drought variations. The period around 2005 indeed was simulated by the ARPEGE climatic model as the most humid of the period. Afterwards, drought increased considerably, inducing an important growth deficit that CO<sub>2</sub> direct effect did not compensate.

#### *Combined simulations*

The four simulations were rather similar in average over hundred years (Fig. 4), due to the chosen biomass intakes (one tenth and one twentieth per year for crops and forests resp.). The lowest biomass production was found for landscape A ( $I_b = 0.40 \pm 0.032 \cdot 10^3$  t) and the highest for landscape R<sub>CO2</sub> ( $I_b = 0.51 \pm 0.028 \cdot 10^3$  t) (Table 1). Landscape R and A<sub>CO2</sub> converged to similar biomass productions (Fig. 4a). A and A<sub>CO2</sub> landscapes showed higher biomass production standard deviations ( $\Delta I_b \sim 0.03 \cdot 10^3$  t) than R and R<sub>CO2</sub> landscapes ( $\Delta I_b \sim 0.028 \cdot 10^3$  t), but their biomass production always remained significantly different. As expected, atmospheric CO<sub>2</sub> concentration absence were always prejudicial to biomass production, R and A simulations showing decreasing trends in these cases.

Transport cost computations did not lead to the same simulation order (i.e. hierarchy, Table 1). A landscape exhibited quite low transport costs, but only during the second part of the simulation. R landscape had a lower averaged transport cost ( $I_c = 0.17 \pm 0.01$  t × km/unit). R<sub>CO2</sub> showed a quite high averaged transport cost, but A<sub>CO2</sub> had a higher averaged transport cost ( $I_c = 0.21 \pm 0.022$  t × km/unit). Atmospheric CO<sub>2</sub> concentration absence clearly reduced, by indirect effects, transport costs at landscape scale. Transport cost standard deviations along to each simulation appeared to be closely linked to random or agricultural scenarios and not to climate influences (Fig. 4b), and were lower for R and R<sub>CO2</sub> simulations ( $\Delta I_c \sim 0.01$  compared to 0.022 t × km/unit). Averaged transport costs are not significantly different between simulations.

Finally, biomass production ratios / transport costs appeared to be the lowest for A<sub>CO2</sub> landscape ( $r_1 = 2.16$  unit/m), the most realistic one (Table 1). Unrealistic R and R<sub>CO2</sub> simulations showed the highest and more relevant conversion inefficiencies ( $r_1 \sim 2.77$  unit/m). Averaged values of each index were mainly related to land cover proportions imposed by agricultural practices. The trend of biomass and transport cost evolutions was mainly due to effects of climate change on tree growth, as agricultural land cover proportions were stabilized along to every simulation. Landscape biomass maps highlighted the spatial distribution of biomass according to both anthropogenic and natural drivers and their articulation (Fig. 4a inset).

#### *Visualizations*

3D visualizations of the contrasted R and A<sub>CO2</sub> simulations helped to infer landscape esthetic at the end of the twenty-first century (Fig. 5). We clearly observed (about 1.65 times) more grasslands and (about 24 %) higher forests in the more realistic A<sub>CO2</sub> simulation image than in the former one. A real 2004 photograph of the landscape chosen as a template is shown for reference (Fig. 5b). We

configured, for each layer in the land cover of these images, a texture that was draped over the terrain when rendering and a list of possible objects in this landscape including: i) the type of object (plants, rocks, human buildings...); ii) object densities in a specific landscape units and iii) the size variation information used to generate variations in the appearance of objects. The R simulation appeared to be the closest simulation ( $I_d = -1.22$ ) because the camera was located in the middle of a maize field with a lot of plants reducing the image depth (table 1). The  $R_{CO_2}$  simulation was the most open in these terms ( $I_d = 0.91$ ). A and  $A_{CO_2}$  simulations are more interesting to be compared, with the  $A_{CO_2}$  landscape being slightly more open.

## Discussion

### *Specific crop and forest dynamics*

On the one hand, the agricultural production simulation (A) was close to landscape evolutions observed in the recent years, for which all farms adopted the same production system. This point combines with past studies based on connectivity indices (Gaucherel et al. 2006) to confirm a correct calibration of the DYPAL model in this case study. Dominant grassland frequencies (roughly equal to 0.25, 0.7 and 0.9 over one century) were close yet less pronounced than for real landscape observations during the past two decades. Such modes of frequency distribution were caused by empirical farm allocation properties chosen by farmers (Gaucherel et al. 2006; Verburg et al. 2002). Our approach here is original, as we have modeled a patchy landscape with mechanistic rules intending to mimic human decisions and directly impacting land cover distributions. It suggests that more elaborated rules (using mixed agricultural managements for example (Houet and Gaucherel 2005) or bioenergy dedicated scenarios) and scenarios (using multiple plausible futures) would improve the simulation realism and assessment.

On the other hand, the MAIDEN model, once calibrated, has shown a correct ability to simulate tree growth of oak species under various environmental conditions (Fig. 3a). This model has for example already been used with *Quercus Ilex* under Mediterranean environment as well as *Quercus petraea* under temperate environment (Misson et al. 2004). Some previous works succeeded in such modelling using remote sensing (LAI) calibration (Anselmi et al. 2004). Our approach is, in a way, different and original, as we have calibrated a complex ecophysiological model, using dendrochronological time series (Gaucherel et al. 2008a; Misson 2004). The simulation is realistic from year 1960 to 1997. If we do not take into account for  $CO_2$  fertilization effect, we find that tree growth has reached a maximum around year 2005 (Fig. 3a): this should not be taken as a precise date for the optimum of these species; it rather shows that the climate changes might not beneficiate to these species in the future in terms of ecophysiological processes at large scales in average. With the direct effect of  $CO_2$ , oak species has a significant increase in productivity (+24.1 %, Fig. 3b). Higher  $CO_2$  concentration allows the tree to close its stomata, leading to a better efficiency in the water use, even if the water budget decreases,

such as after year 2030. This fertilizing effect even has a stronger impact than climate change on the basis of our data and modelling. We are confident about the simulation of this forcing because CO<sub>2</sub> fertilizing effect has been calibrated and validated by using the observed atmospheric CO<sub>2</sub> concentrations for the 20<sup>th</sup> century. However, this effect might not be reasonable because the model does not take into account for acclimation of photosynthesis to progressive increase in CO<sub>2</sub> in the atmosphere.

#### *Quantitative biomass assessment*

Once independent models have been calibrated, we finally modelled contrasted simulations of landscape dynamics to estimate biomass production evolution up to year 2100 in this virtual landscape. For this purpose, we combined two process-based models dedicated to either (human-based) agricultural practices or to tree growth under (natural-based) climate forcing, thus leading to four simulations (A, A<sub>CO2</sub>, R to R<sub>CO2</sub>). Such combination of mechanistic models at landscape scales has, to our knowledge, never been done (Monticino et al. 2007). Each model, independently, would have been capable assessing biomass production in the respective parts of this landscape (crops on one hand, forests on the other hand (Gaucherel et al. 2008b)), but not for the whole landscape.

These simulations led to three main results. First, the transport cost at landscape scale is not correlated to total biomass production (table 1). Such calculation supposed knowing how much and where each biomass quantity is produced to sum their respective contributions and would not have been possible without such mechanistic spatially explicit models. Second, absolute (averaged) index values along to simulations were conditioned by agricultural practices, while relative values (temporal trends) were conditioned by gradual climate changes (Fig. 4). Such processes have different causes and were due to our choices of (i) a generalized intensive agricultural context combining dairy and bioenergy production in the landscape, (ii) a specific landscape configuration corresponding to a crop / forest surface ratio close to unity (1.17) and (iii) the fact that on tenth of the crop production and one twentieth of the wood production is collected every year (Rambal et al. 2004). These choices led to comparable crop and forest biomass productions, yet having different dynamics.

Third, among the R and R<sub>CO2</sub> realistic scenarios, the highest conversion inefficiency ratio (biomass production ratio over hundred years / the averaged transport cost  $r_l$ ) was associated to the less biomass productive scenario (table 1, A<sub>CO2</sub> column). As farmers would usually seek minimizing transportation costs and maximizing biomass production, we expect high conversion inefficiency ratio to be preferred and be more relevant. This point confirmed our main hypothesis that the landscape scenario providing the highest biomass should not be the one leading to the highest economical benefits. Hence, to spatially organize biomass production in landscape would likely increase economical profits too. Process-based simulations were necessary to observe that simulation A has a higher ratio ( $r_l = 2.28$ ) than the simulation A<sub>CO2</sub> ratio (2.16). This scenario ranking suggested that CO<sub>2</sub> increase and LUCC may interplay to lead to an optimum landscape configuration for which the conversion



inefficiency ratio would be maximized. It offers the opportunity, at least in this case, to manage subtle land use and cover changes in order to reduce the effect of CO<sub>2</sub> increase (Lambin et al. 2000). This may have strong ecological implications, as species conservation or environmental threats are closely dependant at landscape scales to agricultural practices too.

#### *Qualitative assessment*

In parallel, we have shown here that there exist today powerful tools to estimate future esthetical aspects of landscape simulations. With such methods, visual changes of the landscape can be shown very impressively and can allow for an intuitive assessment of the visual landscape simulation quality (Fig. 5). The users can explore the landscape, find environmental issues that are relevant (here to mitigate threshold effect of an increased biomass production), compare scenarios and discuss their opinions to form strategies for overcoming them (Ervin 2001; Griffon and Auclair 2009; Tyrväinen and Tahvanainen 2000). The results can then be used either individually by the policy-maker as a decision tool, or as a support for discussion and negotiation. Such esthetical criterion is obviously one of the possible constraints of future landscape studies (Nassauer and Corry 2004). Other economical or environmental constraints should be quantified too (see this *landscape ecology* special issue), before managing a landscape and finally deciding its required trajectory. These indicators could be presented using different 2D, 3D and iconic world-views (Bishop et al. 2005). For example, an abstract 3D view which does not display the landscape as realistic, but rather displays abstract symbols that show the dispersion of the indicator over the landscape.

In this case, the A<sub>CO2</sub> simulation showed a landscape with more grasslands and highest forests, probably closer to what decision-makers would favour in such landscape managements. In addition to the communication tool, such 3D visualisations may become a scientific tool if associated with objective indicators to rank them. A measure of the landscape openness (or its closure, when landscape units reduce the overall landscape visibility) viewed from the same view-points indicated here that simulation A was slightly closer than simulation A<sub>CO2</sub>, thus corresponding to a higher esthetical quality according to the French culture. Other view-points (randomly chosen, in random directions) and other esthetical indices may be added to improve this visual assessment of a scenario and to statistically confirm this rough estimation.

#### *Process-based model advantages and limits*

Mechanistic landscape models are still simplistic, but the few major agricultural / ecophysiological processes today taken into account already give some clues about future biomass productions. It has been explained how process-based models help to better understand ecosystems (Guiot et al. 2008). We may be more confident when extrapolating this kind of models, because they are based on causal relationships such as with human agricultural practices here. Biases are often well controlled,



whatever if they concern distribution of the extremes or some external constraints, such as atmospheric CO<sub>2</sub> increase in this study.

At the contrary, mechanistic models need to be fed by numerous parameters, to be carefully calibrated.

510 To achieve our goal, we chose various parameter values for these biomass simulations that may be tuned and should be discussed. We simulated a precise landscape configuration, with a defined forest/crop composition ratio (~ 1.17); we imposed constant biomass production ratios for each land cover and a constant bioenergy / biomass conversion rate between vegetation types (one ton equivalent petrol (tep) is equivalent to three tons of vegetal biomass (Cormeau and Gosse 2008)), a precise  
515 industry location for biomass transformation, considered to be unique for various land covers; and we supposed only part of the landscape to be dedicated to bioenergy production. Finally, we built a virtual landscape gathering properties of both French agricultural and Mediterranean climate landscapes.

Yet, we argue that such choices and the associated results are not decisive. The idea was rather to illustrate that such a methodology is relevant and reproducible in more concrete study cases. For this  
520 work, we also assumed that production, transport and transformation occurred at landscape scale. Nevertheless, we are conscious how idealistic is this assumption. Bioenergy is often produced at one place (depending on various geographical scales), transported over large distances and transformed at another remote place (Cormeau and Gosse 2008). Yet, we highlighted by such study the role of space over the whole energetic chain. As a consequence, it is crucial to start defining limits of the studied  
525 agro-ecosystem.

### *Conclusions and recommendations*

We reached our first objective by showing that the new generation of landscape models allow estimating spatial and temporal bioenergy distributions that are helpful for an integrated assessment of  
530 the bioenergy production. As a key result for this study, economical benefits would not always be related to biomass production increase. The spatial distribution of biomass in landscapes may be critical too, as it partly conditioned transport costs. We should keep this observation in mind when (locally) managing bioenergy. When trying to develop a sustainable future on the basis of bioenergy, these results highlighted that: i) to adjust biomass production will not straightforwardly affect this  
535 benefit (as transport and other transformation costs may play important roles); that ii) to improve our economical benefit is possible in some cases; and that iii) we may manage various and possibly compensating causes to counteract unwanted changes. For example, it should be possible to compensate trends of climate effects by an opposite biomass production with LUCC changes. As a recommendation, we should remember that the spatial arrangement of LUCC at landscape scale is  
540 probably one of the most powerful manners to mitigate negative (or magnify positive) effects of climate and human decisions on landscapes.

Our second objective for this work adopted a more methodological point of view. As shown in this illustration, mechanistic models should be developed for their extrapolation qualities. Yet, we would

certainly gain at modelling a real coupling between anthropogenic and natural drivers of the landscape and, thus, of biomass and bioenergy productions (Stokstad 2008). This coupling has not been investigated in this study, for which crop-growth and/or silvicultural modules should be developed. Models exist for each of these processes (e.g. (De Coligny 2006; de Noblet-Ducoudre et al. 2004)). As far as we know, these models have never been coupled into the same landscape for applied assessments such as bioenergy topics. In particular, it is probable that such coupled modelling should be very sensitive to neighbouring influences between various crop/forest landscape patches. We should not neglect the effort necessary to collect data for calibration and validation of such coupled process-based models, which partly explains why such modelling developments have been delayed up to now. Yet, they would allow testing *in silico* biomass and bioenergy production mosaic in space and time and assessing environmental/esthetical impacts.

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## Figure captions

Figure 1: Methodology of the integrated biomass production assessment performed in this work. The different models used (dark grey), their associated landscape driving factors (light grey), and their relative contributions (arrows) to intermediate and final assessment results (dashed rectangles) are highlighted. Models combine quantitative and qualitative assessments in different ways.

Figure 2: Crop successions for the chosen agricultural production of simulation A (a). Compulsory and authorized rotations (changes) are schematized according to the distance of the farmsteads and to ages of the Temporary Grasslands (noted TG). One example of virtual landscape simulations at year 2100 in case of simulation A (b). Gray levels, from dark to light, successively feature: forest, crop types 1 and 2, and temporary grassland land covers on a (black) unchanged background. Grassland appearance frequencies (c) of the virtual landscape during the hundred-year long landscape simulations are highlighted by arrows. Adapted from (Houet and Gaucherel 2005).

Figure 3: Indexed tree-ring series (dotted line) and bole carbon allocation simulated by the MAIDEN model after MCMC calibration (plain line) evergreen oak series in a Mediterranean site (a). Both simulations are based on a calibration stage obtained after the convergence of five draws (5000 steps each). Evolutions of the mean annual production of oak species were simulated on the basis of the ARPEGE simulation, with (up) and without (down) direct effect of atmospheric CO<sub>2</sub> (b). The two smoothed curves correspond to 20 year window moving averages of both evolution curves.

Figure 4: Total landscape biomass (a, in 10<sup>3</sup> t) and biomass transport cost (b, in t × km per landscape unit) evolutions of the hundred-year long landscape simulation: simulations A (dashed line), A<sub>CO2</sub> (plain line), R (dash-dotted line), and R<sub>CO2</sub> (dotted line). Years 1 to 100 have been assimilated to years 2000 to 2100 for comparison. The inset shows the biomass production map (gray levels in tep/ha/year) at the hundredth year of the most realistic A<sub>CO2</sub> simulation.

Figure 5: 3D visualization of the virtual landscape for A<sub>CO2</sub> (a) and R (c) simulation, compared to a photograph taken from the same view-point and with the same orientation in year 2004 (b). Fields, hedgerows and forest patches are clearly visible and vary from one image to the other.

## References

- Anselmi S, Chiesi M, Giannini M, Manes F and Maselli F (2004) Estimation of Mediterranean forest transpiration and photosynthesis through the use of an ecosystem simulation model driven by remotely sensed data. *Global Ecology and Biogeography* 13: 371-380.
- Bishop ID, Bruce Hull IV R and Stock C (2005) Supporting personal world-views in an envisioning system. *Environmental Modelling & Software* 20: 1459-1468.
- Bloom C (2000) Terrain Texture Composition by Blending in the Frame Buffer (a.k.a."Splatting Textures"). . [www.cbloom.com/3d/techdocs/splatting.txt](http://www.cbloom.com/3d/techdocs/splatting.txt).
- Butler SJ, Vickery JA and Norris K (2007) Farmland biodiversity and the footprint of agriculture. *Science* 315: 381-384.
- Connor D and Minguez I (2006) Looking at biofuels and bioenergy. *Science* 312: 1743-1743.
- Cormeau J and Gosse G (2008) Les biocarburants de deuxième génération. *Economie et stratégies agricoles*, pp. 167-246. Club Demeter, Paris (Fr).
- De Coligny F (2006) Efficient Building of Forestry Modelling Software with the Capsis Methodology. *In PMA06 - Plant Growth Modelling and Applications*, 13-17 Nov. 2006, pp. 216-222. IEEE Computer Society, Los Alamitos, California (USA).
- de Noblet-Ducoudre N, Gervois S, Ciais P, Viovy N, Brisson N, Seguin B and Perrier A (2004) Coupling the Soil-Vegetation-Atmosphere-Transfer Scheme ORCHIDEE to the agronomy model STICS to study the influence of croplands on the European carbon and water budgets. *Agronomie* 24: 397-407.
- Deque M, Drevet C, Braun A and Cariolle D (1994) The Arpege/Ifs Atmosphere Model - a Contribution to the French Community Climate Modeling. *Climate Dynamics* 10: 249-266.
- Ervin SM (2001) Digital landscape modeling and visualization: a research agenda. *Landscape and Urban Planning* 54: 49-62.
- Fargione J, Hill J, Tilman D, Polasky S and Hawthorne P (2008) Land clearing and the biofuel carbon debt. *Science* 319: 1235-1238.
- Gaucherel C, Campillo F, Misson L, Guiot J and Boreux JJ (2008a) Parameterization of a process-based tree-growth model: comparison of optimization, MCMC and particle filtering algorithms. *Environmental Modelling & Software* 23: 1280-1288.
- Gaucherel C, Giboire N, Viaud V, Houet T, Baudry J and Burel F (2006) A domain specific language for patchy landscape modelling: the brittany agricultural mosaic as a case study. *Ecological Modelling* 194: 233-243.
- Gaucherel C, Guiot J and Misson L (2008b) Changes of the potential distribution area of French Mediterranean forests under global warming. *Biogeosciences* 5: 1-12.
- Gibelin AL and Deque M (2003) Anthropogenic climate change over the Mediterranean region simulated by a global variable resolution model. *Climate Dynamics* 20: 327-339.

Griffon S and Auclair D (2009) Visualising changes in agricultural landscapes. *In* Brouwer F and Van Ittersum M (eds.), Environmental and agricultural modelling: integrated approaches for policy impact assessment. Springer Verlag.

635 Guiot J (1986) ARMA techniques for modelling tree-ring response to climate and for reconstructing variations of palaeoclimates. *Ecological Modelling* 33: 149-171.

Guiot J, Hély C, Haibin W and Gaucherel C (2008) Interactions between vegetation and climate variability: what are the lessons of models and paleovegetation data. *CRAS Geoscience* 340: 595-601.

640 Houet T and Gaucherel C (2005) Simulation dynamique et spatialement explicite d'un paysage agricole bocager: validation sur un petit bassin versant breton sur la période 1981 -1998. *European Journal of GIS and Spatial Analysis Revue Internationale de Géomatique* 17: 491-516.

Houet T and Hubert-Moy L (2006) Modelling and projecting land-use and land-cover changes with a cellular automaton considering landscape trajectories : an improvement for simulation of plausible future states. *In* EARSel eProceedings, pp. 63-76.

645 JRC Europe (2006) Well-to-Wheels analysis of future automotive fuels and powertrains in european context. EUCAR, JRC.

Lambin EF, Rounsevell MDA and Geist HJ (2000) Are agricultural land-use models able to predict changes in land-use intensity? *Agriculture Ecosystems & Environment* 82: 321-331.

650 Lindenmayer A (1968) Mathematical models for cellular interaction in developments, parts I and II. *Journal of Theoretical Biology* 18: 280-315.

Misson L (2004) MAIDEN: a model for analyzing ecosystem processes in dendroecology. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 34: 874-887.

Misson L, Rathgeber C and Guiot J (2004) Dendroecological analysis of climatic effects on *Quercus petraea* and *Pinus halepensis* radial growth using the process-based MAIDEN model. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 34: 888-898.

655 Monticino M, Acevedo M, Callicott B, Cogdill T and Lindquist C (2007) Coupled human and natural systems: A multi-agent-based approach. *Environmental Modelling & Software* 22: 656-663.

Nassauer JI and Corry RC (2004) Using normative scenarios in landscape ecology. *Landscape Ecology* 19: 343-356.

660 Prusinkiewicz P (2004) Modeling plant growth development. *Current Opinion in Plant Biology* 7: 79-83.

Rambal S, Joffre R, Ourcival JM, Cavender-Bares J and Rocheteau A (2004) The growth respiration component in eddy CO<sub>2</sub> flux from a *Quercus ilex* mediterranean forest. *Global Change Biology* 10: 1460-1469.

665 Sheppard SRJ (2005) Landscape visualisation and climate change : the potential for influencing perceptions and behaviour. *Environmental Science Policy* 8: 637-654.

Stokstad E (2008) Dueling visions for a hungry world. *Science* 319: 1474-1476.

- 670 Thenail C and Baudry J (2004) Variation of farm spatial land use pattern according to the structure of the hedgerow network (bocage) landscape: a study case in northeast Brittany, France. *Agriculture, Ecosystem and Environment* 101: 53-72.
- Tyrväinen L and Tahvanainen L (2000) Landscape visualisation in rural land-use planning. *In XXI IUFRO world congress. Forests and society: the role of research*, pp. 338-347, Kuala Lumpur (Malaysia).
- 675 Verburg PH, Soepboer W, Veldkamp A, Limpiada R, Espaldon V and Mastura SSA (2002) Modeling the spatial dynamics of regional land use: The CLUE-S model. *Environmental Management* 30: 391-405.

Table 1

Compilation of the mean index values over the four hundred-year simulations: simulations A, A<sub>CO2</sub>, R, and R<sub>CO2</sub>. Indices concern dominant grassland frequencies as well as total landscape biomass (in 10<sup>3</sup> t), the transport costs (in t × km per landscape unit) and an adimensional depth index for visualization ranking. The most favourable situation between agricultural simulations are highlighted in bold.

| <i>Indices /<br/>Simulations</i>                                        | <i>Agricultural<br/>simulation A</i> | <i>Agriculture with<br/>CO<sub>2</sub> increase A<sub>CO2</sub></i> | <i>Random<br/>simulation R</i> | <i>Random with<br/>CO<sub>2</sub> increase<br/>R<sub>CO2</sub></i> |
|-------------------------------------------------------------------------|--------------------------------------|---------------------------------------------------------------------|--------------------------------|--------------------------------------------------------------------|
| <i>Grassland<br/>frequencies</i>                                        | 0.25, (0.7), 0.9                     | 0.25, (0.7), 0.9                                                    | 0.33                           | 0.33                                                               |
| <i>Biomass<br/>(I<sub>b</sub> in 10<sup>3</sup> t)</i>                  | 0.40 ± 0.032                         | <b>0.44 ± 0.031</b>                                                 | 0.47 ± 0.028                   | 0.51 ± 0.028                                                       |
| <i>Transport cost<br/>(I<sub>c</sub> in t × km/unit)</i>                | <b>0.18 ± 0.022</b>                  | 0.21 ± 0.022                                                        | 0.17 ± 0.010                   | 0.19 ± 0.010                                                       |
| <i>Transport cost /<br/>Biomass ratio<br/>(r<sub>I</sub> in unit/m)</i> | <b>2.28 (rank 3)</b>                 | 2.16 (rank 4)                                                       | 2.77 (rank 1)                  | 2.57 (rank 2)                                                      |
| <i>Depth index (I<sub>d</sub>)</i>                                      | <b>0.15 (rank 2)</b>                 | 0.16 (rank 3)                                                       | -1.22 (rank 1)                 | 0.91 (rank 4)                                                      |



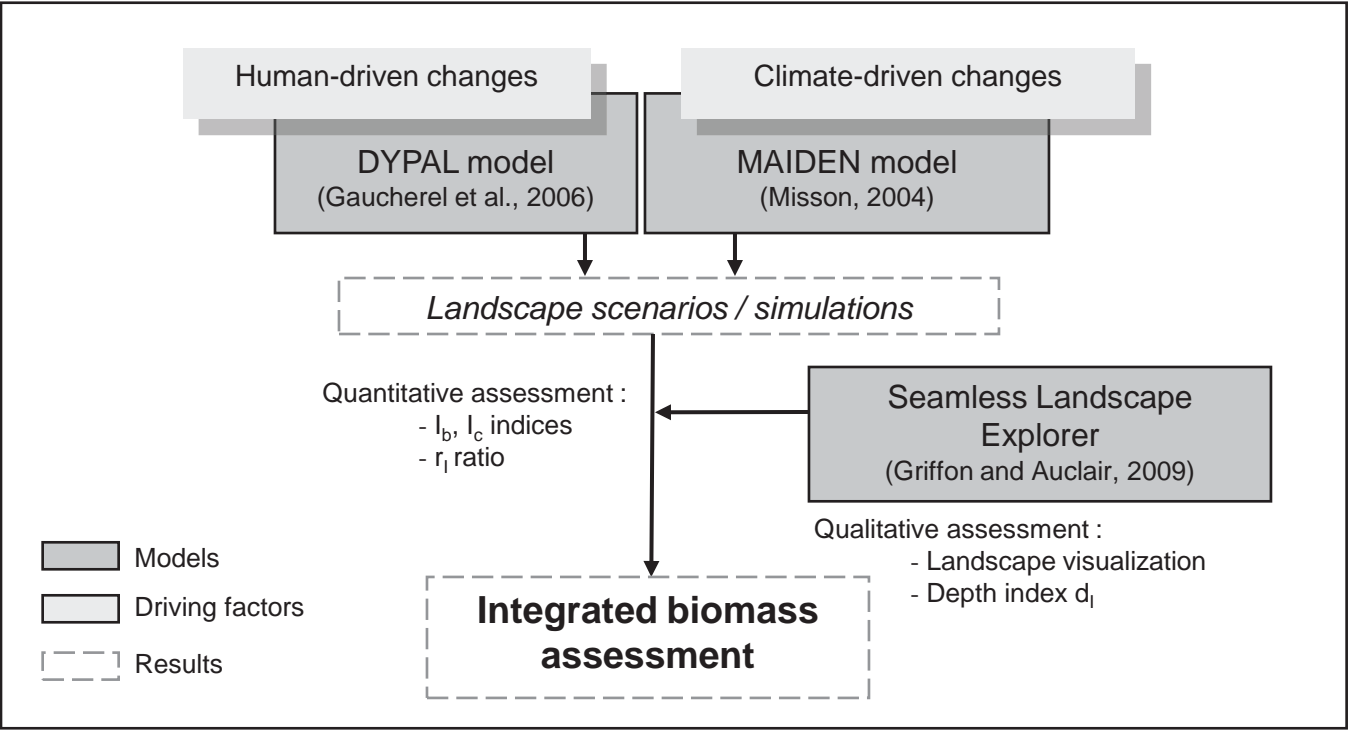


Figure 1

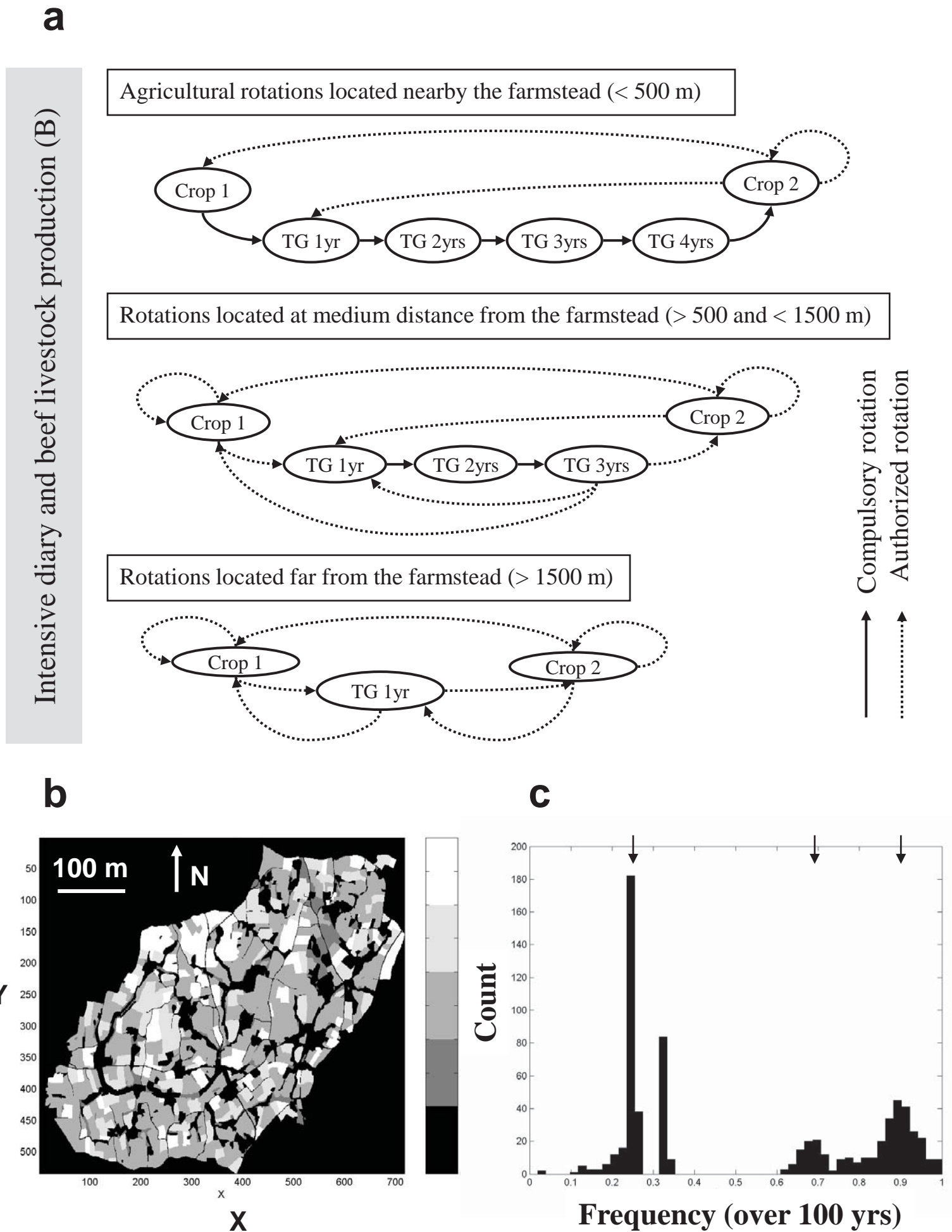
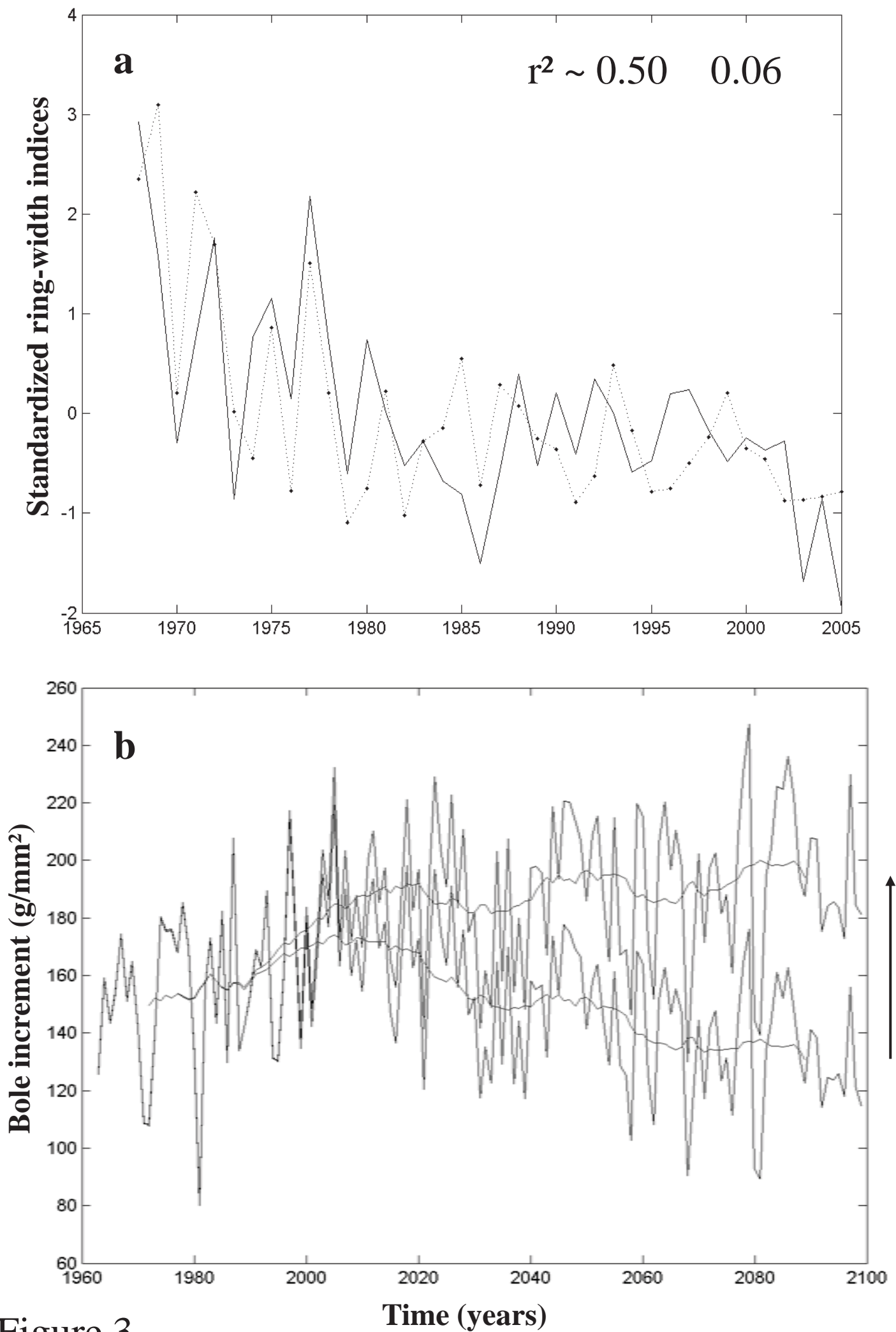


Figure 2



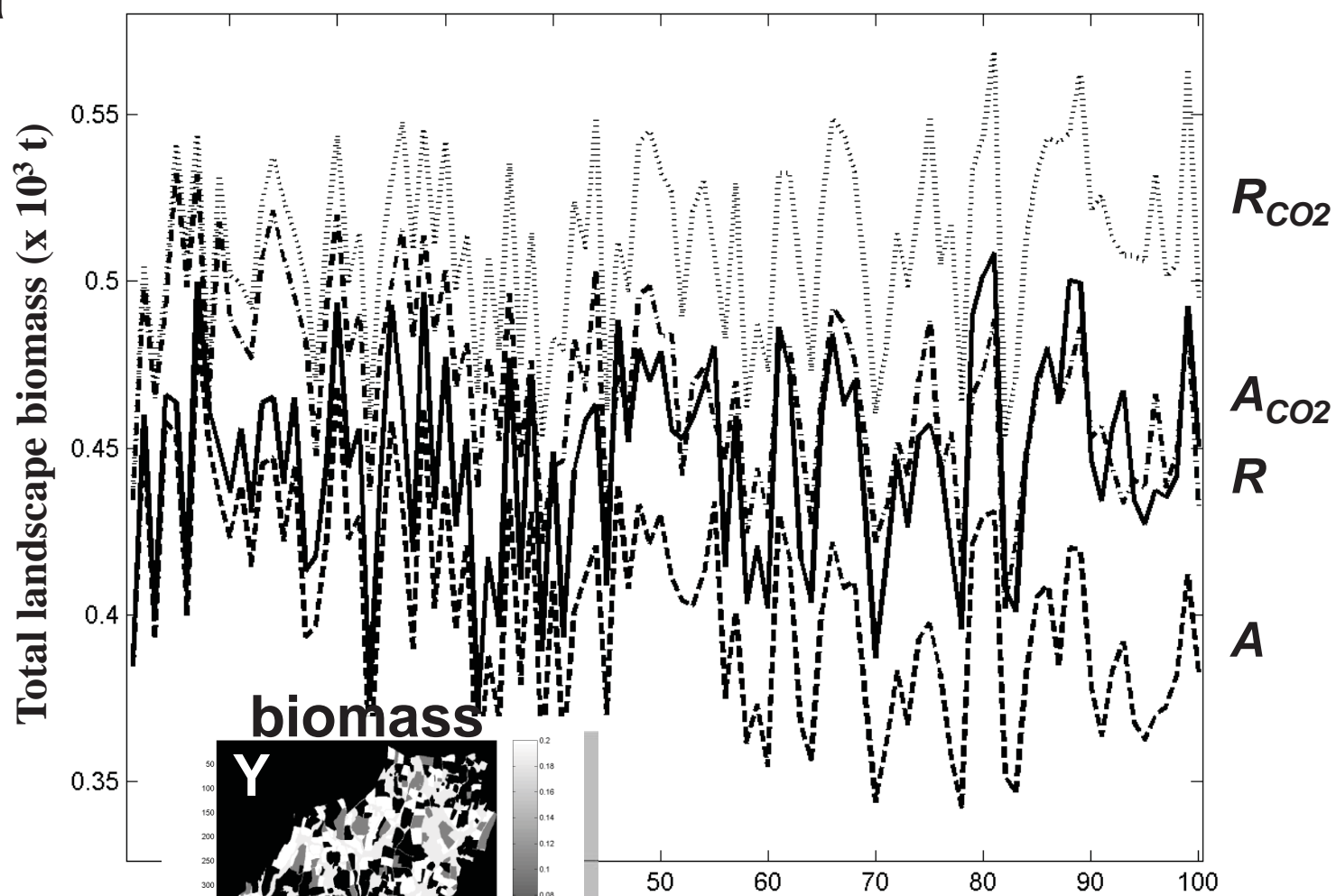
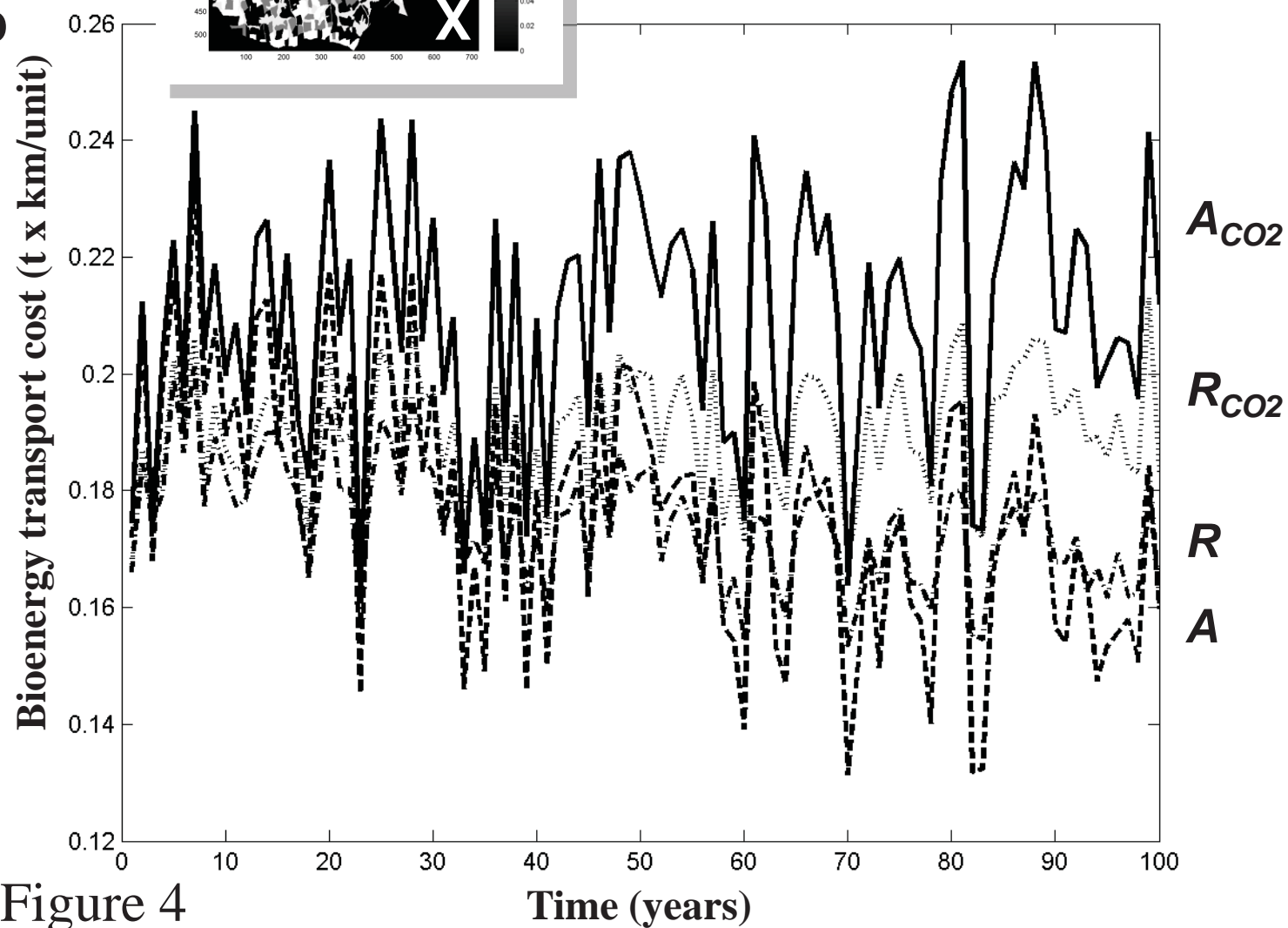
**a****b**

Figure 4

Time (years)





Figure 5