

The importance of multimodel projections to assess uncertainty in projections from simulation models

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Abstract. Simulation models are increasingly used to gain insights regarding the long-term effect of both direct and indirect anthropogenic impacts on natural resources and to devise and evaluate policies that aim to minimize these effects. If the uncertainty from simulation model projections is not adequately quantified and reported, modeling results might be misleading, with potentially serious implications. A method is described, based on a nested simulation design associated with multimodel projections, that allows the partitioning of the overall uncertainty in model projections into a number of different sources of uncertainty: model stochasticity, starting conditions, parameter uncertainty, and uncertainty that originates from the use of key model assumptions. These sources of uncertainty are likely to be present in most simulation models. Using the forest dynamics model SYMFOR as a case study, it is shown that the uncertainty originated from the use of alternate modeling assumptions, a source of uncertainty seldom reported, can be the greatest source of uncertainty, accounting for 66–97% of the overall variance of the mean after 100 years of stand dynamics simulation. This implicitly reveals the great importance of these multimodel projections even when multiple models from independent research groups are not available. Finally, it is suggested that a weighted multimodel average (in which the weights are estimated from the data) might be substantially more precise than a simple multimodel average (equivalent to equal weights for all models) as models that strongly conflict with the data are given greatly reduced or even zero weights. The method of partitioning modeling uncertainty is likely to be useful for other simulation models, allowing for a better estimate of the uncertainty of model projections and allowing researchers to identify which data need to be collected to reduce this uncertainty.

Key words: model uncertainty; modeling assumptions; multimodel; partitioning of the variance; simulation model.

INTRODUCTION

Sustainable use of natural resources and the balance between satisfying human needs and maintaining other ecosystem functions will require quantitative knowledge about the ecosystem's present and future responses (Clark et al. 2001, DeFries et al. 2004). Numerous models have been created to predict ecosystem responses to direct and indirect anthropogenic influence, but if the uncertainty associated with these model projections is not reported adequately, confidence of projections cannot be assessed. At one extreme, this may result in overconfident decisions, while at the other, decision makers may use it as an excuse to postpone or avoid making necessary decisions.

The field of statistics has traditionally acknowledged parametric uncertainty once a particular model form has been chosen. The exclusion of model structure and

model selection uncertainty has been shown, however, to result in overly optimistic predictive or inferential uncertainty, which can have serious implications (Draper 1995, Hoeting et al. 1999). The problem of ignoring model structure uncertainty is likely to be exacerbated in situations in which model extrapolations from available data are needed for decision making, as models that are very different mathematically can have similar fits to the data but wildly different predictions outside the data range (Chatfield 1995, Draper 1995). Multimodel inference has been suggested as a robust method that circumvents the problem of overly optimistic predictive or inferential uncertainty through improved representation of model structure uncertainty (Burnham and Anderson 1998, Wintle et al. 2003, Ellison 2004, Link and Barker 2006).

As in the field of statistics, probably the most-studied source of uncertainty in simulation modeling in the ecological literature is parameter estimate uncertainty. Parameter uncertainty has been assessed in population viability analysis (e.g., Ellner and Fieberg 2003), as well as in models of forest (e.g., Pacala et al. 1996), climate

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(e.g., Wigley and Raper 2001, Murphy et al. 2004, Stainforth et al. 2005), and disease (e.g., Elder et al. 2006). Other sources of uncertainty that are commonly reported in simulation models include model stochasticity (e.g., Gourlet-Fleury et al. 2005, Degen et al. 2006) and effect of starting conditions (e.g., simulations initialized with different forest plots; Phillips et al. 2004, van Gardingen et al. 2006). Model stochasticity is defined here as the changes in model projections, simulated with a fixed model structure and fixed parameter values, solely due to the stochastic nature of the simulated processes (e.g., mortality and recruitment). Model structure uncertainty, on the other hand, is defined here as the changes in model projections due to changes in the structure of the model (e.g., changes in the form of the underlying equations). Because of the large number of general circulation and terrestrial biogeochemistry models built by independent research groups, multimodel projections have been increasingly used for regional and global climate and vegetation predictions. This has allowed for the assessment of the robustness of these predictions in relation to the choice of the model (Cramer et al. 1999, Cox et al. 2008, Malhi et al. 2008). The evaluation of model structure uncertainty for other types of simulation models such as those used for management of natural resources, however, is still uncommon (but see Pascual et al. 1997, Carpenter 2002, Bradshaw et al. 2006).

The objective of this study is to show that, even if multiple models built by independent research groups are not available, multimodel inference is still a valuable tool to assess the uncertainty that originates from the use of key assumptions adopted in the process of model building. In particular, multimodel projections are used to show how the uncertainty resulting from these assumptions can be larger than the uncertainty that arises from other more commonly assessed sources, such as parameter uncertainty, model stochasticity, and effect of starting conditions. To achieve this objective, the method used to partition the overall uncertainty into these different sources is described and a comparison of the uncertainty originating from these sources is made using the forest dynamics model SYMFOR as a case study. Finally, the broader implications of the results from this case study are discussed and general recommendations for ecological modelers are provided.

METHODS

The data set

The series of plots at the Tapajós National Forest, Para, Brazil, are clustered in two regions known as km 67 and km 114. The series of plots at km 114 are composed of 60 permanent sample plots (PSPs), each of 0.25 ha, initially measured (all trees with diameter at breast height [dbh] ≥ 5 cm) in 1981 in an unlogged primary forest. Twelve of these plots were left unlogged while a silvicultural experiment with a randomized block design was installed in the remaining 48 plots. In this

silvicultural experiment, all plots were selectively logged in 1982 and different thinning intensity treatments were applied in 1995. The series of plots at km 67 are composed of 36 PSPs, each of 0.25 ha. This region was selectively logged in 1979, two years prior to the installation of the permanent plots (in 1981). Detailed description of the forest and these experiments can be found elsewhere (Silva et al. 1995, 1996, Alder and Silva 2000, Phillips et al. 2004, Oliveira 2005). This data set was used to calibrate and to initialize SYMFOR (Phillips et al. 2004).

The model and its variants

SYMFOR is a modeling framework for mixed tropical forest that combines a management model with an empirical spatially explicit individual-tree-based ecological model. The management model allows users to specify silvicultural activities, such as harvest, thinning, poisoning, and enrichment planting; the ecological model simulates the natural processes of recruitment, growth, and mortality. SYMFOR has been extensively used for tropical forest management issues in Indonesia (Phillips et al. 2002, 2003, van Gardingen et al. 2003), Brazil (Phillips et al. 2004, van Gardingen et al. 2006, Valle et al. 2007), and Guyana (vanUlf 2004, Arets 2005).

A brief summary of the model, which is described in greater detail elsewhere (Phillips et al. 2004), follows. First, because of the high diversity of tree species present in the data set (see Plate 1), species were assigned to one of 10 ecological species groups using a three-stage method. Cluster analysis, discriminant analysis, and subjective assignments were performed using variables describing growth rates at different competition levels and maximum tree size. Then, growth, recruitment, and mortality functions were calibrated for each species group. The growth submodel predicts annual diameter growth, I (in centimeters per year), as a function of tree diameter at breast height, D (in centimeters), and a diameter-independent competition index, C , with the equation $I = D(a_0 + a_1 e^{-a_2 D}) + a_3 C + a_4$. Annual recruitment probability, F , is predicted for each 10×10 m subplot as a function of the growth, I , of a hypothetical tree with 5 cm diameter centered in the middle of the subplot, with the equation $F = r_1 e^{-r_2 I} + r_3 I + r_4$. Finally, the annual mortality probability, M (as a percentage), is given by the following equation:

$$M = \begin{cases} m_0 & \text{if } D < b_d + 5 \\ m_1 & \text{if } b_d + 5 \leq D \end{cases}$$

where b_d is the upper limit of the first diameter class (in centimeters). This last equation describes how trees in the first diameter class ($D < b_d + 5$) are predicted to have a different mortality rate than those in the other size classes ($b_d + 5 \leq D$). Estimates of the parameters $a_0, a_1, a_2, a_3, a_4, r_1, r_2, r_3, r_4, m_0$, and m_1 for different model variants are given in Appendix A. A flow diagram of SYMFOR with the main simulated processes is provided in Fig. 1.

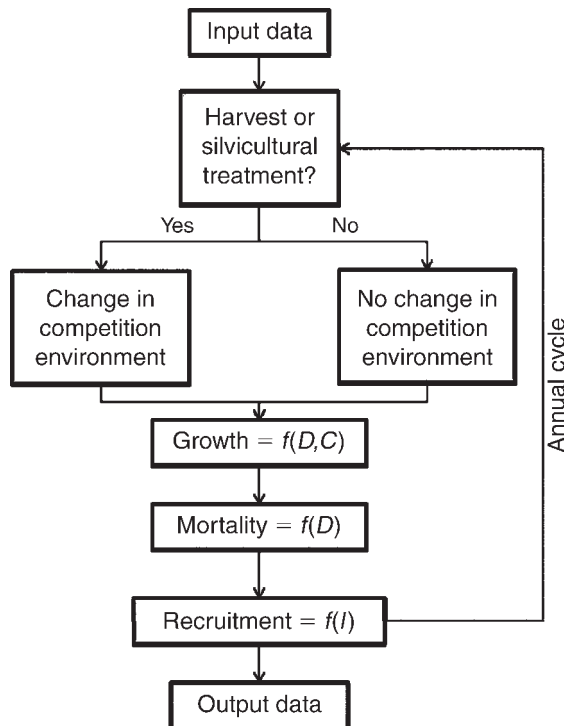


FIG. 1. Flow diagram of the SYMFOR model, illustrating the main processes simulated, where D , C , and I are diameter (cm), a diameter-independent competition index, and diameter increment (cm/yr), respectively.

All results presented in this paper are assessed using SYMFOR's overall basal area (all trees with dbh ≥ 5 cm) projections. Basal area was of primary interest because it is a well-accepted biological measure that integrates the ecological processes within a forest. Moreover, it is highly correlated with variables that are of immediate interest to forest managers and ecologists, such as forest volume and biomass. All 95% confidence intervals reported throughout this article were approximated using an interval around the mean of ± 2 SE.

The baseline model.—The baseline model is the model that was originally parameterized to the Tapajós data set by P. Phillips (*unpublished manuscript*). A summary of the 10 species groups is given in Table 1 and a detailed description of how these species were grouped, model structure, and the statistical procedures used to estimate the baseline model parameters are given in Phillips et al. (2004). Since the parameters shown in Phillips et al. (2004) were fine-tuned (i.e., manually adjusted), the parameter set prior to the fine-tuning process (Appendix A: Table A1) was used as the baseline model. Two other model variants were created by adding selected assumptions to the baseline model.

Dynamic equilibrium assumption model variant.—The dynamic equilibrium assumption is a very common assumption in forest dynamics modeling (Kammesheidt et al. 2001, Porte and Bartelink 2002) and is generally interpreted in the context of forest dynamics modeling as assuming that an undisturbed forest will have a stable basal area and/or tree density on the species group level and/or the stand level. The idea of dynamic equilibrium has a long tradition in fisheries, forestry, and ecology (Sheil and May 1996, Sutherland 2001, Coomes et al. 2003, Kohyama et al. 2003, Brown et al. 2004, Malhi et al. 2004, Muller-Landau et al. 2006, Palace et al. 2008).

The dynamic equilibrium assumption is frequently implemented by fine-tuning the forest dynamics model, regardless of whether the model is empirical or mechanistic (Gertner et al. 1995). We implemented this assumption by iteratively adjusting the parameters from the baseline mortality and recruitment submodels. Parameters were adjusted within their 95% CIs so that species group composition over a 100-year simulation in undisturbed forest was relatively constant. The pragmatic justification for this procedure is that recruitment and mortality data are notoriously noisy; therefore, empirical parameters are likely to be poorly estimated and need to be adjusted. The modified parameters resulting from this fine-tuning procedure are shown in Appendix A: Table A2. The effect of fine-tuning the model is shown in Fig. 2, in which the equilibrium model

TABLE 1. Summary description of each species group in the study plots in the Tapajós National Forest, Para, Brazil.

Species group	Group name (reference)	95th percentile (cm)	I (cm/yr)	Dominant members
1	slow-growing mid-canopy	41.8	0.21	Sapotaceae, Lauraceae, <i>Guatteria poeppigiana</i>
2	slow-growing understory	15.9	0.09	<i>Rinorea flavescens</i> , <i>Duguetia echinophora</i> , <i>Talisia longifolia</i>
3	medium-growing mid-canopy	57.2	0.29	<i>Geissospermum sericeum</i> , <i>Carapa guianensis</i> , <i>Pouteria</i> spp.
4	slow-growing lower canopy	27.7	0.18	<i>Protium apiculatum</i> , <i>Rinorea guianensis</i> , <i>Neea</i> spp.
5	medium-growing upper canopy	72.5	0.26	<i>Couratari oblongifolia</i> , <i>Minuartia guianensis</i>
6	fast-growing upper canopy	76	0.54	<i>Sclerobium chrysophyllum</i> , <i>Trattinickia rhoifolia</i> , <i>Didymopanax morototoni</i>
7	fast-growing pioneers	35.8	0.54	<i>Inga</i> spp., <i>Sloanea froesii</i> , <i>Bixa arborea</i> , <i>Jacaranda copaia</i>
8	emergents, climax	104	0.37	<i>Manilkara huberi</i> , <i>Goupia glabra</i> , <i>Hymenaea courbaril</i> , <i>Dipteryx odorata</i>
9	very-fast-growing pioneers	38.7	1.26	<i>Cecropia sciadophylla</i> , <i>Jaracatia leucoma</i> , <i>Jaracatia spinosa</i>
10	very-fast-growing upper canopy	78.2	0.94	<i>Tachigalia myrmecophylla</i> , <i>Sclerobium tinctorium</i>

Notes: The information provided here is reproduced with permission from Phillips et al. (2004). The 95th percentile is that of the cumulative diameter frequency distribution, and I is the annual mean growth rate.

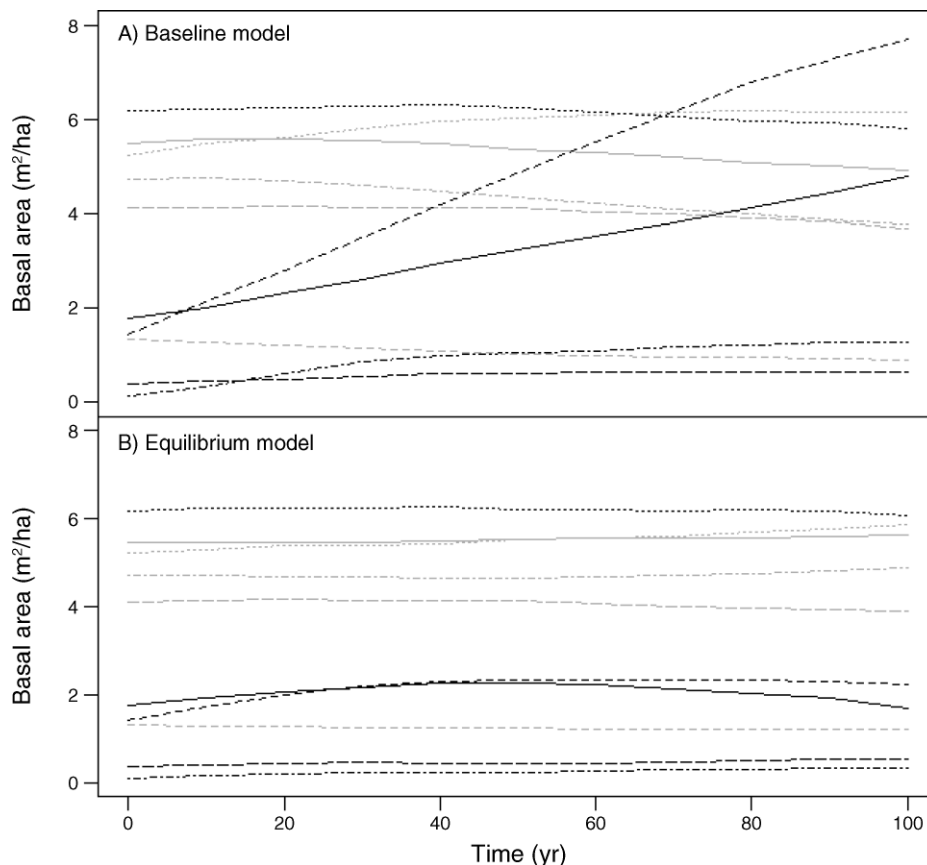


FIG. 2. Comparison of the projected species composition for the unlogged forest simulations using the (A) baseline and (B) dynamic equilibrium assumption models over a 100-year period. Each line represents one of the 10 species groups simulated by SYMFOR. This figure illustrates how the (A) baseline model (which does not exhibit a dynamic equilibrium) can have its parameters fine-tuned to exhibit (B) dynamic equilibrium. Data used to initialize and calibrate the model are from the Tapajós National Forest, Para, Brazil.

is contrasted to the baseline model in relation to the projected species composition of the unlogged forest over a 100-year period.

Growth extrapolation assumption (growthextrap) model variant.—A multi-component iterative model such as SYMFOR can easily start extrapolating outside the range of the calibration data set without an obvious indication to the user that this extrapolation is occurring. This can occur either in relation to individual tree characteristics (e.g., size, growth rate, competition intensity) or stand-level characteristics (e.g., basal area, species composition, tree density). Trees that grow in diameter beyond the range of sizes contained in the original data set are one of the most obvious model extrapolations, and assumptions regarding the dynamics of these trees are often needed. Other extrapolations are far more subtle and frequently go unrecognized. The growth submodel, for instance, might predict diameter increment for covariate combinations that extrapolate the data set used to calibrate it. Preliminary simulations with the baseline model indicated that extrapolation from the growth submodel was required for ~4% of all

trees by the end of 100-year simulations for both logged and unlogged scenarios.

The growthextrap model is exactly the same as the baseline model, except for a modification of the growth submodel. The baseline growth submodel implicitly assumes that the diameter increment is correctly estimated even if used for covariate combinations that extrapolate the calibration data set. The growth submodel in the growthextrap model was modified so that the best point estimate (the species group mean diameter increment) was used whenever the combination of covariates (diameter and competition index) extrapolated outside the data range.

The analysis was limited to these two assumptions (i.e., dynamic equilibrium and growth extrapolation assumptions) in order to keep simulations, results, and discussions concise. However, it is acknowledged that there are numerous other assumptions in forest dynamic models. While the results do not refer to all possible modeling assumptions, they nevertheless help to illustrate how the method can be used and the magnitude of the uncertainty that may arise as a result of the use of a few alternate assumptions.

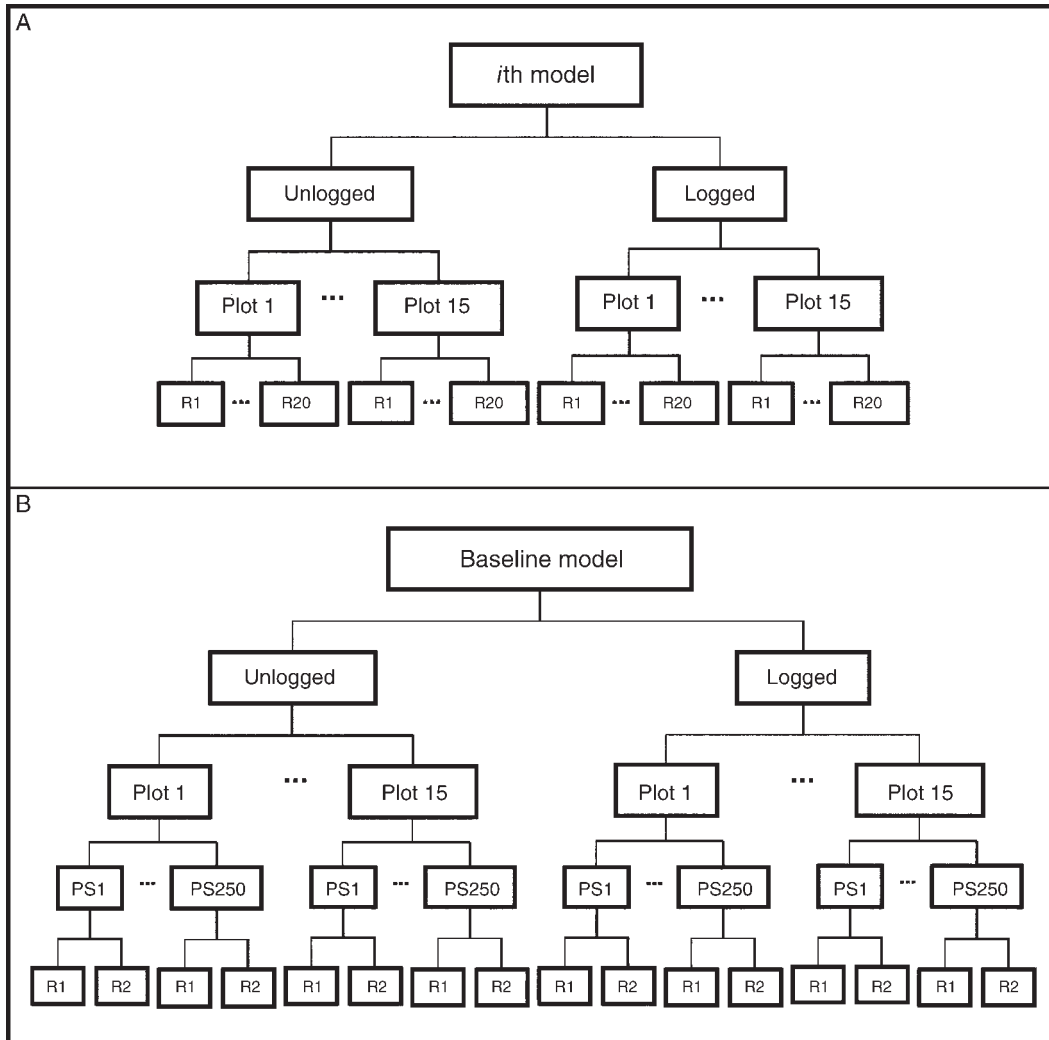


FIG. 3. Nested designs used for simulations. (A) Nested design used to determine the variances associated with starting conditions effect and model stochasticity. This design was used for the three model variants evaluated. (B) Nested design used to determine the variance associated with parameter uncertainty. Only the baseline model variant was used for these simulations. The abbreviations R and PS stand for repetitions and parameter sets, respectively.

Design of simulations

Stand dynamics were simulated for two extreme scenarios: (1) an undisturbed forest and (2) a heavily logged forest, where simulated logging extracted all trees ≥ 45 cm dbh from commercial species resulting in a mean logging intensity of 75 ± 6 m³/ha (mean \pm 95% CI; see Plate 1). Logging was simulated in the beginning of the run and was exactly the same for all simulations in order to ensure an identical starting point for all subsequent stand projections. Both of these scenarios are commonly simulated; the first scenario serves to assess whether the model behaves as expected in undisturbed forest, while the second provides an assessment of the recovery of the forest (particularly in relation to timber stocks and forest biomass) after a major disturbance (e.g., logging). These two extremes

were chosen to evaluate how sensitive the results were to the scenarios being simulated and to determine whether the effect of a given assumption changed according to the scenario being simulated.

One set of simulations was generated for each model variant, each set consisting of 20 100-year simulations for each plot and scenario (undisturbed and heavily logged forest; Fig. 3A). This nested experimental design allowed us to disentangle uncertainty resulting from model stochasticity and from starting conditions. The uncertainty resulting from different starting conditions refers, in this case study, to the variation in mean model projections initialized with different forest plots. Therefore, throughout the text, the terms "uncertainty (or variance) associated with starting conditions" and "uncertainty (or variance) associated with plots" are used interchangeably.

One extra set of simulations was run solely to determine uncertainty associated with parameter estimation, consisting of 500 100-year simulations for each plot and scenario. Parameters of the growth, recruitment, and mortality submodels were drawn randomly every two repetitions and were kept constant throughout the run, resulting in a nested experimental design (individual runs nested within parameter sets nested within plots; Fig. 3B). This allowed us to separate the uncertainty associated with parameter estimation from the uncertainty resulting from model stochasticity and from starting conditions.

Data analysis

Let $L = \{S_1, \dots, S_m\}$ be a finite set of model alternatives, x be the data, and y be the response variable. Furthermore, let μ_i and σ_i^2 be the expected value and the variance, respectively, of the response variable given the data and the i th model alternative (i.e., $\mu_i = E(y|x, S_i)$ and $\sigma_i^2 = \text{Var}(y|x, S_i)$). Let the probability of the i th model given the data be π_i (i.e., $\pi_i = P(S_i|x)$). Draper (1995) showed that

$$\text{Var}(y|x, L) = \sum_{i=1}^m \pi_i \sigma_i^2 + \sum_{i=1}^m \pi_i (\mu_i - \mu)^2$$

where

$$\mu = E(y|x, L) = \sum_{i=1}^m \pi_i \mu_i.$$

In other words, the variance of the response variable is the sum of the within-model variance and the between-model variance, both weighted by the probability of each model given the data.

Following similar arguments, it can be shown that

$$\text{Var}(\bar{y}|x, L) = \sum_{i=1}^m \pi_i \sigma_{\bar{y},i}^2 + \sum_{i=1}^m \pi_i (\mu_i - \mu)^2$$

where $\sigma_{\bar{y},i}^2$ is the variance of the mean of the i th model alternative. This equation can be further expanded by decomposing $\sigma_{\bar{y},i}^2$ into the variances of the mean associated with different uncertainty sources, such as the variance of the mean associated with model stochasticity, with starting conditions, and with parameter uncertainty ($\sigma_{\bar{y},ms,i}^2$, $\sigma_{\bar{y},p,i}^2$, and $\sigma_{\bar{y},pu,i}^2$, respectively). If model variants are created by adding or removing assumptions from a single model, the uncertainty that arises from the use of alternate modeling assumptions can be defined as the variance between these model variants, given by

$$\sum_{i=1}^m \pi_i (\mu_i - \mu)^2.$$

Therefore, the key equation that allows the partitioning of the overall variance of the mean into different sources of uncertainty is given by

$$\begin{aligned} \text{Var}(\bar{y}|x, L) &= \sum_{i=1}^m \pi_i \left(\sigma_{\bar{y},ms,i}^2 + \sigma_{\bar{y},p,i}^2 + \sigma_{\bar{y},pu,i}^2 \right) \\ &\quad + \sum_{i=1}^m \pi_i (\mu_i - \mu)^2. \end{aligned} \tag{1}$$

To illustrate, we could estimate some variable of interest \bar{y} with three independent climate models. If \bar{y} was mean annual temperature ($^{\circ}\text{C}$), for example, μ_i and $\sigma_{\bar{y},i}^2$ would be the expected annual temperature and the variance of the mean annual temperature, respectively, as predicted by model i . Assume we populate the vector μ_i and $\sigma_{\bar{y},i}^2$ with model estimates so that we have $\mu_i = [25, 22, 28]$ and $\sigma_{\bar{y},i}^2 = \sigma_{\bar{y},ms,i}^2 + \sigma_{\bar{y},p,i}^2 + \sigma_{\bar{y},pu,i}^2 = [0.2, 0.2, 0.1] + [0.4, 0.2, 0.1] + [0.4, 0.1, 0.1] = [1, 0.5, 0.3]$, where vectors are ordered from model 1 to model 3. Suppose the probability of each model given the data was estimated to be $\pi_i = [0.2, 0.1, 0.7]$. This implies that

$$\mu = \sum_{i=1}^m \pi_i \mu_i = [0.2, 0.1, 0.7] \begin{bmatrix} 25 \\ 22 \\ 28 \end{bmatrix} = 26.8.$$

The variance of the mean annual temperature, taking into account all three climate models, would therefore be equal to

$$\begin{aligned} \text{Var}(\bar{y}|x, L) &= [0.2, 0.1, 0.7] \begin{bmatrix} 1 \\ 0.5 \\ 0.3 \end{bmatrix} \\ &\quad + ([25, 22, 28] - [26.8, 26.8, 26.8]) \\ &\quad \times \begin{bmatrix} 0.2 & 0 & 0 \\ 0 & 0.1 & 0 \\ 0 & 0 & 0.7 \end{bmatrix} \left(\begin{bmatrix} 25 \\ 22 \\ 28 \end{bmatrix} - \begin{bmatrix} 26.8 \\ 26.8 \\ 26.8 \end{bmatrix} \right) \\ &= 4.42. \end{aligned}$$

A similar calculation could also be performed if the modeler was interested in temporal variability (e.g., the variable of interest \bar{y} could then be the within-year temperature range).

The elements of the within-model variance of the mean ($\sigma_{\bar{y},ms,i}^2$, $\sigma_{\bar{y},p,i}^2$, and $\sigma_{\bar{y},pu,i}^2$) in Eq. 1 can be estimated in several ways. In this paper, we chose to estimate $\sigma_{\bar{y},ms,i}^2$, $\sigma_{\bar{y},p,i}^2$, and $\sigma_{\bar{y},pu,i}^2$ by running the simulations following a balanced nested experimental design and using a variance component analysis assuming normal residuals. These variances were then converted to $\sigma_{\bar{y},ms,i}^2$, $\sigma_{\bar{y},p,i}^2$, and $\sigma_{\bar{y},pu,i}^2$, respectively, by dividing by the appropriate number of observations. The variances associated with starting conditions and with model stochasticity ($\sigma_{\bar{y},p,i}^2$ and $\sigma_{\bar{y},ms,i}^2$, respectively) were determined using the expected means squares from an ANOVA with one random effect (Table 2) estimated at every 10-year time step. Using the simulation set in which parameters were allowed to vary, the uncertainty associated with parameter estimation ($\sigma_{\bar{y},pu,i}^2$) was determined using the variance components analysis summarized in Table 3, also estimated separately for

TABLE 2. ANOVA used to determine the variances associated with plots and model stochasticity ($\sigma_{y,p,i}^2$ and $\sigma_{y,ms,i}^2$, respectively).

Source of variation	df	Expected MS
Plot	$n_p - 1$	$\sigma_{y,ms,i}^2 + n_{rps} \sigma_{y,p,i}^2$
Error	$n_p \times (n_{rps} - 1)$	$\sigma_{y,ms,i}^2$
Total	$n_p \times n_{rps} - 1$	

Notes: These variances were estimated separately for each model variant (i.e., baseline, dynamic equilibrium assumption, and growth extrapolation assumption models), logging scenario (logged and unlogged forest), and 10-year time step. This analysis corresponds to nested design shown in Fig. 3A. The variances $\sigma_{y,ms,i}^2$ and $\sigma_{y,p,i}^2$ are associated with model stochasticity and with plots (i.e., with different starting conditions), respectively, for the i th model; n_p and n_{rps} are the number of plots (i.e., 15) and number of repetitions per plot (i.e., 20), respectively.

every 10-year time step. The variance associated with parameter uncertainty was the only result used from this set of simulations. Because of the computational cost necessary to determine $\sigma_{y,pu,i}^2$ for all models and since we were interested in the magnitude and not the exact value of this parameter, $\sigma_{y,pu,i}^2$ was determined only for the baseline model and assumed to be the same for all models.

The probability of each model given the data (π_i) can be estimated using Bayes rule. For instance, if there are two independent data sets (e.g., D_{mort} and D_{rcrt} , the mortality and recruitment data sets, respectively), the probability of model 1 given these two independent data sets would be

$$\pi(M_1 | D_{mort}, D_{rcrt}) = \frac{L(D_{mort} | M_1) \times L(D_{rcrt} | M_1) \times \pi(M_1)}{\sum_{i=1}^m L(D_{mort} | M_i) \times L(D_{rcrt} | M_i) \times \pi(M_i)}$$

where L is the likelihood, and $\pi(M_i)$ and $\pi(M_i | D_{mort}, D_{rcrt})$ are the prior and posterior probabilities, respec-

tively, of model M_i . Equal priors were assigned to each model (i.e., $\pi(M_i) = 1/3$). The likelihood of each data set given each model i , $L(D_{mort} | M_i)$, and $L(D_{rcrt} | M_i)$, was determined for each data set using SYMFOR's equations and inserting random effects to circumvent the lack of independence of individual observations (as described in Appendix B).

RESULTS

The results were in general consistent for the unlogged and the logged scenarios. The 95% CIs describing the uncertainty around the average projection from each model variant tended to remain relatively constant and small (Fig. 4A, B), and the variance of the mean was mainly dominated by the effect of starting conditions (Fig. 5A, B). A comparison of the projections from the individual model variants, however, revealed that they tended to diverge with increasing simulation length (Fig. 4A, B) and, as a consequence, after 100 years of simulation, most 95% CIs did not overlap. These results highlight the fact that, by neglecting simulation results that could have originated had a different set of assumptions been chosen, users of model projections based on a single model variant tend to underestimate the uncertainty associated with these projections. For instance, users of the equilibrium model variant would have predicted that basal area would recover to pre-logging levels 50–70 years after logging, ignoring that, in the absence of the dynamic equilibrium assumption, the model (i.e., the baseline model variant) would predict complete recovery of the basal area after 20–30 years. Similarly, equilibrium model users would have predicted an increase of the original basal after 100 years in the unlogged scenario of 14–20% while the model without this assumption (i.e., the baseline model variant) would predict an increase of 26–32%.

As is often done in climate models, the overall trend was initially described using a simple multimodel average (i.e., equal weights are assigned to each model). As simulation length increased, the width of the 95% CI around the simple multimodel mean increased, reflecting

TABLE 3. ANOVA used to determine the variance associated with parameter uncertainty ($\sigma_{y,pu,i}^2$) for the baseline model variant.

Source of variation	df	Expected MS
Plot	$n_p - 1$	$\sigma_{y,ms,i}^2 + n_{rps} \sigma_{y,pu,i}^2 + n_{rps} n_{ps} \sigma_{y,p,i}^2$
Parameter uncertainty	$n_p \times (n_{ps} - 1)$	$\sigma_{y,ms,i}^2 + n_{rps} \sigma_{y,pu,i}^2$
Model stochasticity	$n_p \times n_{ps} \times (n_{rps} - 1)$	$\sigma_{y,ms,i}^2$
Total	$n_p \times n_{ps} \times n_{rps} - 1$	

Notes: The variances $\sigma_{y,ms,i}^2$, $\sigma_{y,pu,i}^2$, and $\sigma_{y,p,i}^2$ were estimated separately for each logging scenario (logged and unlogged forest), and 10-year time step. This analysis corresponds to the nested design shown in Fig. 3B. The variances $\sigma_{y,p,i}^2$, $\sigma_{y,pu,i}^2$, and $\sigma_{y,ms,i}^2$ are associated with plots (i.e., with different starting conditions), with parameter uncertainty, and with model stochasticity, respectively, for the i th model; n_p , n_{rps} , and n_{ps} are the number of plots (i.e., 15), the number of repetitions per parameter set (i.e., 2), and the number of randomly drawn parameter sets per plot (i.e., 250), respectively.

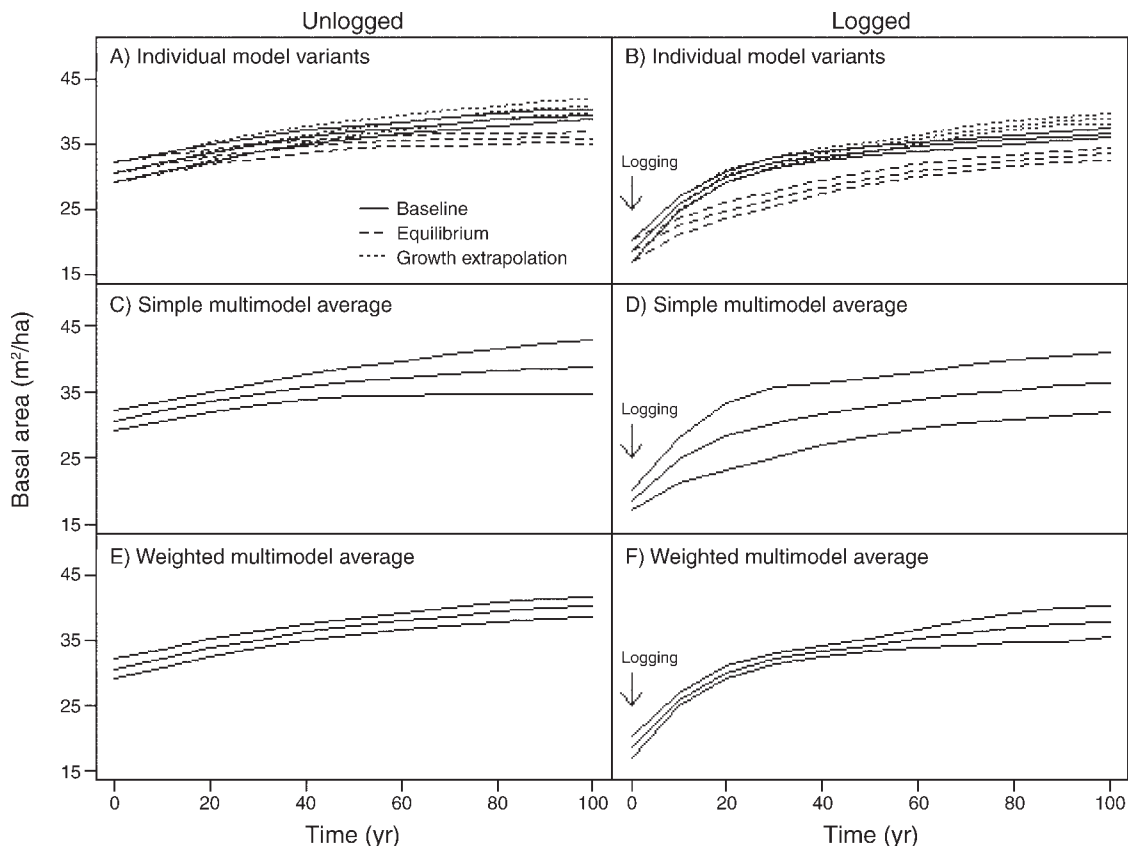


FIG. 4. Mean model projections (and their associated 95% CIs) showing forest dynamics for an unlogged and a logged forest. Results from (A, B) the individual model variants (the baseline, dynamic equilibrium assumption, and growth extrapolation assumption models), (C, D) the simple multimodel average (i.e., equal model probabilities are assigned to each model variant), and (E, F) the weighted multimodel average (i.e., model probabilities are estimated from the data) are contrasted. The simple multimodel average (C, D) incorporates the uncertainty associated with the contrasting mean results from the individual model variants (A, B) but ignores the negligible probability, given the data, associated with the dynamic equilibrium model variant. The weighted multimodel average (E, F) takes the probability of each model variant into account, which results in a narrower confidence interval when compared to the simple multimodel average (C, D).

the divergence of results from the individual model variants (Fig. 4C, D). The variance of the mean for the simple multimodel average after 100 years was 21- and 29-fold larger than the average variance of the mean from the individual model variants (for the unlogged and logged scenarios, respectively). As shown in Fig. 5C, D, the uncertainty around the mean from the simple multimodel average was dominated by the uncertainty that arises from the use of the adopted assumptions. More specifically, the variance of the mean associated with the adopted assumptions represented 95% and 97% of the overall variance of the mean, for the unlogged and logged simulation results after 100 years, respectively.

These results, however, ignore the fact that some of the model variants are more consistent with the data than others. When using the data to estimate model probabilities, it became clear that the equilibrium model strongly conflicted with the data (i.e., the posterior probability associated with this model was approximately zero) whereas the growthextrap and the baseline

models were equally supported by the data (Table 4). This was not unexpected since the growthextrap and the baseline model variants differed only in relation to the growth submodel and the available growth data did not distinguish between these two models. As a consequence of the low weight of the equilibrium model, the variance of the mean (at year 100) for the weighted multimodel average (where the weights were estimated from the data) was ~13–28% of those values when equal probabilities were used (Fig. 5E, F; note narrower 95% CI in Fig. 4E, F). The practical implication of these results is that by using the weighted multimodel projections, forest managers would expect that the forest would recover its original basal area within 20–30 years after logging vs. 20–80 years if a simple multimodel average (i.e., equal weights) had been used. Likewise, the projected increase in basal area after 100 years for the unlogged forest with the weighted multimodel average is equal to 26–36% of the basal area in year 0 vs. 13–40% with the simple multimodel average. Despite the use of

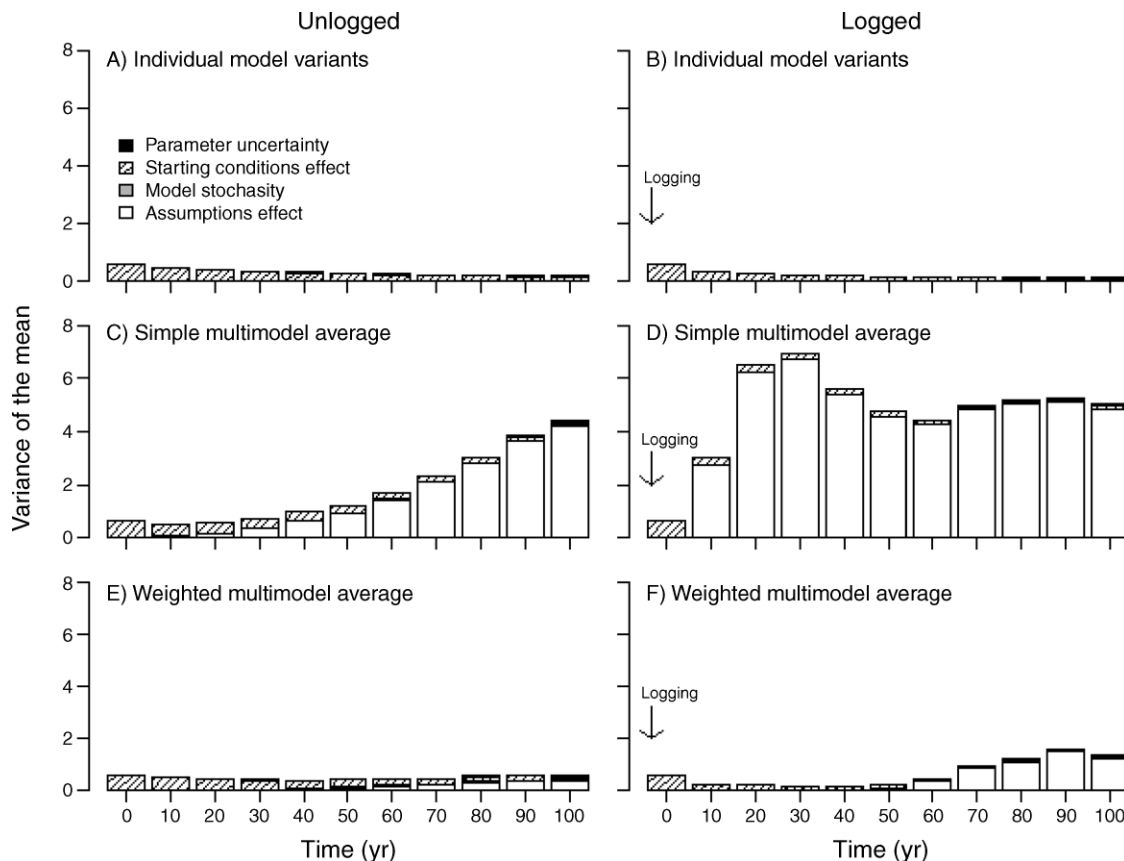


FIG. 5. Variance of the mean for the overall basal area projections, partitioned between parameter uncertainty, starting conditions effect, model stochasticity, and assumptions effect. Results are shown separately for logged and unlogged simulations. Results from (A, B) the individual model variants (variances were averaged over the three model variants), (C, D) the simple multimodel average (i.e., equal model probabilities are assigned to each model variant), and (E, F) the weighted multimodel average (i.e., model probabilities are estimated from data) are contrasted. The individual model variants (A, B) exhibit an excessively small mean overall variance of the mean that does not account for the uncertainties associated with model structure. Model structure uncertainty, shown as “Assumptions effect” (open bars), is taken into account in the simple multimodel average (C, D) and the weighted multimodel average (E, F), but the simple multimodel average assumes all models are equally likely while the weighted multimodel average effectively excludes the equilibrium model variant since this model variant has a negligible probability given the data.

the data to estimate model probabilities and the corresponding decrease in overall uncertainty, modeling assumptions were still the greatest source of uncertainty (Fig. 5E, F). The variance of the mean associated with the used assumptions corresponded to 66% and 89% of the overall variance of the mean, for the unlogged and logged simulation results after 100 years, respectively.

DISCUSSION

Multimodel projections

Simulation model projections are frequently perceived by modelers as conditional on the assumptions embedded in the construction of the model (Haefner 1996). Users of model projections, in contrast, are likely to overlook this fact. In fact, it is impossible to assess the uncertainty associated with these assumptions if projections are based on a single model variant. Multimodel

TABLE 4. Posterior probability of each model variant (i.e., baseline, growth extrapolation assumption [growthextrap], and dynamic equilibrium assumption [equilibrium] models) given the recruitment data, the mortality data, and both data sets combined.

Model variant	Recruitment data	Mortality data	Both data sets combined
Baseline	0.5	0.33	0.5
Growthextrap	0.5	0.33	0.5
Equilibrium	0.0	0.33	0.0

Notes: The posterior probability was estimated with Bayes’ theorem by combining the prior probability (each model had an equal prior probability, one-third) and the likelihood (estimated using WinBUGS; see Appendix B). Recruitment and mortality data came from logged and unlogged forests (at km 67 and km 114 at the Tapajós National Forest, Para, Brazil).



PLATE 1. (Left) A mixed tropical forest in the Brazilian Amazon. (Right) Logs of a tropical tree species at a sawmill in the Brazilian Amazon. The person standing close to the logs is approximately 1.75 m tall. Photo credits: forest, C. L. Staudhammer; logs, Simone Bauch.

projections, on the other hand, are a multiple working hypothesis (Chamberlin 1965) approach. The case study illustrated that multimodel projections, even when based on variants of a single model, can help mitigate this problem by quantifying and including the uncertainty that arises from the use of modeling assumptions, particularly because these assumptions can be the greatest source of uncertainty (e.g., Fig. 5C–F). The effect of alternative model assumptions has been evaluated elsewhere (e.g., Chambers et al. 2004, Cropper and Loudermilk 2006), and this effect has been compared to the uncertainty from other sources using an approach based on sensitivity analysis (e.g., Knorr and Heimann 2001, Jung et al. 2007). However, to our knowledge, the comparison of the magnitude of uncertainty from different sources has never been done in a statistically comprehensive way. The case study also exemplified that multimodel averaged projections can be substantially different from projections based on a single model variant (Fig. 4C–F vs. Fig. 4A, B).

Users and modelers may assume that even if simulations are biased, the comparison of different scenarios (e.g., logged vs. unlogged forest) or management strategies simulated with the same set of assumptions would generally be unbiased (e.g., Ellner and Fieberg 2003, Phillips et al. 2003, Arets 2005). The case study results, however, show that this is not always true given that the assumption effect may depend on the scenario being simulated (e.g., compare baseline and equilibrium model projections in Fig. 4A vs. 4B).

The use of the best model, as chosen from a model selection procedure, is equivalent to using a multimodel projection in which the best model has a probability of one and all the other alternative models have zero probability. If all the other alternative models have

indeed zero probability, the use of the best model instead of multimodel projections is clearly advantageous since it reduces the number of simulations to be performed. If, however, some of the other alternative models have a nonzero probability (e.g., have similar fits to the data), then the use of the best model might be worrisome as the best model may have wildly different predictions in relation to other potential models when extrapolated. Many ecological models are built for the purpose of extrapolation (e.g., to predict the future) and, assuming there is a set of plausible models that have similar fits to the data, multimodel projections are essential to avoid underestimating the uncertainty on model predictions. The use of multimodel inference could have, for instance, prevented such dramatic events as the disaster of the U.S. space shuttle Challenger. In this example, engineers and managers had to predict the probability of failure of the O-rings for a temperature that was outside the range for which these rings had been previously tested. A multimodel inference on the probability of failure of the O-rings for the low temperature at the time of launching could have indicated the unacceptably high risk associated with the space shuttle launching (Draper 1995).

Simple vs. weighted multimodel averaging

The case study suggests that simple multimodel averaging, as often used with global vegetation and climate models (Cramer et al. 2001, Koster et al. 2004), might result in an overestimation of variability (similar to results in Murphy et al. [2004]). Indeed, multiple models (or model variants) can be created based on many biologically reasonable alternatives representing a given phenomenon. For instance, to avoid trees from getting too large, a forest modeler might use an equation

that predicts zero growth for large trees (e.g., Alder and Silva 2000, Gourlet-Fleury and Houllier 2000, Kamme-sheidt et al. 2001, Kohler et al. 2003) or increase the mortality rate of large trees as a result of senescence (e.g., Phillips et al. 2003, 2004, Chambers et al. 2004, Valle et al. 2007). Similarly, the dynamic equilibrium assumption can be implemented by fine tuning the model (e.g., Phillips et al. 2004, Gourlet-Fleury et al. 2005, Valle et al. 2007) or by replacing every tree that dies by a newly recruited tree (e.g., Chambers et al. 2004). To reduce the uncertainty that arises from the use of assumptions and consequently reduce overall uncertainty around the mean, it is crucial to evaluate which of these alternative representations are more consistent with the data and weight them accordingly. Multimodel projection, in which the individual models are weighted according to their past performance, has been shown elsewhere to result in a higher prediction ability than individual models and simple multimodel averages (Krishnamurti et al. 1999).

Even if the available data do not help to discern between these alternative representations, the acknowledgment of this fact can guide researchers to conduct experiments or collect observational data in order to strategically reduce model structure uncertainty. In the case study, despite the fact that model parameters were carefully fine tuned within the confidence interval of each parameter, the equilibrium model was shown to be inconsistent with the data. On the other hand, the data supported equally well model variants that only differed in relation to how growth submodel extrapolations were handled (e.g., baseline and growthextrap models). A carefully designed experiment might have helped to further discern between the baseline and the growthextrap models.

General applicability of the uncertainty partitioning methodology

It has been illustrated how a balanced, nested simulation design facilitates in partitioning the within-model variance into various sources of uncertainty and how multimodel projections allow estimation of uncertainty that arises as a result of the use of different model assumptions (between model variance). This method can potentially be applied to other types of simulation models since the sources of uncertainty analyzed here (i.e., parameter uncertainty, model stochasticity, effect of starting conditions, and uncertainty associated with model assumptions) are likely to be jointly present in other models as well. This method might help model developers and users to identify which are the greatest sources of uncertainty and, more importantly, which type of data should be collected or experiment conducted to decrease the uncertainty from these sources. However, depending on the computational power needed for a single run of some models (e.g., global biogeochemical/biosphere models), the numerous simulations needed for this methodology might limit its

use. One could reduce the number of simulations by eliminating part of the nested simulation design at the cost of additional assumptions in the data analysis. For instance, in the case study described above, parameter estimation uncertainty could have been assessed for only one plot and one model and assumed to be the same for all other plots and models. Also, simulations might eventually become too numerous when using this method if too many modeling assumptions are analyzed. The number of simulations can be somewhat reduced by discarding those modeling assumptions that are not supported by the data; however, modelers, and potentially other stakeholders, will ultimately have to decide which are the key modeling assumptions that should be included in their uncertainty analysis.

Simulation models have and will increasingly be used to predict the outcomes of direct or indirect human-induced changes (e.g., logging, burning, fragmentation, or carbon accumulation in the atmosphere), sometimes with millennium-long time windows (e.g., Chambers et al. 2001). The uncertainty associated with these model projections is underestimated, however, if the uncertainty resulting from assumptions used in model building is not taken into account. This has the potential to mislead decision makers, reduce public confidence in model projections, hamper the ability to anticipate extreme events and devise robust policies, and could potentially have dire consequences (Clark et al. 2001, Pielke and Conant 2003). Simulation modelers in ecology should follow the lead of those in the field of statistics, taking model structure uncertainty into account through multimodel projections.

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APPENDIX A

Parameters used for different model variants of SYMFOR (*Ecological Archives* A019-068-A1).

APPENDIX B

Estimating the likelihood of each data set given each model (*Ecological Archives* A019-068-A2).