Incorrect representation of uncertainty in the modeling of growth leads to biased estimates of future biomass

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Abstract. Biomass is a fundamental measure in the natural sciences, and numerous models have been developed to forecast timber and fishery yields, forest carbon content, and other environmental services that depend on biomass estimates. We derive general results that reveal how dynamic models that simulate growth as an increase in a linear measure of size (e.g., diameter, length, height) result in biased estimates of future mean biomass when uncertainty in growth is misrepresented. Our case study shows how models of tree growth that predict the same mean diameter increment, but with alternative representations of growth uncertainty, result in almost a threefold difference in the projections of future mean tree biomass after a 20-yr simulation. These results have important implications concerning our ability to accurately predict future biomass and all the related environmental services (e.g., forest carbon content, timber and fishery yields). If the objective is to predict future biomass, we strongly recommend that: (1) ecological modelers should choose a growth model based on a variable more linearly related to biomass (e.g., tree basal area instead of tree diameter for forest models); (2) if field measurements preclude the use of variables other than the linear measure of size, both the mean and other statistical moments (e.g., covariances) should be carefully modeled; (3) careful assessment be done on models that aggregate similar individuals (i.e., cohort models) to see if neglecting autocorrelated growth from individuals leads to biased estimates of future mean biomass.

Key words: deterministic vs. stochastic models; growth; Jensen's inequality; linear vs. nonlinear relationships; simulation models; timber yield projections; tree growth models; uncertainty representation; variance.

INTRODUCTION

Biomass is a fundamental measure in the natural sciences; for instance, the biomass of a population often dictates its expected importance in the ecosystem (Power et al. 1996), yield is often expressed in biomass (e.g., Pauly et al. 2003), and forest carbon content is often estimated as a simple linear conversion of its biomass (Houghton 2007). Numerous dynamic models have been created to predict timber and fishery yields, forest carbon content, and other environmental services that depend on biomass estimates, often by iteratively simulating growth, recruitment, and mortality of individuals (i.e., individual-based models) or groups of individuals (i.e., cohort models). Here we show that incorrect representation of uncertainty on linear measures of growth in these models leads to substantially biased estimates of future mean biomass.

It has been known for decades that even when models have the same structure and parameter values, mean differences arise between deterministic and stochastic models (e.g., Zhou and Buongiorno 2004, Boyce et al.

2006). This counter-intuitive result is due to a mathematical property of nonlinear functions called "Jensen's inequality" (Ruel and Ayres 1999). On the other hand, examples have recently emerged showing that alternative representations of uncertainty within stochastic models can also lead to different mean model outcomes, a fact that is still underappreciated. For instance, Clark et al. (2007) have shown that different representations of uncertainty affect tree-diversity projections. Similarly, Melbourne and Hastings (2008) have shown how extinction risk is strongly affected by the specific combination of factors that contributes to stochasticity (e.g., the uncertainty regarding sex of individuals, demographic heterogeneity in vital rates, demographic and environmental stochasticity) even when total variance remains unchanged.

Here we show that incorrect representation of linear-growth uncertainty results in biased estimates of future mean biomass. We first motivate this with a case study on timber yield projections. We then provide a general description of this phenomenon. Finally, we provide some general recommendations regarding growth modeling.

METHODS

In this section, we describe forest-dynamics simulations used to illustrate the impact of alternative

TABLE 1. Summary description of the functions/distributions used to predict diameter increment for each simulation of forest dynamics.

Simulation	Description of growth model	Formulas†
1	deterministic	$\ln(D_{i,t} - D_{i,t-1}) = \beta_0 + \frac{\sigma^2_{ind} + \sigma^2_{proc}}{2}$
2	stochastic, with uncorrelated growth	$\ln(D_{i,t} - D_{i,t-1}) \sim \mathcal{N}(\beta_0, \sigma^2_{ind} + \sigma^2_{proc})$
3	stochastic, with random individual effects (RIEs)	$\ln(D_{i,t} - D_{i,t-1}) \sim \mathcal{N}(\beta_0 + \varepsilon_i, \sigma^2_{proc})$ where $\varepsilon_i \sim \mathcal{N}(0, \sigma^2_{ind})$
4	stochastic, with autocorrelated growth	$\ln(\mathbf{I}) \sim \mathcal{N}(\beta_0, (\sigma^2_{ind} + \sigma^2_{proc})\boldsymbol{\Sigma})$

Notes: The four growth models used have different representations of uncertainty, but the same mean diameter increment. Simulations were based on the growth of trees from the tropical timber species *Simarouba amara* for a period of 20 years to determine timber yields. For details see Appendix A.

† $D_{i,t}$ is the diameter of tree i at time t, β_0 is a constant, σ^2_{ind} is the individual random effects variance, σ^2_{proc} is the process variance, $\mathbf{I}$ is a vector of diameter increments, and $\boldsymbol{\Sigma}$ is the lag-1 autoregressive correlation matrix with correlation parameter ρ.

representations of uncertainty on the growth model. We simulated the growth of trees from the tropical timber species *Simarouba amara* for a period of 20 years to determine timber yield. A complete description of the data used and how the parameters were estimated are given in Appendix A. Despite similar mean structures (i.e., all of them use growth models that predict the same mean diameter increment), they differ in relation to how diameter increment uncertainty is represented.

We simulated the growth of 100 000 trees with initial diameter of 15 cm over 20 years. As is standard in forest dynamic models (Vanclay 1994), annual diameter increments were added sequentially to the initial diameter to estimate the size of these trees after 20 years. All simulations had the same mean diameter increment. In the first simulation (hereafter referred to as "Deterministic"), diameter increment was modeled as a deterministic phenomenon (i.e., $D_{i,t+1} - D_{i,t} = \exp[\beta_0 + (\sigma^2_{ind} + \sigma^2_{proc})/2]$, where β_0 is a constant, $D_{i,t}$ is the diameter of tree i at time t, and σ^2_{ind} and σ^2_{proc} are the variances of the random individual effects [RIEs] and process error, respectively). The term $(\sigma^2_{ind} + \sigma^2_{proc})/2$ ensures that this simulation has the same mean diameter increment as the other simulations because diameter increments in the other models we examined are log-normally distributed. In the second simulation (hereafter referred to as "Uncorrelated Growth"), log diameter increment was drawn at each time step from a normal distribution with mean β_0 and variance equal to $\sigma^2_{ind} + \sigma^2_{proc}$ [i.e., $\ln(D_{i,t+1} - D_{i,t}) \sim \mathcal{N}(\beta_0, \sigma^2_{ind} + \sigma^2_{proc})$]. This simulation represents a scenario where the different sources of variation are lumped into a single variance term. In the third simulation (hereafter referred to as "Random Individual Effects"), we first drew a random individual effect ε_i for each individual from a normal distribution with mean zero and variance σ^2_{ind} and then drew at each time step the log diameter increment from a normal distribution with mean $\beta_0 + \varepsilon_i$ and process error σ^2_{proc}. This can be summarized as $\ln(D_{i,t+1} - D_{i,t}) \sim \mathcal{N}(\beta_0 + \varepsilon_i, \sigma^2_{proc})$, where $\varepsilon_i \sim \mathcal{N}(0, \sigma^2_{ind})$. Finally, a set of simulations (hereafter referred to as "Autocorrelated growth") was performed. For each simulation in this set,

we drew a vector of log diameter increments from a multivariate normal distribution $\mathcal{N}(\beta_0, [\sigma^2_{ind} + \sigma^2_{proc}]\boldsymbol{\Sigma})$, where $\boldsymbol{\Sigma}$ is a correlation matrix with a lag-1 auto-regressive structure and correlation parameter ρ. Each simulation in this set had a different correlation parameter ρ. A summary of each of these simulations is given in Table 1. Tree biomass (B) was estimated using the empirical allometric equation $B_{i,t} = 42.69 - 12.8D_{i,t} + 1.242D_{i,t}^2$ (Brown 1997). All simulations and statistical procedures were conducted in R (R Development Core Team 2007).

We emphasize that all simulations had the same mean diameter increment. Furthermore, simulations 2, 3, and 4 had the same one-step-ahead variance (i.e., Var $[\ln(D_{i,t+1} - D_t) | D_t] = \sigma^2_{ind} + \sigma^2_{proc}$). Thus, two naïve hypotheses can be made. One of these hypotheses is that all simulations will predict the same mean basal area and volume because all have the same mean diameter increment. Another hypothesis is that stochastic simulations 2, 3, and 4 will predict the same mean basal area and volume because they have the same mean diameter increment and one-step-ahead variance.

Results

Simulation results

As predicted, mean tree diameter was almost identical among all simulations; the range of projected mean tree diameter after 20 years was 258–259 mm. However, there were major differences in projected mean basal area and biomass, and thus both naïve hypotheses were rejected (Fig. 1). Mean tree basal area and biomass were smallest for the deterministic simulation and they were largest for the simulations that represented random individual effects and highly autocorrelated growth (i.e., large ρ values). In particular, increasing correlation ρ led to increasing estimates of mean tree biomass. After 20 years, the estimated mean tree biomass ranged from 542 to 1627 kg, almost a three-fold difference. These differences were a direct effect of increasing tree-diameter variance (Fig. 2) on the nonlinear relationship between tree diameter and biomass. Finally, differences among the forward simulations increased with the
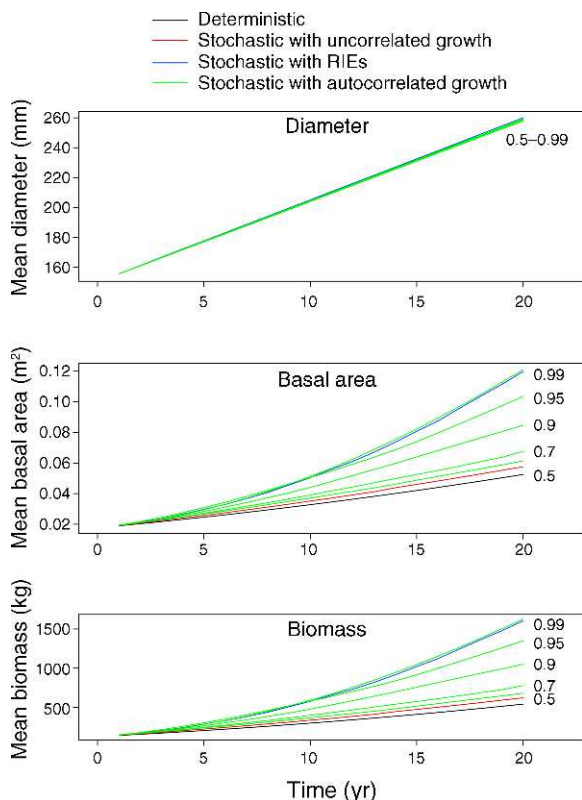
FIG. 1. Simulation results for three tree characteristics from the deterministic (black lines), stochastic with uncorrelated growth (red lines), stochastic with random individual effects (RIEs; blue lines), and stochastic with autocorrelated growth (green lines) models. The correlation parameter ρ is given at the right-hand side of each panel and is depicted close to the mean results from the corresponding simulation.

simulation time window, suggesting that these differences may be even greater for typical timber yield or forest biomass projections.

It might be argued that these differences emerge because simulations were performed with models that are not identical to the fitted model. To show this is not the case, we also fitted the individual models described in Table 1 to the data. Simulations using the fitted parameters revealed the same overall pattern (Appendix B). In particular, for realistic levels of autocorrelation in growth or individual random effects, mean estimated biomass after 20 years can be up to 258% and 63% greater than the mean estimated biomass for the deterministic simulation and the simulation with uncorrelated stochastic growth, respectively.

General description of the phenomenon

Here we describe why our findings from the timber-yield case study are expected to be valid for other ecological models. To show how the incorrect representation of linear growth uncertainty results in biased estimates of future mean biomass, we first describe the iterative process of predicting future length at time t (L_t).

We refer to the linear measure of size L_t simply as length but the concepts of this article also apply to other linear measures of size such as diameter, height, or width, as long as these linear measures of size have an exponent $\gamma > 2$ in the allometric relationship $B \propto L^\gamma$, where B is the organism's biomass and γ is a scaling parameter. Then, we highlight the biases resulting from alternative representations of uncertainty in the growth model when estimating the mean of the quantity A_t, where A_t is defined to be proportional to L_t squared (i.e., $A_t \propto L_t^2$). Finally, we show how these biases on A_t are aggravated for estimates of future mean biomass at time t (B_t). We provide suggestions for how one can quickly determine if these consequences are of significance or can be neglected.

The basic idea arises from the fact that $A_t \propto L_t^2$ is a nonlinear relationship. Assuming that L_t is a random variable, the mean of A_t is not equal to A_t calculated at the mean value of L_t (i.e., $E[A_t] = E[f(L_t)] \neq f(E[L_t])$), a consequence of Jensen's inequality. For instance, a uniform distribution for L_t results in an asymmetric distribution of A_t (Fig. 3). Not only does the distribution change, but also mean A_t (red and green lines) is shifted when compared to A_t calculated at the mean value of L_t (black line). Furthermore, different distributions with
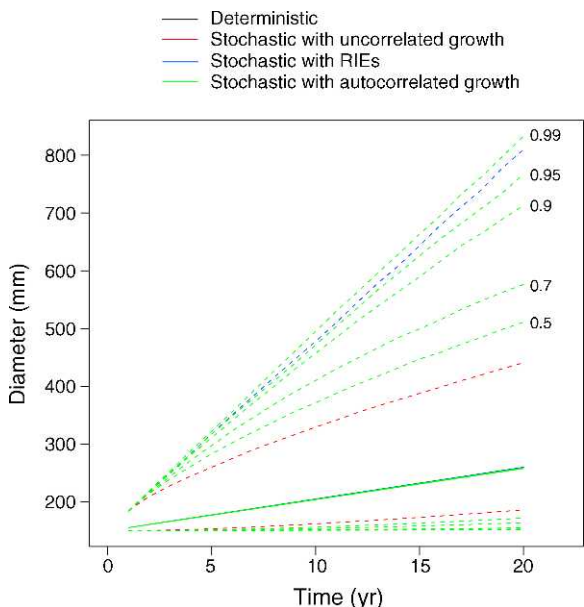

FIG. 2. Mean tree diameter (continuous lines) and 95% confidence intervals (dashed lines) for the simulation results from the deterministic (black lines), stochastic with uncorrelated growth (red lines), stochastic with random individual effects (RIEs; blue lines), and stochastic with autocorrelated growth (green lines) simulations. The correlation parameter ρ is presented at the right-hand side of the panel and is depicted close to the upper 95% confidence-interval results from the corresponding simulation. Note that the lines depicting the deterministic simulation results and the average tree-diameter lines for the other simulations are drawn almost on top of one another.
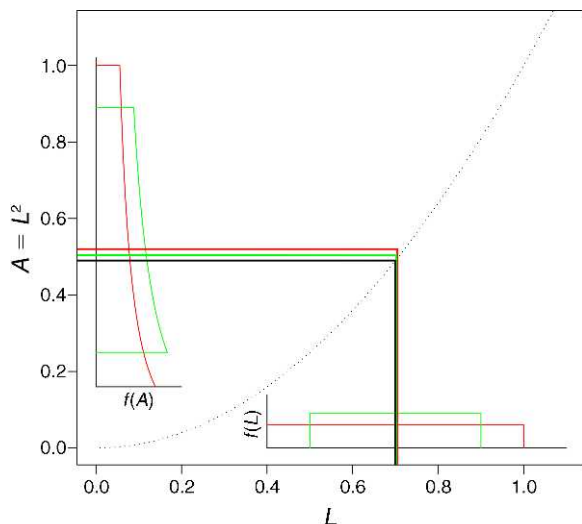
Fig. 3. The relationship between length (L) and the quantity A, where A is defined to be equal to L^2 (dotted black line). Thick lines are the means of L and A, assuming that L is deterministic (black line), L is a random variable with a uniform distribution between 0.5 and 0.9 (green line), or with a uniform distribution between 0.4 and 1.0 (red line). In all cases, the mean of L is 0.7. The probability density functions of L and A are denoted by $f(L)$ and $f(A)$, respectively.

the same mean L_t result in different mean A_t (red vs. green lines). This phenomenon has already been described in the context of a particular forest model in Duursma and Robinson (2003). We take a step further to show how different representations of uncertainty in growth directly influence the final distribution of L_t, thus changing mean A_t and mean biomass. We also emphasize that this is a broad phenomenon, applicable to a number of growth models of different organisms, not only trees.

We conceptualize the process of growth as increments in length being added sequentially to the initial length at time 0 (i.e., L_0). Let $L_{i,t}$ and $I_{i,t}$ be the length and length increment, respectively, for a given organism in realization i and time t. Thus,

$$L_{i,t} = L_0 + \sum_{k=0}^{t-1} I_{i,k}.$$

Assume that $I_{i,t}$ is a random variable with mean $\bar{I}_t$ and variance σ_t^2. Then,

$$E[L_{i,t} \mid L_0] = L_0 + \sum_{k=0}^{t-1} E[I_{i,k}] = L_0 + \sum_{k=0}^{t-1} \bar{I}_k.$$

Expectation is over all realizations i. While $E[L_{i,t} \mid L_0]$ may or may not be influenced by how uncertainty is modeled, the mean of other nonlinearly related quantities, such as $A_{i,t}$, will definitely be influenced by how uncertainty is modeled, above and beyond the effect uncertainty may have on $E[L_{i,t} \mid L_0]$. For instance, a deterministic growth model might predict mean $A_{i,t}$ as

$$E[A_{i,t} \mid L_0] \propto \left(L_0 + \sum_{k=0}^{t-1} \bar{I}_k \right)^2. \tag{1}$$

However, it is easily shown (see Appendix C) that the correct formula should be

$$E[A_{i,t} \mid L_0] \propto \left(L_0 + \sum_{k=0}^{t-1} \bar{I}_k \right)^2 + \sum_{k=0}^{t-1} \sigma_t^2$$

$$+ 2\sum_{k=0}^{t-1} \sum_{l=k+1}^{t-1} \mathrm{Cov}(I_{i,k}, I_{i,l}). \tag{2}$$

Eq. 2 reveals that growth models that predict the same mean diameter increment (i.e., $E[I_{i,t}]$) generally predict different $E[A_{i,t} \mid L_0]$ depending on the variances and covariances. In particular, a deterministic growth model will generally predict a smaller mean biomass when compared to a stochastic one (i.e., compare Eqs. 2 and 1). Similarly, a stochastic growth model that omits correlation between length increments (i.e., set $\mathrm{Cov}(I_{i,k}, I_{i,l}) = 0$ in Eq. 2) will result in smaller estimates of $E[A_{i,t} \mid L_0]$ than a stochastic growth model that includes autocorrelated growth (i.e., set $\mathrm{Cov}(I_{i,k}, I_{i,l}) > 0$ in Eq. 2). For example, models that aggregate individuals of similar age/size (i.e., cohort model) to increase computational efficiency will ignore the strong autocorrelated growth that individuals typically exhibit (e.g., Fujiwara et al. 2004, Brienen et al. 2006), potentially generating biased estimates of $E[A_{i,t} \mid L_0]$.

So far, Eq. 2 shows how uncertainty affects mean A_t. How are these changes in mean A_t related to changes in mean biomass? Whether we assume a conventional scaling ($L_t \propto B_t^{1/3}$) or a "fractal biological scaling" ($L_t \propto B_t^{1/4}$) (West 1999), one percent change in A_t usually results in more than one percent change in biomass at time t (B_t). In other words, $(\Delta B/B)/(\Delta A/A) > 1$. Thus, the relative bias in mean A_t introduced due to incorrect representation of uncertainty of the stochastic growth model is exacerbated for estimates of mean biomass.

Are these biases biologically relevant? To answer this question, we start by defining an empirical allometric equation $B_t = f(L_t)$. We can approximate future mean biomass using the delta method. This approximation can be further simplified if we assume a correlation matrix Σ with a lag-1 autoregressive structure and correlation parameter ρ. Then, the approximation becomes

$$E[B_{i,t} \mid L_{i,0}] \approx f(E[L_{i,t}]) + \left\{ \frac{f''(E[L_{i,t}])}{2} t\sigma^2 \right\}$$

$$+ \left\{ f''(E[L_{i,t}])\sigma^2 \sum_{i=1}^{t-1} (t-1)p^i \right\} \tag{3}$$

(Appendix C). Eq. 3 allows a rough comparison between a deterministic simulation (set the second and third term in Eq. 3 to zero), a stochastic simulation without correlated growth (set the third term in Eq. 3 to zero),

and a stochastic simulation with correlated growth. Eq. 3 only includes $E[L_{i,t}]$, the variance σ^2 and the correlation ρ. If the correlation parameter is unknown, one can use the lower and upper bounds for Eq. 3. These bounds are $f(E[D_{i,t}]) + [f''(E[D_{i,t}])/2(t\sigma^2)$ when $\rho = 0$ and $f(E[D_{i,t}]) + [f''(E[D_{i,t}])/2](t^2\sigma^2)$ when $\rho = 1$, respectively. All else being equal, Eq. 3 reveals that the bias introduced by ignoring the variance and covariance terms is small (1) for large organisms (i.e., large $f(E[L_{i,t}])$); (2) when simulation length is short (i.e., t is small); (3) when variance and/or correlation are small; and/or (4) when $f''(E[L_{i,t}])/2$ is small.

Discussion

We have explored how very different timber yield projections can result from simply converting a deterministic model into a stochastic one or by allowing for persistent individual tree differences in our stochastic growth model. Our findings, however, do not take into account other forest processes typically represented in forest dynamics models such as local tree interactions (e.g., competition for light) and differential mortality. These biases are likely to be even larger if we take differential mortality into account, as individuals growing slower than average are often less vigorous and thus have a higher mortality rate (Chao et al. 2008, Rozendaal et al. 2010). In that case, the culling of these individuals would lead to even greater differences in the estimate of future mean biomass. For simplicity, we also assumed that trees grew independently. This is a widely used assumption in tropical forest models (e.g., Chambers et al. 2004, Dauber et al. 2005, Brienen and Zuidema 2007, Grogan et al. 2008, Schulze et al. 2008, Sebbenn et al. 2008), but it is often not a very realistic assumption. We acknowledge that allowing for interaction among trees may change our results but, unfortunately, we were not able to derive general results that accounted for these interactions because this would depend on the peculiarities of how growth, mortality and tree interaction are modeled (e.g., different competition indexes; Moravie et al. 1999). Nevertheless, preliminary results using an individual-based forest simulator, parameterized with extensive permanent plot data from North Carolina (USA), suggest that these biases arise even in the presence of competition for light (S. McMahon and J. Clark, *unpublished manuscript*). It remains an open question if this would be the case for other forests as well.

Although we have focused on forest dynamics in our case study, the same concepts apply to dynamic models of other organisms that also simulate growth based on a linear measure of size (e.g., crocodile length, Richards et al. 2004; curved carapace length of sea-turtles, Mazaris and Matsinos 2006; fish length, Charles et al. 2008). To our knowledge, this is the first time it has been generalized how different representations of uncertainty on growth affect future biomass estimates. This has important implications because there is still extensive use of models with deterministic growth or stochastic growth that do not allow for persistent individual differences (e.g., Chambers et al. 2001, 2004, Coates et al. 2003, Valle et al. 2007, Purves et al. 2008).

Given these results, how can we accurately forecast timber and fishery yields, forest carbon content, and other environmental services that depend on biomass estimates? Three overall recommendations emerge from our general results. Because second and higher central moments (variance, skew, and so on) are generally more difficult to estimate than the first moment (i.e., mean), our first recommendation is that growth models should be based on the variable more linearly related to biomass, thus decreasing the dependence of the estimates of future mean biomass on the correct estimation of second or higher central moments. For example, tree growth should be preferentially modeled as basal area growth instead of diameter growth. The second recommendation is that, if linear measures of growth are unavoidable (e.g., this is the only available field-based measurement), careful consideration should be given in the modeling of the mean *and* other statistical moments. This implies the use of sophisticated statistical tools to correctly partition and estimate the magnitude of the different sources of uncertainty. Finally, modelers that aggregate similar individuals into cohorts and represent them with a single mean individual for computation efficiency should consider whether or not neglecting autocorrelated growth from individuals will affect estimates of future mean biomass.

To anticipate future environmental challenges, management and policy decisions will increasingly depend on forecasts from ecological models (Clark et al. 2001, Purves and Pacala 2008). However, skepticism will dominate if these models predict disparate results. Thus, the time has come to give careful consideration on how uncertainty within these models is represented.

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APPENDIX A

Description of parameter-estimation method (*Ecological Archives* A021-048-A1).

APPENDIX B

Simulation results from the individually fitted models (*Ecological Archives* A021-048-A2).

APPENDIX C

Derivation of equations used in the main text (*Ecological Archives* A021-048-A3).