

CHAPTER FOURTEEN

Detecting and projecting changes in forest biomass from plot data

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14.1 Introduction

Increasing atmospheric carbon dioxide, changing climates, nitrogen deposition and other aspects of anthropogenic global change are hypothesised to be changing forest productivity and biomass stocks in tropical forests and elsewhere (Clark 2004; Lewis, Malhi & Phillips 2004; Lewis *et al.* 2009a; Luo, 2007; Myeni *et al.* 1997). These hypotheses continue to be much debated, with contrary views on the plausibility of particular mechanisms and on the status of current evidence for or against them (Clark 2007; Friedlingstein *et al.* 2006; Holtum & Winter 2010; Körner 2009; Wright 2005, 2010). The influence of atmospheric and climate change on forest biomass is of particular interest because of the potential for positive or negative feedbacks. Increases in forest biomass and associated carbon pools would slow the rise in atmospheric carbon dioxide, producing a negative feedback, whereas decreases in forest biomass would have the opposite effect. Uncertainty surrounding these feedbacks is considerable at the global scale, with important implications for global carbon budgets (Luo 2007).

In view of this, it is essential to know whether forests are experiencing changes in productivity and biomass in excess of those typical for their age. Successional forests, those regrowing after disturbances, increase in biomass over time, with the trajectory and duration of this increase varying with forest type (Bormann & Likens 1979; Odum 1969). In the absence of global change, such forests are expected to eventually reach a dynamic equilibrium in which biomass gains from growth and recruitment are balanced by biomass losses from tree death and branchfall, and these old-growth forests thus experience no directional changes in biomass (Odum 1969; Yang, Luo & Finzi 2011). Accordingly, detection of directional changes in biomass in old-growth forests is generally considered evidence of global change influences. When and where such changes are detected, the next critical question concerns

prediction of future net carbon fluxes and ultimate carbon stocks of such altered forests.

Detecting influences of global change on forest biomass is complicated by the fact that biomass is always changing on small spatial scales even in old-growth forests. In old-growth forests, gap-phase dynamics mean that forests in most areas and at most times are increasing modestly in biomass as trees grow, while a few are experiencing large decreases in biomass where one or more large trees have died ('slow in, rapid out', in the words of Körner 2003). It is only on a landscape scale that we expect the biomass of old-growth forests to be at equilibrium in the absence of global change or other temporal climate variability (note that this applies only to biomass; soil carbon stocks, for example, may show long-term directional change even in old-growth forests). Regional and global climate cycles could lead forests to be out of equilibrium even on landscape scales at any given time. Thus, detecting global change in old-growth forests requires a large enough sample size with adequate distribution in space and time to be able to confidently distinguish global change influences from the natural gap-dynamic cycle and cyclical climate variation. The question of what constitutes an adequate sample size has been addressed in the recent literature (Fisher *et al.* 2008; Gloor *et al.* 2009).

Because of the large area of old-growth forests in the tropics, and their high carbon density, potential alteration of their biomass stocks is of particular importance to the global carbon cycle (Saugier, Roy & Mooney 2001; Schimel 1995). Many studies have evaluated changes in biomass stocks in tropical forests using recensuses of field plots (Baker *et al.* 2004; Chave *et al.* 2008; Lewis *et al.* 2009b; Phillips *et al.* 1998, 2008), and some have also examined changes in coarse woody productivity (Lewis *et al.* 2004; Phillips, 1996). Field measurements of tropical forest biomass stocks have focused largely on aboveground woody biomass of trees. Generally biomass is estimated from measurements of trees greater than 10 cm in diameter at breast height (dbh) and from allometric relationships. These trees constitute the vast majority of biomass stocks in these forests, with smaller trees and shrubs, lianas and herbaceous vegetation making up a small minority that few studies have measured directly. Belowground biomass pools (roots, etc.) can also be estimated from allometric relationships, typically by assuming that they are proportional to aboveground biomass. Empirical evidence suggests that this is true on average, although there is considerable variation among sites in the observed proportions (Wolf, Field & Berry 2011; Yang & Luo 2011). More precise methods of estimating above- and belowground biomass rely on destructive techniques that disturb the forest and prohibit repeat measurements and assessments of change. Soil carbon pools are also hypothesised to be affected by global change (Luo 2007; Rustad *et al.* 2001),

but to date there have been few studies of repeated measurement of soil carbon in the tropics.

In this contribution, we address the issues of how to detect and project biomass change in old-growth forests from plot data, focusing on tropical forests. We focus solely on aboveground biomass (hereafter referred to simply as ‘biomass’), the pool for which the most data are available. We first evaluate some key contributions to uncertainty and bias in estimates of biomass change from plot data. We specifically examine the scaling of sampling error with plot area and census interval, and the potential for biases resulting from different kinds of measurement errors and data entry errors and their interaction with error-correction routines. We then discuss alternative approaches to projecting future biomass of old-growth forests, and present a new approach based on Markov chain models of small plot biomass transitions. Throughout, we use the 50-ha forest dynamics plot on Barro Colorado Island (BCI) as a case study. We close with recommendations for future work.

14.2 Estimating biomass change

14.2.1 Sampling errors in biomass change

A major contributor to uncertainty in biomass change estimates from plot data in old-growth forests is sampling error. On small scales, some areas are expected to have strong decreases in biomass due to deaths of big trees, whereas most areas are expected to witness no such mortality and thus will have smaller increases in biomass that reflect tree growth. Samples based on larger plot areas and longer census intervals are expected to encompass more representative distributions of these changes. Quantification of sampling uncertainty is important for developing confidence intervals on estimates of biomass change, and associated tests of whether observed changes are significantly different from zero.

It is important to note that sampling errors are inherently unbiased. A measurement is by definition biased if its expected value, i.e. the mean of the distribution of its values, is different from the true value. For any random sample, the expectation of the sample mean is the true mean. Statements by Fisher *et al.* (2008) and Körner (2009) that the sample mean of biomass change is biased because of the ‘slow in, rapid out’ phenomenon are incorrect and reflect a misunderstanding of the meaning of bias. The ‘slow in, rapid out’ phenomenon can indeed lead to an asymmetric (skewed) sampling distribution, in which the median exceeds the mean, but the mean of this distribution is still the true mean provided the plots are an unbiased sample of the landscape. One real concern is that the ‘slow in, rapid out’ phenomenon could exacerbate biases associated with non-random plot placement across the landscape. For example, biomass change estimates will be biased in the

positive direction if site selection is biased towards locations that experience less disturbance during the census interval (Körner 2009).

Fisher *et al.* (2008) and Gloor *et al.* (2009) recently explored the influence of sampling error on true power to reject the null hypothesis of no change in biomass given the potential for large-scale disturbances. These studies use simulation analyses to explore the importance of clustered disturbances combined with the 'slow in, rapid out' nature of biomass change, and the sample size needed to confidently reject a null hypothesis of no change. The studies come to contrasting conclusions on the sufficiency of available evidence to reject the hypothesis of no change, reflecting two key differences in assumptions. Fisher *et al.* (2008) underestimate the available sample size in time – assuming one-year census intervals, when in fact intervals were more typically 10 years. Fisher *et al.* (2008) also use a flawed procedure to fit the size distribution of disturbance events, and thus almost certainly overestimate the probability of large disturbance events. Gloor *et al.* (2009) corrected these errors, and concluded that sample sizes in area and time were sufficient to demonstrate that average biomass change in 135 forest plots, typically 1 ha or larger, across the Amazon basin is significantly positive, under the assumptions that plots were an unbiased sample of the landscape and that individual plot biomass change estimates were unbiased. It is important to note that these results are sensitive to the frequency of large disturbance events, and that there are very limited existing data relevant to estimating these frequencies.

Quantification of sampling errors is of considerable interest, in part for tests of whether observed changes are significantly different from zero. Here, we first examine how sampling uncertainty scales with plot area and time period for individual plots, an issue that is critical to determining the appropriate weighting when plot size and census interval vary. We then address the issue of sampling uncertainty for mean biomass change in ensembles of plots.

14.2.1.1 *Spatial and temporal scaling of sampling uncertainty for single plots*

Spatial and temporal autocorrelation in biomass change, or its absence, is critical to the scaling of sampling errors in biomass change. In the absence of such autocorrelation, the variance of the observed change in biomass per area is expected to decrease in proportion to $1/(\text{area} \times \text{time})$, because $\text{area} \times \text{time}$ is the effective total sample size. (Therefore, the standard deviation and the coefficient of variation, CV, are expected to decline in proportion to $1/\sqrt{\text{area} \times \text{time}}$.) When spatial and/or temporal autocorrelation is present, however, uncertainty will decrease more slowly with increasing area (for contiguous or nearby plots) and time interval. Previous studies of the spatial scaling of uncertainty in biomass (not biomass change) have found that the

coefficient of variation declines with area to the power -0.43 between 0.05 and 6 ha for biomass of trees >10 cm in Paracou, French Guiana (Wagner *et al.* 2010), and to the power -0.37 between 0.125 and 4 ha for biomass of trees >35 cm in Tapajos, Brazil (reanalysis of the data plotted as Figure 14.4 in Keller *et al.* (2001)). Earlier studies have examined similar questions for basal area (e.g. Higuchi, dos Santos & Jardim 1982). The difference from scaling with a power of -0.5 suggests some spatial autocorrelation in biomass at these scales and sites. Wagner *et al.* (2010) further found that the CV of biomass productivity and biomass losses scaled with area to the power -0.429 and -0.451 , respectively, suggesting that net biomass change would be likely to scale with similar exponents, again reflecting some spatial autocorrelation.

We used the 25-year, 50-ha dataset for the BCI forest dynamics plot to examine the spatial and temporal scaling of uncertainty in biomass change at this site. We found that the decrease in the standard deviation with increasing plot size from 0.025 to 1 ha matched the theoretical expectation if there is no spatial autocorrelation, with the standard error of biomass change declining almost exactly with $1/\sqrt{\text{area}}$, i.e. with area to the power -0.5 (Figure 14.1A). Linear regression of the log-transformed standard deviation on log-transformed area produces an estimated slope of -0.493 (95% CI -0.496 to -0.491). This is consistent with the lack of spatial structure in biomass change at these scales: the semivariogram is flat (results not shown), as is the wavelet power spectrum (Figure 14.2A). Temporal autocorrelation also appeared to be unimportant on the time scales considered, as the standard deviation declined with the inverse square root of census interval in accordance with the theoretical prediction for the case of no autocorrelation (Figure 14.1B).

Bootstrapping over subplots can be used to quantify sampling uncertainty for single plots. Since the biomass change on the plot is known more exactly, this bootstrapping procedure is technically estimating sampling uncertainty associated with the stochastic process operating within this plot (and that could potentially have produced other outcomes) (e.g. Chave *et al.* 2008). When dividing a plot into subplots for the purposes of within-plot bootstrapping, it is essential that the subplot scale be greater than the integral length scale, the scale at which the spatial semivariogram plateaus, i.e. there should be no spatial autocorrelation between subplots. Violation of this could lead to artificially low confidence intervals. On BCI, as Chave *et al.* (2008) previously reported for this and other large plots, the confidence intervals are insensitive to the subplot scale for subplot sizes between 0.025 and 1 ha (Figure 14.2B), consistent with the lack of spatial structure at these scales (Figure 14.2A). The sampling uncertainty for the full 50-ha plot that is estimated by bootstrapping over subplots is exactly consistent with the spatial scaling of sampling uncertainty for smaller areas (Figure 14.1A).

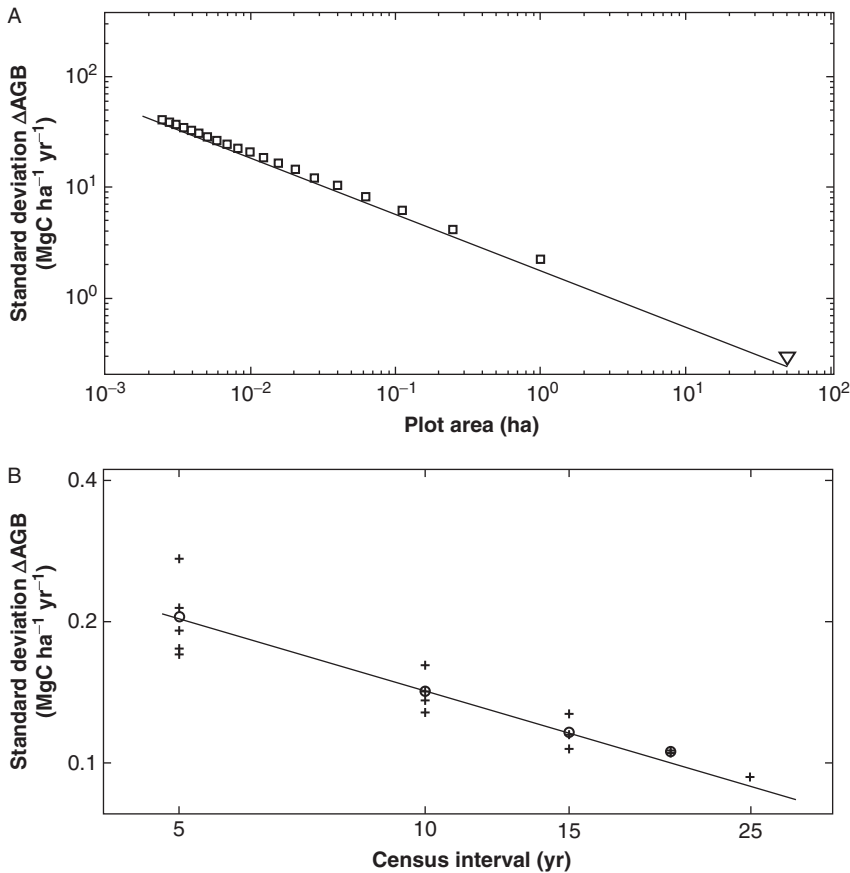


Figure 14.1 Sampling uncertainty in estimated biomass change as a function of plot area and census interval for the 50-ha plot on Barro Colorado Island, Panama, quantified here as the standard deviation of the biomass change over replicate plots and/or census intervals of the relevant size. (A) Observed standard deviations for square plots of different area (squares) and the standard deviation of the estimate for the whole plot obtained from bootstrapping over subplots (triangle) for the 2005–2010 census interval, compared with the expected decline with square root of area (line). (B) Standard deviations for the entire 50-ha plot from bootstrapping over 10×10 m subplots for census intervals of different length using the six censuses between 1985 and 2010 (plus signs), and the average of the standard deviations for any census interval (circles), compared with the expected decline with the square root of time (line).

One perhaps obvious limitation of plot-based assessments of the spatial scaling of sampling error in biomass change is that they provide no information on how error scales over larger areas than the largest sample taken. This is because differences in habitat, land-use history, climate or other factors may exist beyond the sampled area, which could cause the variogram to rise at

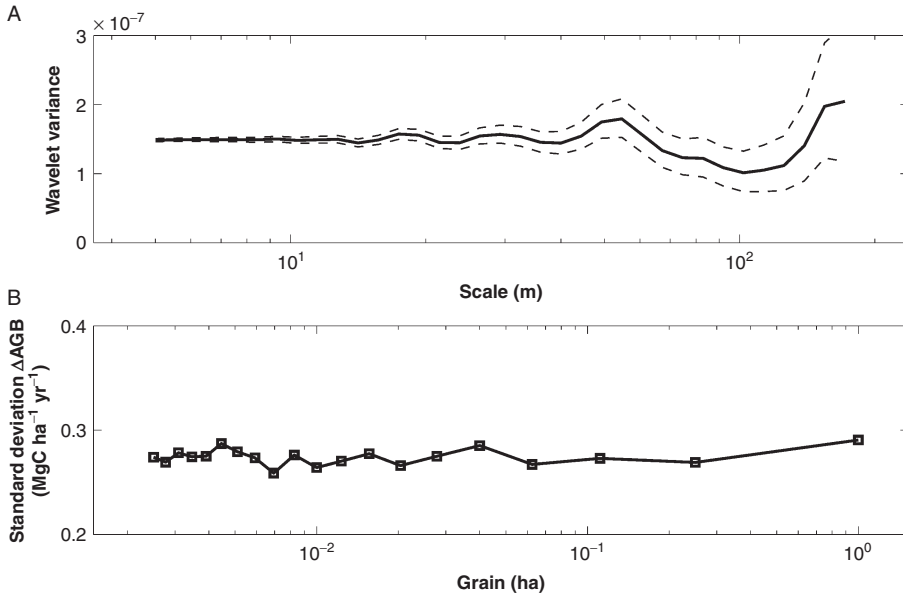


Figure 14.2 The spatial structure of biomass change on the BCI 50-ha plot. (A) The wavelet power spectrum, with 95% confidence intervals (dashed line), shows little significant spatial structure or autocorrelation. (B) The bootstrapped standard deviation (1000 bootstraps) of biomass change estimates on BCI is insensitive to the spatial grain over which bootstrapping is done, as expected given the lack of spatial structure at these scales.

a different rate than within the sampled area. For example, although we found no spatial autocorrelation of biomass change within the BCI 50-ha plot, we expect that there might be spatial autocorrelation at larger scales within central Panama due to spatially structured variation in rainfall, soil type and past land-use. We also expect that other sites of similar scale might show very different patterns of spatial and temporal scaling of sampling errors. In particular, sites that have experienced recent large-scale patchy disturbances (unlike BCI) might show significant spatial and temporal autocorrelation in biomass and biomass change, and thus slower declines in sampling error with area and time. Parallel issues regarding how patterns change with spatial scale have long been a focus of research on diversity; e.g. the distinction between alpha, beta and gamma diversity (MacArthur & Wilson 1967; Ricklefs 2004).

14.2.1.2 Sampling uncertainty for ensembles of plots

If samples are available from different plots within a landscape or region, it becomes possible to estimate landscape biomass or biomass change within an

appropriate statistical framework. Biomass change estimates may come from plots of different areas and census intervals of different lengths. If the plots are randomly situated in the landscape, then the best unbiased estimate of the overall landscape biomass change is obtained by taking a weighted mean of the individual site estimates, where each weight is proportional to the reciprocal of the variance of the corresponding site estimate. Let $X(a,t)$ be a random variable representing the biomass estimate at a randomly chosen site of area a and census interval t . Then the variance of $X(a,t)$ is

$$\text{var}(X(a,t)) = \frac{1}{t} \left(\sigma^2 + \frac{\tau^2}{a} \right)$$

where σ^2 is the between-site (landscape) variance and τ^2 is the within-site variance (e.g. between individual hectares within the site). In practice, the variances may be difficult to estimate. The formula above assumes that temporal autocorrelation in biomass change can be ignored. If temporal autocorrelation is substantial, then plots should be weighted more evenly with respect to census interval, with the exact weighting depending on the form of temporal autocorrelation.

The proper weighting of plots varying in area thus depends critically on the relative size of the variance within sites (τ^2) and the variance among sites (σ^2). In the limit that landscape variance is much larger than within-site variance (very heterogeneous landscapes), the weighting formula reduces to simply t , meaning equal weighting if the census intervals are equal across sites, regardless of plot area. In the limit that landscape variance is much smaller than within-site variance and within-site variance is identical across plots (very homogeneous landscapes), the weighting formula reduces to ta . Intermediate situations call for weighting by the product of time and of area to a power between zero and one, e.g. $t\sqrt{a}$.

The choice of weightings can make a small but noticeable difference in the mean change across plots (Table 14.1), emphasising the importance of choosing an appropriate weighting scheme or at least testing the robustness of results to different plausible weighting schemes (as done by Baker *et al.* 2004). Of course, if information on underlying landscape heterogeneity is available and if the available plots are not proportionally representative of this heterogeneity, weighting should also take account of this, if possible. De Grijter *et al.* (2006) provides an excellent treatment of the broader issues surrounding sampling design in environmental monitoring.

One approach to determining the best weighting for biomass change estimates is to search empirically for the weighting that minimises trends in residuals plots of site biomass change versus site area and census interval (Phillips *et al.* 2009; Lewis *et al.* 2009b). Specifically, one graphs the product of

weights and squared residuals vs area and vs time. This approach is in principle excellent; however, to produce useful results it requires sufficiently large numbers of sites of different areas and census intervals, a condition that is rarely met in practice. (For example, the vast majority of plots used in the abovementioned papers are 1 ha in area, and there are too few plots at other areas to gain much insight into the best weighting by area.) Combining the datasets from all the references in Table 14.1 provides a somewhat better basis for choosing a weighting with area, and suggests that the ideal weighting would be the product of time and of area to a power between 0 and 1. Weighting by t or ta leads to significant trends in the residuals plots, while weighting by $t\sqrt{a}$ (among others) produces no significant trends.

Once the appropriate weighting has been determined, confidence intervals for sampling uncertainty for an ensemble of sites can be estimated by bootstrapping over plots or sites (e.g. Phillips *et al.* 2009). If multiple plot data are available, it is possible to bootstrap at both the within-plot and between-plot levels to produce a confidence interval on the landscape biomass change estimate, providing that appropriate weighting schemes are used on the between-plot bootstrapped data. It is important to note that this only captures uncertainty due to sampling error.

14.2.2 Influences of measurement errors and data 'cleaning' procedures

Measurement errors are ubiquitous and inescapable in field data collection. Variation in the height of the measuring tape or caliper on the stem and variation in the hydration status of the stem introduce random errors into stem diameter measurements. Further, error in positioning the measuring tape to be exactly perpendicular to the long axis of the stem can lead to systematic overestimation of diameter. Additional and potentially larger errors enter during data recording and data entry, including digit switching, missed or added digits, and switching data between two trees. Careful field and data entry procedures can reduce the incidence of such errors, but never completely eliminate them. All these errors, hereafter referred to simply as measurement errors, introduce uncertainty into estimates of standing biomass and biomass change. Further, because of the non-linear relationship between diameter and biomass, random errors in diameter can and do induce systematic errors in biomass. In tropical forests, trees with buttresses or other types of irregular trunks present additional challenges for accurate and precise measurements of biomass and biomass growth (Clark 2002; Phillips *et al.* 2002; Sheil 1995).

Most studies have attempted to minimise the influence of measurement errors and changing height of measurement on buttressed trees through what we will call data cleaning procedures. These typically include screening data

Table 14.1 Estimated mean change in aboveground biomass of trees 10 cm or more in diameter. Estimates are for different datasets under alternative schemes for weighting data points as a function of plot area and census interval, with 95% confidence intervals for sampling uncertainty only; that is, confidence intervals based on bootstrapping over plots (or sites in Phillips et al. 1998). If there is no spatial autocorrelation in biomass change, the best unbiased estimator of overall biomass change is based on weighting by area \times time (assuming plots are an unbiased sample of the landscape). If there is strong spatial structure in biomass change such that landscape variance among plots greatly exceeds sampling variance within plots, then the best unbiased estimator is based on weighting by time (see text). Numbers were recalculated from the datasets provided with the original publications, to be in units of $\text{MgC ha}^{-1} \text{ yr}^{-1}$, with carbon stocks calculated as 47% of dry biomass, and to include only trees greater than or equal to 10 cm in diameter. Note that numbers in the original publications were in some cases based on analyses assuming carbon was 50% dry biomass; were for total biomass, not just carbon; included estimated carbon stocks in lianas, small trees and belowground biomass; involved different weightings; and/or include other sources of error in confidence intervals.

Publication	Region	Dates	Number of plots	Total ha-yrs	Tree AGB change ($\text{MgC ha}^{-1} \text{ yr}^{-1}$)			
					Unweighted	Weighted by time	Weighted by time \times area	Weighted by time \times sqrt(area)
Phillips et al. 1998	Pantropic	1947–1997	68	2350	0.33 (0.15,0.52)	0.18 (0.02,0.34)	0.12 (-0.10,0.31)	0.15 (0.00,0.30)
Phillips et al. 1998	Neotropics	1956–1997	50	1621	0.48 (0.26,0.71)	0.41 (0.23,0.57)	0.15 (-0.11,0.35)	0.26 (0.07,0.45)
Phillips et al. 1998	Lowland Neotropics	1956–1997	45	1577	0.46 (0.21,0.71)	0.35 (0.17,0.54)	0.14 (-0.12,0.35)	0.23 (0.03,0.43)
Phillips et al. 1998	Amazon	1956–1997	40	877	0.41 (0.18,0.67)	0.38 (0.19,0.56)	0.24 (0.10,0.43)	0.31 (0.15,0.48)
Baker et al. 2004	Amazon	1980–2003	59	864	0.57 (0.37,0.77)	0.50 (0.28,0.70)	0.46 (0.25,0.65)	0.48 (0.28,0.68)
Chave et al. 2008	Pantropic	1985–2005	10	3156	0.22 (-0.02,0.45)	0.23 (-0.03,0.51)	0.24 (-0.06,0.56)	0.24 (-0.04,0.54)
Phillips et al. 2009	Amazon	1972–2006	123	2410	0.44 (0.30,0.57)	0.39 (0.28,0.50)	0.45 (0.33,0.56)	0.41 (0.31,0.51)

Phillips <i>et al.</i> 2009	Amazon	1972–2007	136	2607	0.29 (0.14,0.44)	0.35 (0.23,0.47)	0.42 (0.30,0.53)	0.37 (0.26,0.49)
Lewis <i>et al.</i> 2009b	Africa – raw ¹	1968–2007	79	1206	0.54 (0.07,0.98)	0.54 (0.19,0.90)	0.63 (0.27,0.94)	0.57 (0.25,0.89)
Lewis <i>et al.</i> 2009b	Africa – corrected ¹	1968–2007	79	1206	0.60 (0.12,1.05)	0.66 (0.32,0.99)	0.74 (0.37,1.05)	0.68 (0.35,0.99)
Lewis <i>et al.</i> 2009b	Africa – mean ¹	1968–2007	79	1206	0.59 (0.11,1.02)	0.64 (0.31,0.97)	0.75 (0.37,1.06)	0.67 (0.35,0.99)
Lewis <i>et al.</i> 2009b	Africa – perturbed ¹	1968–2007	79	1206	0.55 (0.11,0.95)	0.59 (0.28,0.89)	0.67 (0.33,0.95)	0.61 (0.32,0.90)
Lewis <i>et al.</i> 2009b	Pantropic ²	1947–2007	156	5483	0.53 (0.27,0.76)	0.49 (0.30,0.67)	0.35 (0.15,0.58)	0.43 (0.27,0.60)
All combined	Pantropic ³	1947–2007	251	8243	0.36 (0.18,0.53)	0.34 (0.23,0.47)	0.32 (0.17,0.47)	0.34 (0.23,0.45)

¹ Lewis *et al.* (2009b) presented four different sets of results corresponding to four different procedures for dealing with changes in the point of measurement.

² Lewis *et al.* (2009b) report Pantropical results obtained by combining the results of Baker *et al.* (2004) for the Amazon, Lewis *et al.* (2009b) Africa corrected, the undisturbed Chave *et al.* (2008) (excluding Lenda and Egoro to avoid double-counting, as these are also in Lewis *et al.* 2009b) and the Phillips *et al.* (1998) Asia plots.

³ Our Pantropical compilation includes the Lewis *et al.* (2009b) Africa raw data, the Phillips *et al.* (2009) Amazon data through 2007, the undisturbed Chave *et al.* (2008) data (excluding the Lenda and Egoro plots to avoid double-counting), and the Phillips *et al.* (1998) non-Amaزون plots.

for outliers that are considered so unlikely as to almost certainly be errors, and substituting a corrected value for these outliers; we will refer to these steps as data screening and gap-filling, respectively. In addition, most studies in which points of diameter measurement change on some trees between censuses have devised algorithms to 'correct' the diameter change on these trees. The data cleaning steps that are taken typically seem reasonable, but multiple alternative procedures meet the 'reasonable' test. Where authors have, to their credit, examined multiple alternatives, they often find that these produce different results (Chave *et al.* 2003; Lewis *et al.* 2009a). Such sensitivity analyses are laudable, but do not shed light on which alternative is best. Choice among data cleaning procedures should ideally be based on analyses of the potential for the data cleaning itself to introduce errors and biases. For studies of forest change, systematic errors are arguably of more concern than random errors.

To demonstrate the potential influences of different data cleaning procedures on estimates of biomass change, we estimated biomass change over two census intervals on BCI using a variety of procedures to deal with extreme outliers, hemiepiphytes (strangler figs) and trees whose point of measurement changed. The estimated aboveground biomass (AGB) change between 1985 and 1990 is greatly affected by the choice of data cleaning procedures: it varies from -0.61 (95% confidence interval, CI, $-1.22, -0.05$) $\text{MgC ha}^{-1} \text{yr}^{-1}$ if the raw 'uncorrected' data are analysed, to $+1.31$ (0.83, 1.70) if using a gap-filling procedure for AGB-change outliers and stems that have point-of-measurement changes (Table 14.2). The high sensitivity to data cleaning procedures for this census interval in part reflects the large number of problematic cases in this census interval, owing to changes in details of census procedures (especially with respect to buttressed trees) and changes in field personnel between these two censuses. The estimated AGB change between 2005 and 2010, when detailed census procedures and supervisory personnel were consistent across both censuses, is considerably less sensitive to the data correction method used, but still varies from -0.47 ($-0.98, -0.08$) to -0.07 ($-0.54, 0.27$) $\text{MgC ha}^{-1} \text{yr}^{-1}$ (Table 14.2). In the earlier census interval, the choice of data cleaning procedure makes the difference between significant biomass decline and significant biomass increase. In the later interval, it makes a difference between statistically significant biomass decline and no significant biomass change.

Clearly, then, procedures for data screening, gap-filling and modelling growth in trees with changing points of measurement are critically important to estimating biomass change in tropical forests. Many previous authors have discussed the potential qualitative impact of different types of measurement errors or measurement procedures (Clark 2002; Phillips *et al.* 2002; Sheil 1995). Here, we focus on just two issues – issues that our analyses show are

Table 14.2 Effects of alternative data cleaning routines on AGB change estimates (95% CI) for the BCI 50-ha plot for 1985–1990 and 2005–2010. Census methodology and supervisory personnel changed somewhat between the 1985 and 1990 census, and not at all between 2005 and 2010. Plot census methods are described in Condit (1998). See Appendix 14.1 for details on the AGB calculations. Three classes of problematic measurements were screened: (1) hemiepiphytes (strangler figs) for which diameter measurements do not reflect basal area; (2) stems that were extreme outliers in biomass change; and (3) stems whose height of measurement changed. Biomass changes for hemiepiphytes were simply set to zero. Biomass changes for the other classes of screened individuals were either set to zero or changed to the value obtained from a biomass growth model fitted to non-screened data.

Screened stems and their treatment				
	\DeltaAGB	POM	\DeltaAGB 1985–1990	\DeltaAGB 2005–2010
Hemiepiphytes ¹	outliers ²	change ³	(MgC ha ⁻¹ yr ⁻¹)	(MgC ha ⁻¹ yr ⁻¹)
\DeltaAGB =0			-0.61 (-1.22 -0.05)	-0.46 (-1.04 -0.08)
\DeltaAGB =0	\DeltaAGB =0		-0.58 (-1.26 -0.04)	-0.47 (-0.98 -0.08)
\DeltaAGB =0	Model		0.04 (-0.48 0.47)	-0.43 (-0.99 -0.08)
	growth ⁴		0.13 (-0.31 0.55)	-0.43 (-0.89 -0.06)
\DeltaAGB =0	\DeltaAGB =0	\DeltaAGB =0	0.49 (0.04 0.89)	-0.28 (-0.78 0.07)
\DeltaAGB =0	Model	Model	1.31 (0.83 1.70)	-0.07 (-0.54 0.27)
	growth ⁴	growth ⁴		

¹ Hemiepiphytes encompass six species of strangler figs: *Ficus bullenei*, *F. citrifolia*, *F. colubrinae*, *F. costaricana*, *F. pertusa* and *F. popenoei*. In total, there were 36 individuals of these species that were alive in one or more censuses between 1985 and 2010, and between 12 and 20 alive in any given census.

² Stems that had a rate of change in biomass (increase or decrease) of more than 2 MgC yr⁻¹, and that were not recorded as stem breaks or point of measurement changes.

³ Change in the point of measurement between the two censuses greater than 0.2 m.

⁴ AGB change substituted with the value obtained from the fits of non-screened trees to a third-order polynomial model $Y = a_3X^3 + a_2X^2 + a_1X + a_0$ where $Y = \log(AGB_{t+1} - AGB_t)$ and $X = \log(AGB_t)$. All individuals of all species (except the hemiepiphytes) were combined in this model; individuals were binned into 50 classes of equal numbers of elements, and the logs of the class-wise arithmetic means were regressed against each other to fit the coefficients a_i .

particularly important to determination of biomass change in this forest (Table 14.2). First, we examine the impact of ordinary measurement errors and data cleaning procedures and their interaction on estimates of biomass and biomass change. Second, we discuss issues surrounding measurement and modelling of growth in buttressed trees, or more generally, all trees whose diameter is measured above the standard 1.3 m and whose height of measurement may change substantially over time. In both cases, we focus

especially on the potential to introduce systematic errors (i.e. biases) in estimates of biomass and biomass change.

14.2.2.1 *Ordinary measurement errors and data cleaning*

Most past studies of biomass change have used some sort of data cleaning procedure to identify presumed erroneous values and 'correct' them. Past approaches to error identification most typically involved absolute cutoffs for diameter growth rates, with more extreme values considered unrealistic and thus necessarily erroneous. For example, diameter increases of more than 35 mm yr^{-1} , 40 mm yr^{-1} or 45 mm yr^{-1} , or decreases of more than 5 mm yr^{-1} , have been flagged for correction (Chave *et al.* 2003, 2008; Lewis *et al.* 2009b; Phillips *et al.* 2009). Where multiple census data are available, these presumed errors are corrected by interpolation or extrapolation where possible. In other cases, they are set to the mean (Chave *et al.* 2008; Phillips *et al.* 2009) or median (Lewis *et al.* 2009b) diameter growth rates for trees in the same diameter class. Despite the ubiquity of such procedures, we know of no study that has systematically evaluated their potential influence on estimates of forest biomass change. On first principles, these procedures may well reduce certain kinds of random and systematic errors – but as we show below, this reduction may come at the cost of the introduction of other systematic errors. How large are the systematic errors introduced by data cleaning? Is data cleaning a worthwhile procedure given potential trade-offs between correcting one kind of error and introducing another?

A key problem of error identification is that it is difficult, if not impossible, to design error detection criteria that exactly balance the correction of positive and negative errors in diameter growth, and thus avoid inducing systematic biases. It is often easier to identify large negative errors, because large decreases in measured diameters are biologically implausible unless there are concurrent observations of stem breaks. In contrast, large positive errors may go undetected because it is possible for some individuals to grow very quickly. If measurement errors are symmetric, but negative errors are more likely to be detected and corrected, then this introduces a positive bias on biomass change estimates. Identifying appropriate thresholds to balance positive and negative error correction in diameter growth exactly is possible in principle but very difficult in practice. Thus, such thresholds will almost inevitably introduce systematic errors in estimates of biomass change.

A key problem in gap-filling erroneous measurements is to ensure that the corrections do not introduce systematic errors in statistics of interest. There is a large existing literature on gap-filling methods and their relative performance in terms of bias and root mean square error, RMSE (e.g. Moffat *et al.* 2007), including analyses specific to individual tree growth (Sironen, Kangas & Maltamo 2010; Sironen *et al.* 2008). Nearest-neighbour imputation methods,

in which the missing value is substituted with the mean from the k nearest neighbours as defined by distance in a space of traits of interest (e.g. diameter, forest type), emerge as particularly useful, with minimal bias and RMSE (Sironen, Kangas & Maltamo 2010). The most common gap-filling method applied in tropical biomass studies – substituting the mean diameter growth for similarly sized trees – is in some sense a very limited application of this method, in which size class is the only distance metric considered. However, gap-filling with mean diameter growth for reference populations is problematic when the goal is calculation of biomass growth, because of the non-linear relationship between diameter and biomass and the skewed distribution of growth rates among individuals. Thus, for example, gap-filling with mean diameter growth leads to systematic 10% overestimation of individual tree biomass growth in a test with BCI data, even though this method produces unbiased estimates of diameter growth. In contrast, substituting with mean biomass growth will produce unbiased estimates of biomass growth – but systematically underestimate diameter growth. Because mean growth is typically larger than median growth, substituting median biomass growth will underestimate biomass gain (e.g. by 40% in a test with BCI data). The use of median diameter growth could overestimate or underestimate biomass growth, depending on the statistics of the target population. In sum, the gap-filling algorithms that have been employed to date in tropical forest biomass change studies have almost certainly introduced systematic errors that bias resulting estimates of total biomass change.

The importance of the resulting systematic errors will vary depending not only on the algorithm, but also on patterns of diameter growth at the site. Here, we examine what biases result from commonly used (1) error detection and (2) gap-filling algorithms when applied to the BCI data for 2005–2010.

First, we consider the effects of absolute diameter growth thresholds for error identification. On BCI, the 30 stems that decreased in diameter by less than 5 mm yr^{-1} between 2005 and 2010 together account for a decrease of $0.153 \text{ MgC ha}^{-1} \text{ yr}^{-1}$, whereas the 25 stems that grew by more than 40 mm yr^{-1} together contribute an increase of $0.133 \text{ MgC ha}^{-1} \text{ yr}^{-1}$, together contributing net biomass change of $-0.019 \text{ MgC ha}^{-1} \text{ yr}^{-1}$. (These calculations exclude stems that had a change in point of measurement or a break below the measuring point.) Changing all their growth rates to the mean biomass growth rates for similar diameter stems increases net biomass change by $0.019 \text{ MgC ha}^{-1} \text{ yr}^{-1}$.

Second, we examine the most commonly used gap-filling procedure – mean diameter growth. As mentioned previously, this tends to overestimate mean biomass growth of individual trees on BCI by 10%. Suppose that this correction is applied to 1% of trees (Phillips *et al.* 2009 apply such a correction to 0.9% of trees in their analyses). Applying this correction to 1% of stems on BCI

upwardly biases biomass growth estimates by less than $0.005 \text{ MgC ha}^{-1} \text{ yr}^{-1}$, assuming no bias in error detection. Thus, on BCI, unbalanced error detection is more problematic than biased gap-filling algorithms in terms of the size of resulting biases in biomass change, but both overall biases are relatively small. This suggests, consistent with the results in Table 14.2, that data cleaning for trees whose diameter is measured at the standard height is not a major source of systematic errors at least for the BCI 2005 and 2010 census data (although it may be important in other cases, e.g. the BCI 1985–1990 data). (Trees measured at non-standard heights, which we examine in the next section, appear to be a much bigger source of errors.)

Although effects on BCI are modest, we argue that there remains a need for improvement in data cleaning procedures for studies of biomass change. There are three distinct types of approaches that would yield unbiased estimates of biomass changes. The first approach would be to apply unbiased error detection and gap-filling algorithms. This approach could draw on the large literature on such issues in forestry and other disciplines (Moffat *et al.* 2007; Sironen *et al.* 2010). Analyses should specifically evaluate bias (e.g. Sironen *et al.* 2010). Application of these algorithms, especially for error detection, will have to be tailored to individual sites and their growth patterns. A second approach would be to analyse biomass change using Bayesian methods that explicitly included probability distributions of measurement errors, and explicitly modelled observed growth as the convolution of true growth and measurement errors. Such models would greatly benefit from incorporation of data that specifically constrained the measurement error distribution, such as remeasurement data. Metcalf *et al.* (2009) provide an excellent example of this approach, applied to analyses of tree growth. A third approach would be to eschew data cleaning altogether, and instead quantify the impact of measurement errors on statistics of interest, and then correct those statistics accordingly after they are calculated from uncorrected data. This last approach is in many ways the simplest, and should be successful in eliminating systematic errors. It will, however, leave potentially large random errors.

We now apply this last approach to BCI, where a large dataset on remeasurements of the same stems allows us to quantitatively assess the impacts of measurement errors on biomass. In the 1995, 2000 and 2005 censuses, diameters of 1562 randomly chosen stems were independently remeasured within 30 days of the original measurement. Rüger *et al.* (2011) fitted this error distribution with a sum of two normal distributions (both centred at zero; these errors were purely random not systematic). The first distribution, which has 97.24% of the weight, describes small errors that are proportional to tree diameter (standard deviation $\text{sd} = 0.927 \text{ mm} + 0.0038 \cdot \text{dbh} \text{ mm}$); the second describes larger errors that are independent of diameter ($\text{sd} = 25.6 \text{ mm}$). We

used a Monte Carlo approach to assess the impact of such measurement errors on biomass and biomass change. In particular, we assumed that the 2005 and 2010 BCI census data represent the true diameters, and we examined how applying additional measurement errors drawn from the measured distribution of measurement errors changed estimates of biomass and biomass change. We found that adding such measurement errors led to slight overestimation of biomass, by an average of 0.14% (bootstrapped 95% CI 0.07, 0.21), with no significant effect on biomass change. Thus, for BCI at least, simply ignoring all measurement errors, and leaving data uncorrected, is expected to have a trivial *systematic* impact on estimates of biomass and biomass change – although the uncorrected measurement errors will introduce random errors. Clearly, if measurement error rates were higher, as they may be at some other sites, the impact of measurement errors alone would be larger, and may induce larger systematic errors. For example, if the dbh measurements of 1% of stems in the BCI data have a pair of adjacent digits switched, this results in 1.7% systematic overestimation of biomass. One could quantify the resulting systematic errors through exercises such as these to correct estimates of total biomass and total biomass change calculated from uncorrected individual measurements.

14.2.2.2 *The special challenge of buttressed trees*

One of the greatest potential sources of error in estimates of biomass change is the measurement and analysis of buttressed trees (Clark 2002; Sheil 1995). We use ‘buttressed trees’ to refer to all trees whose diameters are measured at heights above 1.5 m because of buttresses or irregular trunks, and whose heights of measurement are likely to increase over time. The standard measurement height is 1.3 m, and stems with small irregularities only in this area are measured slightly above or below the standard point (1–1.5 m). Thus, we chose 1.5 m as a threshold to capture mainly trees with buttresses or irregular trunks. Trees measured at heights above 1.5 m constituted 59% of estimated tree biomass on BCI in the 2010 census, although these trees represented just 1.4% of stems. Thus, estimates of biomass change and productivity for BCI are very sensitive to the algorithms used to calculate biomass changes for these trees.

Diameter–biomass relationships are likely to differ for buttressed trees, yet these differences are not reflected in current allometric equations. Individual tree biomass is typically estimated from allometric equations relating diameter, wood density and sometimes tree height to biomass, with diameter measured either at 1.3 m height or ‘above buttresses’ (Chave *et al.* 2005). Because trunk diameter generally declines (i.e. tapers) with increasing height, we would expect that trees whose diameter is measured at a height above 1.3 m will have smaller diameters for the same biomass, or equivalently, higher biomass for the same diameter. Consequently, biomass–diameter

relationships for buttressed trees are expected to deviate systematically from those for non-buttressed trees, when the diameters in the former case are measured above buttresses and above 1.3 m height, while diameters in the latter case are measured exactly at 1.3 m height. Surprisingly, we know of no study that has tested for such systematic differences, nor any published dataset that would allow such tests to be made.

As a consequence, buttressed trees represent a large potential source of systematic error in estimates of biomass and biomass change. The application of the same biomass allometry equations to buttressed and unbuttressed trees is likely to lead to systematic underestimation of biomass in buttressed trees, and systematic overestimation in unbuttressed trees. These two opposite types of errors will cancel exactly at the plot level if the frequency of buttressed trees in the plot matches the frequency of buttressed trees in the dataset used to develop the biomass allometry equations, and if diameters of buttressed trees are measured in the same way in both datasets. Plot-level biomass will tend to be systematically overestimated in stands with lower frequencies of buttressed trees, and systematically underestimated in stands with higher frequencies of buttressed trees, assuming diameters of buttressed trees are measured in a consistent manner across the plots and in the biomass calibration dataset.

The lack of standard methods for determining measurement heights on buttressed trees creates additional potential for systematic error. For example, if diameters of buttressed trees are measured at greater heights in the plot than in the biomass calibration dataset, then biomass will be systematically underestimated even if the frequency of buttressed trees is identical. Such differences in measurement methods for buttressed trees are quite likely. For one-time measurements such as those for calibrating biomass equations, diameters are typically measured directly above buttresses, which presumably means within 10–20 cm of the top of buttresses. In permanent plots where repeat censuses are planned, diameters are typically measured at greater heights to ensure that the measurement point will remain above buttresses in the next census; an oft-used rule is to measure 50 cm above the top of the buttress (Condit 1998). In general, there is no quantitative, generally accepted, standard definition of the top of the buttress, or of the distance above the top of the buttress at which diameters should be measured, and thus it is to be expected that different field teams and technicians would make diameter measurements at different heights given the same tree form. The emergence of a universal standard (perhaps 50 cm above as in Condit 1998), applied to both biomass calibration equations and plot censuses, would remove this potential source of systematic error.

On BCI, the proportion of trees measured at heights above 1.5 m has increased greatly over time (Table 14.3). We know that some of these shifts reflect changes in measurement procedures: in the first census, all trees were

Table 14.3 *Number, frequency, and proportion estimated aboveground biomass of tree stems measured above 1.5 m height in the Barro Colorado Island forest dynamics plots in different censuses.*

Census year	Stems with height of measurement >1.5 m			
	Number	Proportion of total stems ≥ 1 cm	Proportion of total stems ≥ 10 cm	Proportion of total biomass ¹
1982	0	0.00%	0.0%	0.0%
1985	1302	0.48%	6.0%	28.4%
1990	2076	0.72%	9.3%	48.5%
1995	2456	0.92%	10.8%	53.0%
2000	2786	1.12%	12.3%	53.7%
2005	2872	1.17%	12.8%	54.3%
2010	3373	1.37%	14.8%	58.6%

¹ Here biomass was calculated by substituting the observed maximum height diameter measurement directly into the biomass allometry equation (no data cleaning, no taper).

measured at 1.3 m even if this was around buttresses, whereas in the second census buttressed trees were measured directly above buttresses, and in the third census, the protocol was changed to place measurement points on buttressed trees high enough that they would be expected to remain above buttresses in the following census even after growth. It is more difficult to interpret the continued, more modest, increases in the proportion of stems measured at height above 1.5 m between 1990 and 2010. These increases are likely in part to reflect increasing conservatism on the part of the field crew, as they sought for ever more round points on the bole, or heights that are ever more certain not to be affected by buttresses in the subsequent census, as well as the fact that measurement points are moved up but never down. However, there is also the possibility that there has been some real increase in buttressed trees, and/or heights of buttresses on trees, on BCI. Regardless of the causes of the increase in height of measurement, the increasing frequency of diameter measurements at heights above 1.5 m would be expected to introduce a negative bias on estimated biomass change on BCI, because of the way the diameter measurements interact with the biomass allometry equation. A larger and larger proportion of trees fall into the category of systematic underestimation of biomass, while an ever smaller proportion fall into the category of systematic overestimation of biomass.

In principle, it should be possible to correct for the biases in biomass and biomass change that are associated with measurements of diameters at heights above 1.3 m. One possibility would be to replace 'diameter at 1.3 m or above buttresses' with 'diameter at 1.3 m, measured or estimated based on

taper' in biomass allometry equations. Taper equations, such as those used by Metcalf *et al.* (2009), could be used to calculate equivalent diameters at 1.3 m height from diameters measured above buttresses. Given the right taper functions, we would expect that biomass–diameter datasets constructed under this definition would show no systematic differences between buttressed and non-buttressed trees. If there were no systematic differences, then one could construct and apply biomass allometry equations without regard to the frequency of buttressed trees. Indeed, in this case, equations could be constructed simply from data on non-buttressed trees, which might be the more practical approach, as older datasets on biomass of buttressed trees do not necessarily include necessary information on the height of diameter measurement for buttressed trees.

We use the BCI dataset for 2005–2010 to illustrate the potential impact of measurement practices for buttressed trees on estimates of biomass and biomass change (Table 14.4). In the 2010 census, 962 stems were measured at two heights. If we use the diameter measurement at the lower height in the biomass allometry equation, total biomass is 4.2 MgC ha⁻¹ larger than if we use the measurement at the greater height (Table 14.4). Inferring diameter at 1.3 m based on taper should in principle make the biomass estimates less sensitive to the exact measurement height, decreasing the difference between these estimates. We used the taper equation $DBH = De^{\alpha(h - 1.3)}$, where D is the measured diameter and h is the height of the measurement, a function previously fitted to empirical data on diameters in similar height ranges for five tropical tree species by Metcalf *et al.* (2009), and values of α that spanned the range for these five species. At higher taper values, biomass estimates were substantially higher (Table 14.4). Biomass estimates were essentially identical between minimum and maximum height diameter measurements for $\alpha = 0.055$, which suggests that this value might best represent average taper in these trees. However, use of realistic taper functions and resulting estimates of equivalent diameters at 1.3 m height with currently available biomass equations (themselves based on dbh or diameter 'above buttresses') will invariably lead to systematic overestimation of biomass, with the degree of overestimation dependent on the relative representation of diameter measurements above buttresses in the biomass calibration datasets.

The treatment of buttressed trees had an even bigger relative effect on estimates of biomass change for BCI (Table 14.4). When we used measured diameters directly in the biomass equation (taper = 0 in Table 14.4), estimates of biomass change varied from -0.56 to 0.31 MgC ha⁻¹ yr⁻¹ depending on the choice of point of measurement (POM): the largest decrease was found when the minimum POM was used in each census, and the largest increase when the same POM was used (where available) and the maximum POM otherwise. Using the diameter from the same POM across two censuses provides better estimates

Table 14.4 *Effect of treatment of diameters measured at non-standard heights on estimates of aboveground tree biomass and biomass change on Barro Colorado Island, Panama. Diameter measurements were available at two (or rarely more) measurement heights for 948 stems in 2005 and 962 stems in 2010 (less than 0.4% of all stems in each census), generally in cases where the measurement point was being moved upwards to ensure that it would remain above buttresses in the next census. The standard treatment for biomass in most studies is to use the lowest available good diameter measurement above buttresses or irregularities (here ‘minimum’), and to insert this diameter measurement directly into the allometry equations (here taper = 0). The standard for estimates of biomass change is to use the same height of measurement across the two censuses if available, and the lowest good measurement when there are multiple options (here ‘same and min’). The default in the BCI database is always to use the maximum diameter measurement available (‘maximum’). Alternatively, a taper equation can be used to estimate equivalent diameter at 1.3 m height, and this equivalent diameter can be used in the biomass equation. We use the taper equation $D_{1.3} = D_i e^{-\alpha(h_i - 1.3)}$, which Metcalf et al. (2009) previously fitted to empirical data on diameters in similar height ranges for five tropical tree species; values of α are chosen to span the range for these five species. No other data cleaning was done. Details of methods for calculating biomass are given in Appendix 14.1.*

POM choice	Taper parameter (α , units of m^{-1})					
	0	0.01	0.02	0.03	0.06	0.12
AGB ($MgC\ ha^{-1}$) in 2010						
Minimum ¹	147.2	153.0	159.3	166.2	190.8	262.3
Maximum ²	143.0	149.4	156.4	164.0	191.3	271.6
Δ AGB 2005–2010 ($MgC\ ha^{-1}\ yr^{-1}$)						
Minimum ¹	-0.559	-0.458	-0.340	-0.206	0.322	2.171
Maximum ²	-0.463	-0.389	-0.307	-0.216	0.123	1.238
Same and min ³	0.217	0.197	0.175	0.152	0.074	-0.122
Same and max ⁴	0.312	0.275	0.234	0.188	0.016	-0.521

¹ Where diameter measurements were available from multiple heights in a given census, the diameter with the *minimum* height of measurement was used. Under this rule, 1540 stems had a change in diameter measurement height between 2005 and 2010.

² Where diameter measurements were available from multiple heights in a given census, the diameter with the *maximum* height of measurement was used. Under this rule, 1374 stems had a change in diameter measurement height between 2005 and 2010.

³ Where the stem was alive in both censuses, diameter measurements that were made at the *same* height in both censuses were used when available. In other cases, the diameter with the *minimum* height of measurement in that census was used. Under this rule, 976 stems had a change in diameter measurement height between 2005 and 2010.

⁴ Where the stem was alive in both censuses, diameter measurements that were made at the *same* height in both censuses were used when available. In other cases, the diameter with the *maximum* height of measurement in that census was used. Under this rule, 976 stems had a change in diameter measurement height between 2005 and 2010.

of the biomass change of the individual trees in question, but introduces systematic errors in biomass change at the plot level, because trees are then measured at different heights relative to the tops of upwardly growing buttresses in the different censuses. When we calculated equivalent diameter at 1.3 m based on taper equations, and used this diameter in the biomass allometry equations, biomass change went from negative to positive as the taper parameter α increased (Table 14.4). This result is consistent with the fact that the later census had a higher proportion of trees with higher POMs. There was no single taper value for which all four POM choices led to similar values for biomass change; overall the standard deviation among the values was lowest for $\alpha = 0.05$, at which point the mean estimate was $0.076 \text{ MgC ha}^{-1} \text{ yr}^{-1}$.

In the absence of better allometric data for buttressed trees, it is difficult if not impossible to say which measurement and analysis protocols produce the best estimates of plot-level biomass and biomass change, but it is clear that current standard practices introduce systematic errors. Given that virtually all tree boles taper, we recommend that height of measurement be recorded for any diameter measurement taken at a non-standard height. Explicit treatment of height of diameter measurement in future biomass allometry measurements, combined with data on height of diameter measurements, would allow large reductions in systematic errors associated with buttressed trees. Studies of trunk taper on buttressed species in the range of heights typically used for measurement would also be useful. Ideally, analyses should incorporate information on taper as well as diameter measurements at one or more non-standard heights to infer true biomass growth (Metcalf *et al.* 2009). In the long run, an even better approach might be to measure trees with buttresses and those liable to develop buttresses at a standard height that remained above buttresses on most if not all trees (e.g. 5 m, 8 m), and combine these with allometric equations for biomass of buttressed trees based on diameter measurements at such heights. Such an approach is already used in Finland, where standard forest inventory practices include measurements of diameters at 6 m height, measurements that are taken from the ground using a device called the Finnish caliper.

14.3 Projecting biomass change

Observations of biomass change in forests provide critical evidence regarding the question of current effects of global change on forests, but they do not provide clear insights into future biomass change. The simplest assumption – that change in a given forest will continue at the most recently observed rate – is obviously wrong when projecting for 50 or more years. The next simplest assumption, of linear extrapolation based on two or more rates of change, is also obviously wrong on longer time scales. Another approach is clearly needed to project how biomass will change in the medium and long

term. In general, there are two broad classes of strategies that can be employed: phenomenological models and mechanistic models.

In the following subsection, we present a phenomenological approach for short- and medium-term projections of biomass, based on Markov chain models and observed small-scale biomass transition probabilities.

14.3.1 Markov chain models of biomass change

A Markov chain model captures stochastic transitions between states (here, tree biomass in small forest plots) with a matrix of transition probabilities. First-order Markov chain models were first used to model successional changes in species composition and/or vegetation type in the 1970s (e.g. Horn 1975; Usher 1979; Waggoner & Stephens 1970). Their application in this context was criticised for the models' inability to capture historical and spatial dependence of succession (Facelli & Pickett 1990). In particular, the simplest Markov chain models assume that (1) transition probabilities depend only on the current state not on past states (the memory-less property); (2) transition probabilities do not vary in time or space (stationarity); and (3) transitions in different cells are independent (spatial independence). More complex models can relax these assumptions, but the data needed to parameterise them increase accordingly, and even the most basic models require extensive data on observed transitions for parameterisation (Facelli & Pickett 1990). Thus, Markov chain models were superseded as more mechanistic gap models of succession were developed for temperate forests, models that simultaneously predicted changes in species composition, forest structure and forest dynamics (Shugart 1984). However, these mechanistic models require extensive, species-level information on individual growth, mortality, and recruitment and how this varies with gap age, or in later models, neighbourhood (Pacala *et al.* 1996). Similar models have been constructed at the functional type level for some tropical forests (e.g. Chave 1999), but we lack the information needed to build such mechanistic models for most sites. This suggests a reconsideration of the 'black box' approach of Markov chain models, especially in cases where extensive transition data are available to parameterise such models.

A Markov chain model for forest biomass can be parameterised from census data from a large plot or many small plots. With this approach, the data on biomass and biomass change within small subplots are used to parameterise a linear matrix model that describes the dynamics of the probability distribution of biomass. This approach captures gap dynamics, as small subplots can transition in and out of low-biomass states with realistic probabilities based on the observed relationship of biomass to biomass change. Kellner *et al.* (2009) used this approach to model transitions in canopy height, a proxy for forest biomass, parameterising their model with airborne LiDAR data for large areas. We argue that such models provide a useful basis for projecting

biomass distributions (and thus mean biomass) forward into the future under the assumption that transition probabilities continue as currently observed.

To parameterise a Markov chain model for biomass change, we first divide the range of observed biomass densities into N classes. Let $\mathbf{V}(t)$ be a vector of length N , with elements $v_i(t)$ corresponding to the proportion of subplots having biomass density in class i at time t . Let \mathbf{M} be a transition probability matrix, whose elements m_{ij} give the probability that a subplot that was in state j transitions to state i in one time step. Then, $\mathbf{V}(t+1) = \mathbf{M}\mathbf{V}(t)$. (That is, following the standard rules of matrix multiplication, each element $v_i(t+1) = \sum_j m_{ij}v_j(t)$.) Provided \mathbf{M}

is not singular, there exists a single equilibrium probability distribution \mathbf{V}^* such that $\mathbf{V}^* = \mathbf{M}\mathbf{V}^*$, and this equilibrium can be obtained analytically from the first eigenvector of \mathbf{M} (Anderson & Goodman 1957). That is, over time, given a fixed transition probability matrix \mathbf{M} , any and every initial frequency distribution that is non-zero will converge on the equilibrium.

We parameterised a Markov chain model for the biomass density of 10 m \times 10 m subplots on the Barro Colorado Island 50-ha plot. We first divided the 50-ha plot into contiguous 10 m \times 10 m subplots (5000 in total), and calculated total biomass in each subplot by summing estimated biomass of each tree within it. Individual tree biomass was calculated from uncorrected diameter data for the highest diameter for each stem in each census using a pantropical allometric equation (Chave *et al.* 2005) (details in Appendix 14.1). We log-transformed total biomass in each subplot (to achieve normality), and used a two-dimensional Gaussian kernel density estimator with fixed width to estimate the continuous joint probability distribution (Haan 1999; Scott 1992; Silverman 1986) for log biomass density at census t and census $t+1$. This resulted in estimates of p_{ij} , the probability that a given 10 m \times 10 m plot is in biomass density class j at one time step and in biomass density class i during the next time step. The Gaussian kernel estimator essentially obtains a smoothed version of the empirically observed joint probability surface (Figure 14.3). The transition matrix is calculated as the conditional probability from the joint probability density function:

$$m_{ij} = \frac{p_{ij}}{p_j} = \frac{p_{ij}}{\sum_k p_{kj}} \quad (14.1)$$

where p_j is the marginal probability that a subplot has biomass density class j in the first census interval. The matrix \mathbf{M} is independent of t because of the memory-less property of Markov chains.

The advantage of the Gaussian kernel estimator is that the probability density function (PDF) is independent of the discretisation of the probability domain (here the number of biomass categories), in contrast to a histogram or

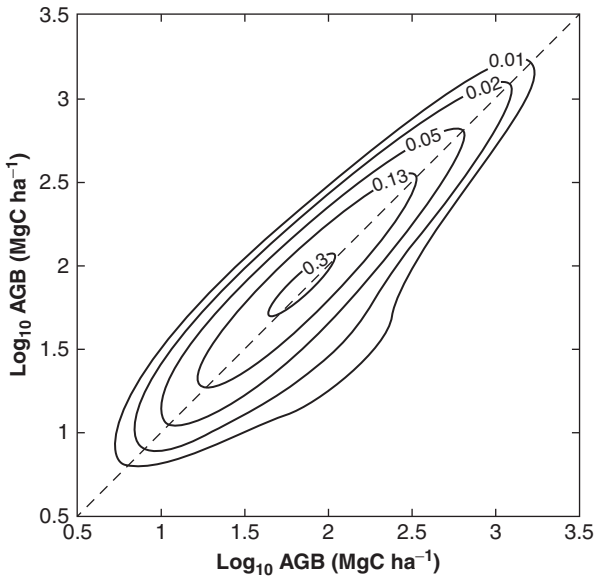


Figure 14.3 Ensemble joint probability density function of biomass density over two successive census intervals, t and $t + 1$, estimated from transitions for all 5-year census intervals between 1985 and 2010 using a Gaussian kernel estimator (see text), and using the raw census data without ‘data cleaning’ or correction for increasing heights of measurement. Correcting for increasing heights of measurement over time would increase biomass in later censuses relative to earlier ones, and thus alter transition probabilities.

box counting method. This allows us to use a large number of biomass categories without increasing errors in estimates of the transition probabilities. The use of a large number of categories improves estimates of dynamics (Zuidema *et al.* 2010). The PDF is dependent on the width of the Gaussian kernel estimator, which has a role similar to the bin size for box counting approaches. The width of the Gaussian kernel estimator is critical for estimating the PDF and is chosen as a best compromise between minimising the bias caused by smoothing (which increases for large width, causing excessive smoothing of the peaks of the distribution) and minimising the variance (which increases for small width in areas where little information is present, causing noise at the tails of the distribution) (Haan 1999). In our case, we use 100 classes (from 0 to 10 on a log scale of MgC ha^{-1}) and the width of the estimator was 0.25. All analyses were done in MATLAB (Version 7, The Mathworks Inc.).

We took advantage of the six censuses, and thus five census intervals, at BCI, which allowed us to increase the sample sizes used to estimate transition probabilities and also to investigate temporal variation in the transition

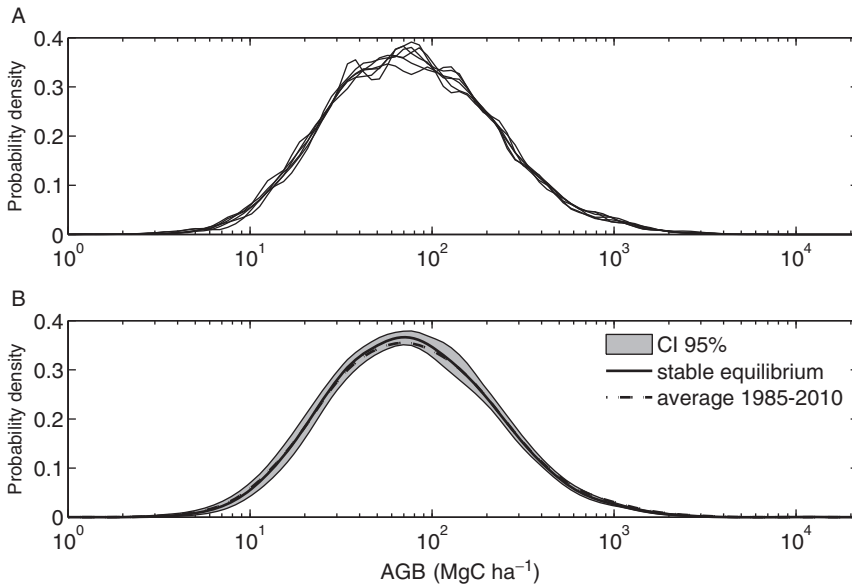


Figure 14.4 (A) The probability density functions (PDFs) of biomass densities in 10×10 m subplots for the different census intervals on BCI. (B) The PDF for the projected stable equilibrium and its 95% confidence interval from stochastic simulations, compared with the average observed PDF. Biomass was calculated using the raw census data without data cleaning or correction for increasing heights of measurements.

matrix. We computed five separate 5-year transition probability matrices, and calculated a mean transition matrix by taking arithmetic means of joint and marginal probabilities for each element of the five matrices. The equilibrium mean biomass was computed from the equilibrium probability distribution of log biomass classes, P^* . The equilibrium mean biomass was 140 MgC ha^{-1} , which is slightly higher than the most recent census (137.5), and lower than other censuses (Figure 14.4). We also explored the influence of stochastic variation in transition probabilities by simulating biomass dynamics over time when one of the five transition matrices was randomly selected at each time step. We found that over 1000 iterations (equivalent to 5000 years given our 5-year time step), this led to biomass fluctuations over a range from 133 to 147, and a mean value of 140 MgC ha^{-1} (Figure 14.5). The projected stable equilibrium from the mean transition matrix lies within the 95% confidence intervals of the PDF from the simulations (Figure 14.4B).

Analysis of the Markov chain model for biomass transitions on BCI, when biomass is calculated without correcting for changing points of measurement (see previous section), thus suggests that the plot is currently at its dynamic equilibrium in biomass given current environmental conditions, and is not undergoing directional change. It further suggests that variability among

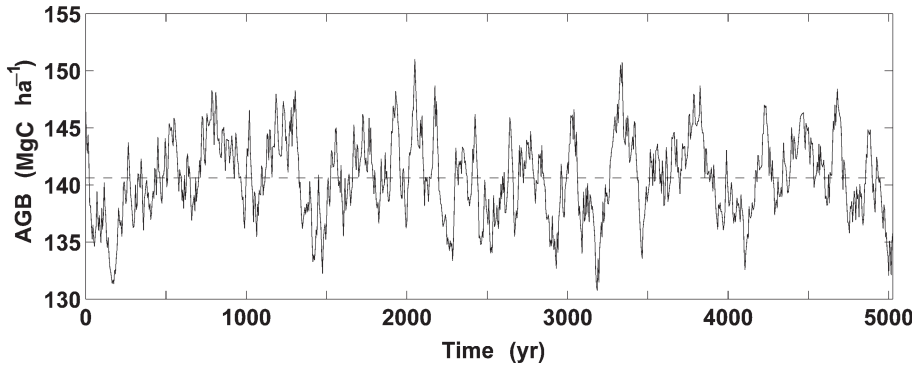


Figure 14.5 Stochastic simulations of the Markov chain model of BCI, in which one of the five projection matrices (corresponding to one of the five 5-year census intervals) is randomly selected at each iteration. The dashed line indicates the deterministic equilibrium value. The projection matrices were based on biomass calculated using the raw census data without data cleaning or correction for increasing heights of measurements.

censuses may be explained by stochastic temporal environmental variation. This is consistent with the similarity in the biomass distribution across all six censuses evaluated here (Figure 14.4A), and with the lack of consistent directional change observed in the past 25 years (Chave *et al.* 2003, 2004). However, it is important to note that this approach has clear limitations, related to the limitations of the underlying data. The current analysis uses biomass estimated in the standard way – by using observed diameter at the maximum height of measurement in a given census, and plugging this directly into biomass equations without any adjustment for height of measurement. Monitoring is unlikely to capture rare, but potentially large, transitions such as major disturbances, and if these are missed in monitoring, their effects will also be absent from the resulting model. Further, as we showed above, estimates of biomass change can vary considerably and systematically with error correction routines, and with procedures for dealing with diameters measured at non-standard heights. Correcting for the increasing heights of measurement in later censuses would increase biomass in later censuses relative to early ones, thus leading to transition matrices with more weighting towards biomass increases, and thereby increased equilibrium biomass relative to current and past observed biomass. We are currently collecting field data on taper in order to develop accurate corrections for increasing heights of measurements, and will revisit this analysis once those data are in hand.

The Markov chain approach has some clear limitations, corresponding to the key assumptions stated above (Facelli & Pickett 1990). First, the first-order Markov chain models that we parameterised assume that transitions depend

only on the current state of the system, and are invariant in space. Thus, for example, all areas of low biomass have the same transition probabilities to various higher (and lower) biomass states. In reality, some areas of low biomass may represent arrested gap succession owing to liana tangles (Schnitzer, Dalling & Carson 2000), or may be likely to stay in low biomass because of habitat effects such as location in a swampy area (Chave *et al.* 2003). Second, projections are made under the assumption that future transition probabilities are distributed in the same way as previously observed probabilities, in our case choosing randomly among the observed census intervals. Thus, this approach inherently cannot capture influences that are causing ongoing changes in transition probabilities – it only informs us about the logical endpoint of extrapolating current transition probabilities into the future. Increasing abundances of lianas, increasing atmospheric carbon dioxide and changing climates (Lewis *et al.* 2009a), among others, may be directionally changing transition probabilities over time, effects that are not reflected in projections of Markov chain models parameterised from past observed transitions. Third, the model assumes that biomass changes in adjacent subplots are independent. Our own analyses found no spatial autocorrelation in biomass change within the plot (Figure 14.2), suggesting that this assumption is appropriate for our site. The direct causal influence between patches is, in general, likely to be small most of the time; although gaps are commonly believed to be contagious and may be modelled as such (Sole & Manrubia 1995), a recent study found that areas next to existing canopy gaps have disturbance rates that are similar to those of areas far from existing gaps (Jansen, Van der Meer & Bongers 2008). On the other hand, large-scale disturbances, e.g. from hurricanes, blow-downs, fires and drought, are generally spatially structured with adjoining areas likely to transition to low-biomass states at the same time, whether or not they causally influence each other.

As we have shown here, parameterisation of Markov chain models for biomass transitions within subplots is potentially a useful way to capture gap dynamics and project future trajectories of biomass. This approach requires data for a large and fairly uniform area to obtain reliable transition matrices; large plots of 16–50 ha such as those in the CTFS/SIGEO (Center for Tropical Forest Science/Smithsonian Institution Global Earth Observatories) network are well suited to such analyses. Given that LiDAR-derived canopy height metrics are well correlated with biomass in tropical forests (Asner *et al.* 2011), landscape-scale LiDAR data are also well suited to such studies. Kellner *et al.* (2009) examined the canopy height distribution over 444 ha in a wet tropical forest in Costa Rica using LiDAR, and found that the observed distribution at 5 m grain is consistent with the stationary distribution of a Markov model parameterised using the transitions observed over an 8.5-year interval. Similar studies over larger areas would provide important information about

whether and how tropical forest biomass is changing, and a first basis for projecting future changes. Future work should explore how statistical power is related to sample size (area and census interval) for this type of model. It is important to keep in mind that this phenomenological approach only projects forward based on currently observed dynamics, and that it cannot capture the effects of potential future changes in dynamics due to further changes in the environment.

14.4 Conclusions and recommendations

Forest biomass change in tropical forests is spatially variable, reflecting stochastic local variation as well as deterministic influences of topography, soil type, forest type, etc. Sampling uncertainty associated with stochastic local variation contributes random error in estimates of biomass change. The associated sampling errors can be quantified for individual sites by examining spatial autocorrelation patterns and then bootstrapping appropriately over subplots whose scale exceeds the local correlation length. When combining data from multiple sites differing in area and/or time interval, the appropriate weighting depends critically on the relative magnitude of within- and among-site variability, which in turn depends on landscape-level spatial patterns. Sampling errors for ensembles of sites can be assessed by bootstrapping over sites and subplots within sites (e.g. Chave *et al.* 2008). We recommend that all studies of biomass or biomass change examine autocorrelation patterns for the scales relevant to the study, and use this information to quantify sampling errors and determine appropriate weighting schemes, if necessary. Autocorrelation patterns are likely to differ among forests, and need to be considered carefully in any given application. Ideally, their assessment would be based on large-scale, fine-grained data such as that provided by airborne LiDAR, but in the absence of such information, plot data themselves can be used to assess this (e.g. through semivariograms).

Although sampling errors are inherently random, measurement errors and data cleaning routines can introduce systematic as well as random errors in estimates of forest biomass and biomass change. Even random ordinary diameter measurement errors on non-buttressed trees can introduce systematic errors in biomass because of the non-linear relationship of diameter to biomass. Further, common error detection and gap filling algorithms can actually introduce systematic errors in biomass change. On BCI, where measurement error frequencies are fairly low, these effects are currently small, but they have the potential to be larger depending on error rates and data cleaning practices (e.g. in earlier BCI censuses). It is important that all studies carefully document data cleaning practices, and describe these practices in publications in sufficient detail that they can be reproduced. We further recommend that studies quantify measurement errors, if at all possible; such information is extremely useful

in quantifying any bias that may result from measurement errors, or changes in measurement error rates over time, and in enabling corrections for such biases. In general, data cleaning procedures should be carefully planned *a priori*; *post hoc* development or adjustment of such procedures is problematic as it raises the potential for conscious or unconscious biases towards expected results to influence outcomes. Research is needed to thoroughly evaluate alternative error detection and gap filling procedures for tropical forest biomass, and develop general recommendations for procedures that induce no systematic errors in key quantities of interest.

Trees whose diameter is measured above the standard height because of buttresses or other stem irregularities constitute a large proportion of biomass in tropical forests and create a very large potential for systematic errors in biomass and biomass change. Their potential to introduce bias follows from the interaction of current biomass allometry equations, which do not consider height of measurement, with variation among sites and over time in the heights of measurement. On BCI, different approaches to data analysis for buttressed trees produce very large differences in estimates of biomass change, including reversals in the sign of biomass change; at this time, it is not clear which approach and which estimate are best. It is critical that the methods for choosing measuring points and handling changes in measurement heights are clearly documented and reported. We strongly recommend that the height of diameter measurements always be measured, and that publications provide statistics on the distribution of measurement heights (and especially, any changes in this distribution over time, as seen on BCI). Ideally, the height of the top of the buttress would also be recorded, because existing biomass data often include only diameter measured immediately above buttresses. We further recommend the development and application of allometric equations that explicitly take the height of diameter measurement into consideration, and thus automatically correct for non-standard heights of measurement. Research that explicitly evaluates alternative approaches in simulated datasets could make clear the best approaches for obtaining unbiased estimates of biomass and biomass change for buttressed trees and stands that contain such trees.

A key challenge in predicting the future trajectory of forest biomass change is to control appropriately for the gap age distribution in the current dataset and/or landscape (the gap age distribution reflects the disturbance history of the site). Markov chain models for biomass offer a potentially useful means to do this. They require data for many transitions for reliable parameterisation, but this is within the realm of what is available for single large plots, such as BCI, or collections of small plots. In general, Markov models are a worthy area for future exploration, although it is important to keep in mind that these are purely phenomenological models, and only provide the ability to extrapolate

current dynamics to their equilibrium. A critical question we did not address here concerns the confidence intervals on the probabilities and the projections of the Markov model; this is something that should be addressed in future work. The quantities estimated as part of parameterising Markov models are also themselves worthy of further examination – in particular, global change in forest dynamics would be expected to be evident in directional changes in transition probabilities over time.

This chapter has focused almost entirely on aboveground biomass data from field measurements, currently the main source of data on tropical forest carbon pools. This is likely to change in the future, as airborne LiDAR and other remote sensing tools become increasingly useful for quantifying biomass in tropical forests (Asner *et al.* 2011; Mascaro *et al.* 2011b), and as measurements of belowground pools become more common. LiDAR metrics such as mean canopy height correlate well with aboveground biomass in tropical forests (e.g. Mascaro *et al.* 2011a), and thus LiDAR is well placed to provide information on the spatial autocorrelation structure of biomass at landscape scales. Both LiDAR and other remote-sensing tools can provide landscape-scale data on canopy disturbance rates and the size distribution of disturbance events – critical quantities for determining the true power of a given plot sampling effort (Fisher *et al.* 2008; Gloor *et al.* 2009). However, most remote-sensing tools are likely to have limited if any ability to detect small increases in biomass in high-biomass forests (because most remotely sensed metrics saturate at high biomass), limiting their usefulness for quantifying potential subtle changes in old-growth forests. LiDAR, in contrast, can directly measure changes in canopy heights (e.g. Kellner *et al.* 2009) and in the density of vegetation beneath the canopy, both potential effects of global change that could affect biomass. Belowground stocks in soil and roots are also gaining attention, with standard methods increasingly applied across plot networks such as RAINFOR and SIGEO/CTFS. Future research should quantify random and systematic errors in associated estimates of carbon pools and fluxes.

Overall, ground plots remain an essential tool for quantifying impacts of global change on tropical forests, especially old-growth forests. Carbon stocks in these forests depend greatly on the diameters and heights of big trees, which are still poorly measured remotely. However, measurement methods and errors for ground plots can introduce random and systematic errors in estimates of biomass and biomass change. Methods should always be carefully documented and fully reported, and should include data cleaning procedures. Measurement errors should be quantified. It has generally been assumed that measurement errors and data correction routines have little or no effect. Here we show that although some effects are small, others are potentially large, and more worryingly, systematic. More investigation of the effects of these errors and procedures is warranted.

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Appendix 14.1 Details of methods for calculating AGB and AGB change for Barro Colorado Island

We calculated individual stem AGB (in kg dry biomass) using the moist forest equation based on wood specific gravity (wsg) and diameter (dbh, in cm) from Chave *et al.* (2005):

$$\text{AGB} = \text{wsg} \times \exp \left[-1.499 + 2.148(\ln \text{dbh}) + 0.207(\ln \text{dbh})^2 - 0.0281(\ln \text{dbh})^3 \right]$$

We assumed dry biomass was 47% carbon (Martin & Thomas 2011), and we report AGB and AGB change in MgC.

We calculated AGB change per year in a quadrat as the sum of AGB changes per year for individual stems in that quadrat, thus taking into account differences in measurement intervals for different stems. Stems that were recruits in the final census were assigned an initial AGB of zero and an initial date corresponding to the date in which their quadrat was censused. Stems that were newly dead in the final census were assigned a final AGB of zero and a final date corresponding to the date in which their quadrat was censused.

We used species-level wood density values for 306 species, most obtained from field measurements in central Panama (Wright *et al.* 2010 and S. Joseph Wright, unpublished data), genus-level values for 12 species, and a plot-level basal-area-weighted mean of 0.521 for the remaining taxa and unidentified individuals (the later censuses have no unidentified individuals).