AN ABSTRACT OF THE DISSERTATION OF

Judith C. Jobse for the degree of Doctor of Philosophy in Wildlife Sciences presented on September 25, 2008.

Title: Impacts of Forest-to-Agriculture Conversion on Aboveground and Soil Carbon and Nitrogen Stocks along a Bioclimatic Gradient in Costa Rica.

Abstract approved:

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Tropical forest-to-agriculture conversions contribute to ~20% of contemporary global C emissions. Current global C flux estimates assume C is lost from vegetation and soils over time due to this conversion, and that C stocks in agricultural lands are fairly uniform across the tropics. Global C stock and flux estimates may contain large errors if these assumptions are incorrect. I asked the following research questions: (1) Do aboveground and soil C and N stocks and their net changes due to forest-to-agricultural conversion differ among life zones and agricultural land use types in Costa Rica?; (2) Do aboveground and soil C and N stocks and their net changes due to forest-to-pasture conversion differ by pasture age?; and (3) Can life zone specific-estimates reduce potential biases and uncertainty of regional and global C flux estimates for forest-to-agricultural conversions? I sampled soil and aboveground C and N stocks at 62 agricultural sites in Costa Rica stratified by land use and life zone and compared them to mature forests. Ecosystem and soil C and N stocks varied more by life zone than by land use. Net soil C and N stock changes due to forest-to-pasture conversion differed by life zone; soil stocks decreased in the Tropical dry forest and Lower Montane rain forest life zones and increased in the other life zones. Generally, ecosystem C and N stocks in pastures decreased with pasture age, but the effect of age was smaller than life zone and conversion effects. My estimates of Costa Rican ecosystem C stocks in agricultural lands were 2-fold greater and my ecosystem C flux estimates due to forest-to-agricultural conversions were 8-19% lower than Intergovernmental Panel on Climate Change (IPCC)-endorsed estimates. Therefore to reduce uncertainty and bias, incorporation of ecosystem C stock variability related to life zone into regional and global models is more important than including variability related to pasture age or land use type. Overall, my results confirm that forest-to-agriculture conversions represent a significant alteration to global C cycles, and contribute to reducing uncertainty in the magnitude of such changes.

Impacts of Forest-to-Agriculture Conversion on Aboveground and Soil Carbon and Nitrogen Stocks along a Bioclimatic Gradient in Costa Rica

by
Judith C. Jobse

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APPROVED:

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Judith C. Jobse, Author

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CONTRIBUTION OF AUTHORS

Dr. J. Boone Kauffman was involved in the design, analysis, and editing of the first drafts of Chapters 2 and 3 of this dissertation. Dr. R. Flint Hughes was involved in the design. Dr. Miguel Cifuentes Jara was involved in the analysis and data interpretation. Vicente Watson was involved in the design, all stages of field work, and provided essential data for Chapter 4.

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CHAPTER 1

GENERAL INTRODUCTION

Chapter 1 General introduction

1.1 Introduction

Knowledge about carbon (C) and nitrogen (N) cycling and related uncertainties is essential to our understanding of ecosystems and the biosphere. Human activities, such as fossil fuel burning, mining, land use change and agriculture, have altered C and N cycles since long before the beginning of the Industrial Revolution (Solomon et al. 2007). In the 1980s and 1990s land use change, primarily tropical forest-to-pasture conversion, contributed to ~20% of the global atmospheric C emissions (Denman et al. 2007). Moreover, these tropical C flux estimates had the highest uncertainty of all the fluxes in the global C budget (Denman et al. 2007). In addition, land conversion may affect C storage indirectly due to changes in soil nitrogen (N) and uncertainties in the effects of forest-to-pasture conversion on the N-cycle are also substantial (Neill et al. 2005).

An improved understanding of global C and N cycling and its response to land use change is needed to include N feedbacks in climate-C cycle models (Thornton et al. 2007). The coupled climate-C cycle models used in the Intergovernmental Panel on Climate Change’s (IPCC) most recent assessment do not include N feedbacks (Denman et al. 2007). Nevertheless, N is the primary limiting nutrient in terrestrial ecosystems at mid and high latitudes, as well as an important co-limiting nutrient for tropical plant growth, and hence, for terrestrial CO_2 uptake (Reich et al. 2006, Thornton et al. 2007).

Global C stock and flux estimates may contain large errors because C stocks in agricultural lands and their changes due to conversion are not as homogenous as global C flux models assume. The IPCC’s most recent 2007 assessment (Denman et al. 2007) assumed that estimates of net C changes due to forest-to-agricultural conversion were fairly similar across the tropics (Houghton 2003). However, the extent of C lost with vegetation change is highly uncertain (Houghton 2007) as is the fate of soil C and N stocks in response to land use change (Guo and Gifford 2002, Murty et al. 2002). Both net losses and gains in soil C and N stocks due forest-to-agricultural conversion have been reported (Guo and Gifford 2002, Murty et al. 2002). Although the causes of this variability are not well understood, climate explained some variability in soil C stock changes (Amundson 2001, Guo and Gifford 2002)

Time since deforestation (land use age) plays an important role in controlling the variability in soil C and N stocks among pastures. Data on aboveground C and N stock changes in agricultural lands over time is limited, but stocks may decline rapidly after forest-to-pasture conversion followed by a slow decrease over time (Kauffman et al 2003). Generally, soil C stocks initially rapidly decrease after forest-to-cropland conversion followed by a slower rate of soil C loss (Murty et al. 2002). Temporal patterns of soil C change after forest-to-pasture conversion vary widely, and soil C stocks have been found to: (1) steadily increase over time, (2) initially increase and then decrease, (3) initially decrease followed by a recovery over time, and (4) rapidly decrease and then stabilize (Veldkamp 1994, Murty et al. 2002). The causes of this variability are not well understood, although changes in soil C may be related to climate (Amundson 2001, Guo and Gifford 2002). Nevertheless, the IPCC’s 2007 estimate (Denman et al. 2007) assumed that: (1) all Neotropical soil C stocks consistently decreased for the first 20 years after forest-to-pasture conversion, and (2) C stocks in the vegetation of all Neotropical pastures were 10 Mg C/ha within 10 years after deforestation (Houghton and Hackler 2001, Houghton 2003). These assumptions may have introduced biases into the global C budget estimates.

Life zone (bioclimatic unit’s *sensu* Holdridge 1947 and 1967) based-estimates of net ecosystem C and N stock changes may substantially reduce possible biases and uncertainties in global C flux models and aid the development of coupled climate-C-N models. Houghton et al. (1991) indicated that life zone-based estimates of croplands and pastures in Latin America increased the ecosystem C flux between 1850 and 1990 by 15% compared to an estimate not stratified by life zone. However, no life zone-based estimate for C stocks in agricultural vegetation was used in that work, probably due to a lack of data. In addition, Houghton et al. (1991) assumed all soil C stocks decreased due to forest-to-agricultural conversion regardless of life zone.

My research objective was to improve our understanding of the impacts of tropical land use change on terrestrial C and N stocks. I asked the following research questions: (1) Do aboveground and soil C and N stocks and their net changes due to forest-to-agricultural conversion differ among life zone and agricultural land use type in Costa Rica?; (2) Do aboveground and soil C and N stocks and their net changes due to forest-to-pasture conversion differ by pasture age?; and (3) Can life zone-specific estimates reduce potential biases and uncertainty of regional and global C flux estimates for forest-to-agricultural conversions? To answer these questions I measured aboveground and soil C and N stocks in 31 Costa Rican pastures representing chronosequence sets within six different life zones. In addition, I measured aboveground and soil C and N stocks in 31 croplands (11 banana, 10 coffee, and 10 sugarcane plantations) across a rainfall gradient in life zones where they are common land uses (Appendix 1). I stratified my sampling efforts using Holdridge’s life zones (1947 and 1967) and included eight different life zones that cover almost 80% of Costa Rica (Bolaños and Watson 1993). I compared C and N stocks in these agricultural lands to C and N stock data from mature reference forests sampled in a companion study (Kauffman et al. unpublished) to estimate C and N stock differences between forests and agricultural lands (N data in croplands are not reported in this dissertation).

Pasture soil C and N stocks and their net changes due to forest-to-pasture conversion are described in Chapter 2. In Chapter 3, I present aboveground C and N stocks in pastures and their net changes due to conversion, as well as ecosystem C and N stocks (sum of soil and aboveground C and N stocks) and changes in ecosystem C and N stocks. Therefore, Chapter 2 and 3 are closely related. In Chapter 4 I first present ecosystem C stock estimates for banana, coffee, and sugarcane plantations. Then, I compare ecosystem C stocks among all agricultural land uses (pastures, banana, coffee, and sugarcane) and mature forests, which combines novel data presented in Chapters 3 and 4. To conclude, I compare my life zone based-estimates of agricultural ecosystem C stocks and their net changes due to forest-to-agriculture conversions for all of Costa Rica with estimates based on Houghton's (2003) assumptions of no variation by life zone.

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CHAPTER 2

SOIL CARBON AND NITROGEN STOCKS AFTER FOREST-TO-PASTURE CONVERSION IN SIX PASTURE CHRONOSEQUENCES ALONG A BIOCLIMATIC GRADIENT IN COSTA RICA

Abstract

In the 1980s and 1990s, forest-to-pasture conversions in the tropics contributed to ~20% of global carbon (C) emissions, and uncertainties in these estimates were the highest of all estimated fluxes in the global C budget. In addition, land conversion may affect C storage indirectly due to changes in soil nitrogen (N). Much of the C and N stored in forest vegetation is lost from the ecosystem when forests are converted to pasture, but the fate of C and N stocks in soils are uncertain. Life zone and pasture age may play important roles in controlling the variability in soil C and N stocks. Our objectives were to: (1) quantify soil C and N stocks in pastures of a wide age range across a broad climatic gradient; (2) quantify net changes in soil C and N stocks due to forest-to-pasture conversion; and (3) determine how soil C and N stocks and associated net changes varied with pasture age and life zone. We measured 0-1 m soil C and N stocks in 31 Costa Rican pastures representing chronosequences within six different life zones comprising a precipitation and temperature gradient from the Tropical dry forest to the Tropical Lower Montane rain forest life zones. High spatial soil variability, potential inadequate reference mature forests, and the use of different sampling tools to estimate soil bulk density in mature forests and pastures contributed to uncertainties in net soil C and N stock changes due to forest-to-pasture conversion. All pastures had higher soil bulk densities than mature forest reference sites throughout the 0-1 m depth profile. After accounting for increases in soil bulk density, soil C and N stocks averaged 15% (22 Mg C/ha) and 16% (2.2 Mg N/ha) higher in pastures than in reference mature forests. However, our results varied by life zone ranging from net decreases (-30% C and -36% N) to net increases (96% C and 52% N) in soil C and N stocks. Decreases were found in the Tropical dry forest and Lower Montane rain forest life zones and increases were found in the other life zones. Generally, soil C and N stocks decreased with pasture age, except in the Tropical Premontane rain forest life zone where we observed an increase. The effect of life zone and land use conversion on soil C and N stocks was greater than pasture age. We

suggest that potential bias and uncertainties of global C stock and flux estimates could be reduced if the variability in soil C stocks and net changes related to life zone are incorporated when estimates are made.

Chapter 2 Soil carbon and nitrogen stocks after forest-to-pasture conversion in six pasture chronosequences along a bioclimatic gradient in Costa Rica

2.1 Introduction

Knowledge about carbon (C) and nitrogen (N) cycling and related uncertainties is essential to our understanding of ecosystems and the biosphere. Human activities, such as fossil fuel burning, mining, land use change and agriculture, have altered C and N cycles since the beginning of the Industrial Revolution (Solomon et al. 2007). In the 1980s and 1990s land use change, primarily tropical forest-to-pasture conversion, contributed to ~20% of the global atmospheric C emissions (Denman et al. 2007). Moreover, these tropical C flux estimates had the highest uncertainty of all the fluxes in the global C budget (Denman et al. 2007). Tropical land use change is also a large source of another important greenhouse gas, nitrous oxide (N_2O), which is released during forest biomass burning, cattle raising, and use of N fertilizers (Denman et al. 2007). The impacts of forest-to-pasture conversion on the N cycle are also highly uncertain (Neill et al. 2005).

An improved understanding of global C and N cycling and its response to land use change is needed to include N feedbacks into climate-C cycle models (Thornton et al. 2007). The coupled climate-C cycle models used in the Intergovernmental Panel on Climate Change’s (IPCC) most recent assessment do not include N feedbacks (Denman et al. 2007). Nevertheless, N is the primary limiting nutrient in terrestrial ecosystems at mid and high latitudes, as well as an important co-limiting nutrient for tropical plant growth, and hence, for terrestrial CO_2 uptake (Reich et al. 2006, Thornton et al. 2007).

The fate of soil C and N stocks in response to land use change is uncertain. Both net losses and gains in soil C and N stocks due forest-to-pasture conversion have been reported. Two global reviews found that on average either: (1) net soil C stocks increased (Guo and Gifford 2002), or (2) net soil C and N stocks remained the same

(Murty et al. 2002). Guo and Gifford (2002) found that sites with precipitation between 2000 and 3000 mm/year had net increased soil C stocks after conversion; whereas sites with higher or lower precipitation had both increased and decreased soil C stocks, suggesting that soil C changes are related to climate. In addition, Amundson (2001) reported that soil C loss rates due to cultivation increased with temperature. Nevertheless, the IPCC's latest estimate assumed that all tropical soil C stocks decreased after forest-to-pasture conversions (Houghton and Hackler 2001, Houghton 2003, Denman et al. 2007), introducing a possible bias into the global C budget.

Time since deforestation (pasture age) also plays an important role in controlling the variability in soil C and N stocks among pastures. Temporal patterns of net soil C change after forest-to-pasture conversion vary widely (Murty et al. 2002). Soil C stocks have been found to: (1) steadily increase over time, (2) initially increase and then decrease, (3) initially decrease followed by a recovery over time, and (4) rapidly decrease and then stabilize (Veldkamp 1994, Murty et al. 2002). The causes of this variability are not well understood. Nevertheless, the IPCC's 2007 estimate (Denman et al. 2007) assumed that all Neotropical soil C stocks consistently decreased for the first 20 years after forest-to-pasture conversions (Houghton and Hackler 2001, Houghton 2003), introducing yet another possible bias into the global C budget.

Because climate explained variability in soil C stock changes (Amundson 2001, Guo and Gifford 2002), life zone based-estimates of net soil C and N stock changes may reduce possible biases and uncertainties in global C flux models substantially and aid the development of coupled climate-C-N models. Life zones (bioclimatic units *sensu* L.R. Holdridge 1947 and 1967) or other climatic variables explain much of the variation in soil C and N stocks found in the tropics (Jenny 1941, Post et al. 1982 and 1985). For example, 0-1 m soil C and N stocks in mature (Kauffman et al. unpublished data) and secondary forests (Cifuentes Jara 2008) varied by life zone when estimated across a broad climatic gradient in Costa Rica.

In this study we determined tropical soil C and N stocks and associated net changes related to life zone and land use duration in Costa Rica. Our objectives were to: (1) quantify soil C and N stocks in pastures of a wide age range across a broad climatic gradient, (2) quantify net changes in soil C and N stocks due to forest-to-pasture conversion, and (3) determine how soil C and N stocks and associated net changes varied with pasture age and life zone. More specifically, we addressed the following research questions: (1) Are life zone and other climate variables predictors of soil C and N stocks in pastures and their net changes due to pasture-to-forest conversion?; (2) Do soil C and N stocks in pastures change with pasture age?; and (3) Does the effect of pasture age on soil C and N stocks differ by life zone?

2.2 Methods

2.2.1 Study areas

Our research was conducted in Costa Rica because it has an extremely high biotic and physical diversity in a relatively small area (51,100 km^2). Costa Rica is bordered by the Atlantic and the Pacific oceans, and is dissected by volcanic mountain ranges from northwest to southeast. Across all sampled pastures, mean annual precipitation ranged from 1512-5126 mm/year and mean annual temperature ranged from 16.8-27.8 ^{o}C (Table 2.1). There are 23 different life zones in Costa Rica including 11 transition life zones (Bolaños and Watson 1993). Transition life zones are transitions between two major life zones, similar to ecotones. The majority of Costa Rica is classified as Tropical moist forest (14%), Tropical wet forest (16%), Tropical Premontane moist forest-warm (9%), Tropical Premontane wet forest-warm (14%), Tropical Premontane wet forest (8%), Tropical Premontane rain forest (9%), and Tropical Lower Montane rain forest (7%). The other 16 life zones cover <5% of Costa Rica (Bolaños and Watson 1993). Deforestation in Costa Rica started in the Tropical dry and moist forest life zones, and later in the Tropical wet and Tropical Premontane moist and wet forest life zones; by 1983, only the less accessible areas in the very wet life zones retained relatively undisturbed forest (Sader and Joyce 1988). In 2002, pastures made up about

46% of Costa Rica and 90% of all agricultural land use types in the country (FAO 2008).

2.2.2 Site selection

We stratified pasture sites by six dominant life zones in Costa Rica (Table 2.1). Within each of these life zones, we sampled one chronosequence, consisting of five or six pastures of various ages. The sites for each chronosequence were selected based upon their proximity to mature forest sites sampled in a companion study (Kauffman et al. unpublished; Appendix 1). We used these mature forests reference sites to infer impacts of forest-to-pasture conversion. We avoided areas of anomalous soils, rock outcrops, and riparian zones. In the Tropical dry forest life zone all pastures were flat while pastures in all other life zones included slopes between 0-47 degrees. At each site, geographic coordinates and elevations (Table 2.1) were derived from global positioning system (GPS) readings.

Our pasture chronosequences represented the broadest age range (time since deforestation) within the sampled area that we could find given time and resource constraints. We determined pasture age by interviews with landowners and other local residents and once with aerial photographs. Chronosequences are space-for-time substitutions and a critical assumption of this approach is that the conditions for all pastures within a chronosequence were initially the same, and thus, differences between pastures of different ages were due to pasture age alone. Assumptions critical to determine net changes due to forest-to-pasture conversion were that our sampled forests were in equilibrium and that forest conditions at the pasture sites prior to conversion were similar among sites within each life zone. These assumptions were impossible to verify, but we carefully selected sites to minimize confounding factors.

Pasture management differed by site and we made no attempt to account for these differences. All the pastures were owned by small to large beef cattle ranchers or dairy farmers, and had been actively grazed since pasture establishment. Prior to pasture establishment, many of the pastures were initially cultivated with rice or corn for 1-2 years after forest clearing. Slashed forests were often burned before pastures were established. In the Tropical dry forest life zone, pastures were burned periodically as part of their maintenance. Pasture owners indicated that environmental and health concerns had reduced the use of fire in recent years. We sampled all pastures from January to March 2002.

2.2.3 Environmental variables

We estimated mean annual precipitation by using the nearest meteorologically station data (Instituto Meteorologico Nacional 1988), corrected for the position of the site location on the life zone map (Bolaños and Watson 1993). For example when the position of the actual pasture site was closer to the border of a drier life zone than the reference meteorologically station, then the precipitation for the actual site was given a lower precipitation estimate than the reference station. These manual corrections were conducted independently by R. Bolaños, Dr. J.A. Tosi and V. Watson (life zone and climate experts at the Tropical Science Center in Costa Rica); we used the mean of their estimates. Mean annual temperature data were obtained by applying equations relating temperature with elevation for five climatic provinces of Costa Rica (Castro 1992).

Costa Rica has very high soil variability and most soil orders can be found in the country (Alvarado 2006). We did not attempt to determine the soil types of our sampled sites due to time and monetary constraints. Based on a coarse-scale soil map (Pérez et al. 1978) our sampled pastures included soils from the following orders: Entisol, Alfisol, Inceptisol, Ultisol, and Andisol. The inaccuracy of the soil classification map at the site-level scale precluded formal analyses of these data.

2.2.4 Soil sampling and analysis

We determined soil C and N stocks through collection of soil samples following methods similar to those outlined in Hughes et al. (2000). One 50- x 100-m macro plot, used to measure total above ground biomass (Chapter 3), was established near the center of a pasture. We sampled soils in each pasture at five locations spaced every 25 m along a 100-m transect bisecting the macro plot (Appendix 2). We collected five soil cores at each of the five locations (25 cores per pasture). The cores were collected down to 1 m depth with a gouge auger for hard soils (Eijkelkamp, Giesbeek, The Netherlands, width between vertical cutting edges = 2.4 cm). An impact absorbing hammer (Eijkelkamp, Giesbeek, The Netherlands) was used if the gouge auger could not be pushed into the soil manually. We partitioned the soil cores by depth into five layers: 0-10, 10-20, 20-30, 30-50 and 50-100 cm. We mixed the five soil cores collected at each sampling location to create a composite soil sample for each depth layer per location. A total of five composite samples of each depth from each pasture (25 composite soil samples per pasture) were prepared for soil C and N analysis. We used the same gouge auger to take soil bulk density samples as for sampling for soil C and N analysis. For each depth layer we determined the soil bulk density once at each of the five sampling locations ($n = 5$ per depth layer for each pasture). At each depth layer, we sampled 3 cm of one soil core (volume = 13 cm^3), which was cut flush with the vertical cutting edges of the gouge auger using a knife. The soil bulk density samples were placed in airtight soil cans. Stone content was negligible at most pasture sites and we did not attempt to correct for it. In pastures in the Tropical dry forest life zone, we reached the depth of impedance or a similar resistance around 50 cm depth, and therefore, we did not collect soil samples for the deepest layers at those sites. We oven-dried all soil samples for 1-3 days at 65 ºC and determined dry weight of the soil bulk density samples. Soil samples were transported to Oregon State University where they were sieved to remove particles >2 mm in diameter, and ground to allow passage through a 60-mesh screen (250-µm pore size). Total C and N concentrations in the soils were determined by induction furnace method (Nelson and Sommers 1996) using a Carlo-Erba NA series 1500 NCS analyzer (Fisons Instruments, Danvers, Massachusetts) at Oregon State University. Soil C and N stocks were calculated by multiplying soil C and N concentrations with soil bulk density estimates, the length of the soil layer, and a unit conversion factor. We assumed that the differences in soil C and N stocks between pastures and mature forests (Δ soil C and N stocks) were due to the conversions from forest-to-pasture.

When comparing pasture soil C and N stocks to mature forests a correction is needed to exclude the confounding effects of soil bulk density change (Ellert and Bettany 1995, Fearnside and Imbrozio Barbosa 1998, Murty et al. 2002). Thus, we applied a correction for the differences in soil bulk density between forests and pastures (Veldkamp 1994, Ellert and Bettany 1995, Power and Veldkamp 2005). This resulted in pasture soil C and N stock estimates for a soil mass equivalent to those sampled in 0-1 m reference forest soils. The correction procedure is complex because the soil C and N stock estimate of any given layer is dependent on the estimates from the layers above (Appendices 3 and 4). For example, soil bulk density in the top soil (0-10 cm) for the 29 year old pasture was 1.2 g/cm^3 and 0.8 g/cm^3 in the reference forest. The 0-10 cm corrected soil C and N stocks in that pasture were calculated by using equations reported in Appendix 4, and the 0-10 cm equivalent soil pasture depth was 7 cm. The remaining 3 cm of sampled pasture soil from the top layer was then included in the calculation of the 10-20 cm corrected pasture soil C and N stocks. The same procedure was followed for the remaining soil layers. The cumulative corrected soil stocks (e.g. 0-30 cm or 0-100 cm) were calculated by summing the corrected stocks for the individual layers. If the soil mass present in 0-1 m reference forest soil was greater than the soil mass present in 0-1 m pasture soil (i.e., the opposite of soil compaction) then the % soil C and soil bulk density of the “missing” soil mass in pastures was assumed to be the same as in the 50-100 cm layer. Soil mass was “missing” in 18 of our pastures when calculating adjusted soil C and N stock estimates (section 2.2.5).

2.2.5 Adjustments of reference mature forest estimates

Most mature forests that served as reference forests for the pastures were sampled using a different gouge auger (tool B [JMC 51-792-8285]: volume = 23.7 cm^3, width between vertical cutting edges = 3.45 cm) than the gouge auger (tool C) used to sample pasture soils. Two reference forests were sampled with the same gouge auger as was used to sample pasture soils (tool C).

We used the relationship between soil bulk density and % soil C (Périé and Ouimet 2008) to investigate the impacts of the different sampling tools on the soil bulk density estimates, assuming that our sampling methods did not influence our % soil C estimates. We made scatter plots of the relationship between all soil bulk density and %soil C estimates stratified by tool for all mature forest data from Kauffman et al. (unpublished) (Appendix 5). We calculated different regression lines for each mature forest data set sampled with a different tool (Appendix 5). If the regression equations were different for each sampling tool then there may have been a sampling tool bias, although, other factors that may have influenced the regression line could not be excluded.

To determine the effect of the potential sampling tool bias on our results we standardized all soil bulk density estimates using regression equations. We calculated soil bulk density estimates of all mature reference forests sampled with tool B with a regression equation based on mature forest data sampled with tool C (Appendix 6). These adjusted forest soil bulk density estimates were used to calculate adjusted (Δ) soil C and N stocks in forests and pastures in sections 2.3.3 and 2.3.4. We report both original and adjusted Δ soil C and N stock estimates in these sections. The adjusted soil bulk density estimates in mature reference forests were compared with the original soil bulk density estimates (Kauffman et al. unpublished) in sections 2.3.1. In this dissertation we specifically state if estimates were adjusted and in all other cases statements refer to our original estimates. Statistical analyses were only applied to our original estimates, except for six tests reported in Table 2.2. The adjusted estimates may have excluded sampling tool bias, but it has introduced an uncertainty because adjusted soil bulk densities are based on a regression equation instead of actual measurements.

2.2.6 Statistical analyses

We determined Pearson coefficients of correlation (*r*) among soil response variables in all 31 pastures and pasture age, elevation, temperature, and precipitation independent of life zone, and used scatter plots to interpret them. We compared six regression lines that described the net change of soil variables with pasture age for the six different life zones for each soil response variable: soil C and N stocks, soil C and N stock difference between pastures and forests (Δ soil C and N stocks), % soil C and N, and soil bulk density. Regression line comparisons tested whether the: (1) slopes of the regression lines were similar to each other (homogeneity of slopes), (2) response variable correlated with pasture age (slope ≠ 0), and (3) chronosequences (and thus life zones) were different from each other, while accounting for the effect of pasture age (unequal intercepts). If the slopes of the regression lines differed among life zones (test 1), we did not conduct test 2 and 3 because of the age by life zone interaction. If we detected an age effect (test 2), then we conducted test 3, which was similar to an analysis of covariance with pasture age as a covariate. If we failed to detect an age effect (test 2), then test 3 resembled an analysis of variance.

We used Bayesian Information Criterion (BIC) to rank a-priori models estimating C stocks using maximum likelihood estimation. We developed our set of a-priori models to test how well life zones predicted soil C stocks compared to individual climate variables, and if pasture age was important. Correlation coefficients and scatter plots revealed that elevation, temperature, precipitation, and life zone were highly correlated and therefore models that include a combination of these variables were excluded to avoid effects of multicollinearity. Models that were within 2 BIC units of the “best” model were considered strongly competing models and models between 2 and 4 BIC units of the “best” model were classified as competing models.

We conducted pair wise multiple comparisons with Tukey-Kramer adjustments to test for differences in soil response variables among life zones without correcting for age. Soil C and N concentrations and stocks were natural log-transformed to correct for unequal variance and we back-transformed those results. Hence we report differences between median life zones estimates (Ramsey and Schafer 2002). All statistical tests were conducted in PROC CORR and PROC MIXED using SAS software, Version 9.1 of the SAS[1] System for Windows (SAS Institute 2002-2003).

Although the ranges of pasture age for the different chronosequences were not identical, they overlapped substantially (Table 2.1), and therefore, we assumed that our comparison of regression lines was an appropriate procedure. In this study insufficient data were available for years immediately after deforestation, therefore only pastures ≥8 years were used to test for age effects in the comparison of regression lines. We conducted the BIC model ranking analysis for all 31 pastures, and for the data set without the two youngest pastures. We could not determine the exact age of five pastures due to constraints in time and resources (Table 2.1). Therefore, the following nominal ages were used for those five pastures in the analyses: >75 years = 75 years, >47 years = 50 years, >69 = 70 years, >35 years = 40 years. We report results on the sensitivity of our regression analyses by using the ages: >75 years (site a) = 100 years, >75 years (site b) = 150 years >47 years = 50 years, >69 = 80 years, >35 years = 50 years. This did not substantially change correlations between 0-1 m soil C and N stocks and age, and did not change the comparison of regression lines for 0-1 m (Δ) soil C and N stocks.

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2.3 Results

2.3.1 Soil bulk density

Comparisons of regression lines indicated that soil bulk densities in pastures ≥8 years, at all depths, did not change with pasture age but differed by life zone (Table 2.2). Pastures in the Tropical dry and moist forest life zones generally had the highest soil bulk density at all depths, while pastures in the Tropical Premontane rain and Tropical Lower Montane rain forest life zones had the lowest (Appendices 7-8). Similarly, soil bulk densities at all depths decreased with precipitation ($r \leq -0.84$, $P < 0.01$) and elevation ($r \leq -0.59$, $P < 0.01$), and increased with temperature ($r \geq 0.73$, $P < 0.01$; Appendices 9-10). In the first 3 soil layers soil bulk density increased slightly with pasture age when all pastures were combined ($r \geq 0.31$, $P < 0.1$; Appendix 9).

Measured soil bulk densities were higher in pastures than forests at all depths, which necessitated correcting soil C and N stock estimates to determine how land use conversion and duration influenced C and N stocks (Appendices 7-8). Average soil bulk densities in pastures were between 1.0 and 3.3 times higher than their reference mature forests, with the most pronounced differences in the upper soil layers. Soil bulk density generally decreased with depth in both pastures and forests (Appendices 7-8).

Adjusted soil bulk densities in mature reference forests that were standardized for different tools used during sampling were generally higher than our measured estimates. Differences between measured and adjusted soil bulk density estimates in mature forests increased by depth and varied by life zone (Appendices 7 and 8). The soil bulk density estimates in pastures were on average 48, 19 and 1% higher than the adjusted soil bulk density estimates in mature forests in the 0-10, 10-20 and 20-30 cm soil layers, respectively, and on average 6 and 13% lower in the 30-50 and 50-100 cm soil layers, respectively (Appendix 8).

2.3.2 Soil C and N concentrations

Soil C and N concentrations (% soil C and N) were strongly correlated in our pastures throughout the soil profile (for all depths: $r \geq 0.98$, $P < 0.01$, Figure 2.1a). Generally, % soil C and N decreased with depth in all pastures (Appendix 11-13). In the 0-10 cm soil layers, % soil C and N were 3-13 times higher than in the 50-100 cm soil layers (Appendices 11-13).

Comparisons of regression lines indicated that median % soil C and N in pastures ≥8 years, differed by life zone at all depths (Table 2.2, N not shown because the patterns were almost identical to C). Median % soil C and N in pastures ≥8 years in each life zone was different from two to four (out of five) other life zones, and the number of differences among life zones decreased with depth (Appendix 11-13). In general, across all depths the pastures in the Tropical dry and moist forest life zones had the lowest % soil C and N and the pastures in the Tropical Premontane rain and Tropical Lower Montane rain forest life zones had the highest (Figure 2.1a, Appendix 11-13). Similarly, when pastures were combined, % soil C and N at all depths increased with precipitation and elevation, and decreased with temperature (Appendices 9-10).

In pastures ≥8 years, pasture age did not affect % soil C and N in most layers except in the 30-50 cm layer where the effect of age on % soil C and N differed by life zone (C: $F_{1,16} = 4.08$, $P = 0.01$; N: $F_{1,16} = 7.34$, $P = 0.001$; Table 2.2). When pastures were combined, % soil C and N slightly decreased with pasture age in some layers (max $r = -0.40$; Appendix 9) but these correlations were weak compared to the relationship with climate variables (Appendix 9).

2.3.3 Soil C and N stocks

Comparisons of regression lines of pastures ≥8 years indicated that median corrected soil C and N stocks differed by life zone (Table 2.2 and Figure 2.2). However, soil C and N stocks within life zones were highly variable, and generally, standard errors increased with increasing C and N stocks but coefficients of variation did not (Table 2.3). Corrected 0-1 m soil C stocks were strongly correlated with soil N stocks in our pastures (r = 0.98, $P < 0.01$; Figure 2.1b), hence our results for soil C and N were similar. Median 0-1 m soil C stocks in pastures ≥8 years formed three different groups: 1) the Tropical dry and moist forest life zones had the lowest estimates, 2) the Tropical wet forest and Premontane wet forest-warm life zone estimates were more than twice as high as the first group, and 3) the Tropical Premontane and Lower Montane rain forest life zone estimates were slightly higher than group 2 (Table 2.3). We did not test for life zone differences for 0-1 m soil N stocks because of the interaction effects between age and life zone (Table 2.2), but median 0-30 cm corrected soil N stocks in pastures ≥ 8 years for each life zone were different from three to four out of five other life zones (Table 2.3). Corrected 0-1 m soil C and N stocks increased with precipitation (C: r = 0.91, $P < 0.01$; N: r = 0.90, $P < 0.01$) and elevation (C: r = 0.70, $P < 0.01$; N: r = 0.72, $P < 0.01$), and decreased with temperature (r = -0.84, $P < 0.01$) (Figures 2.3a-d, Appendix 9).

The effect of pasture age on corrected soil C and N stocks for pastures ≥8 years was inconsistent by depth layers (Table 2.2). Generally, soil C and N stocks decreased with depth (Appendices 14-17). Corrected soil C and N stocks in the first 10 and 30 cm did not change with pasture age (Table 2.2), while 0-1 m corrected soil C stocks decreased slightly with age ($F_{1,22}$=5.70, P=0.03) (Figure 2.2a). Furthermore, the effect of age for 0-1 m soil N stocks differed by life zone ($F_{1,17}$ = 2.95, P = 0.04; Figure 2.2b). The effect of pasture age on corrected soil C stocks adjusted for potential tool bias was similar to our original estimates, while no interaction or age effect was found for adjusted soil N stocks (Table 2.2). When all pastures were combined, soil C and N stocks slightly decreased with pasture age for the entire soil profile (Appendix 9). Soil C and N stocks for the two pastures ≤2 years were highest within their life zone (Table 2.3).

Changes in soil C and N stocks associated with pasture age were relatively small compared to differences among life zones. For example, regression showed that 0-1 m corrected soil C stocks in an average pasture ≥8 years in the Tropical dry forest life zone decreased from 82 Mg C/ha at age 10 to 74 Mg C/ha at age 70, whereas, in the Tropical Lower Montane rain forest life zone 0-1 m corrected soil C stocks decreased from 273 to 246 Mg C/ha for the same age range.

The BIC model ranking results confirmed our findings based on our regression line comparisons. The “best” BIC-ranked model predicting corrected 0-1 m soil C stocks included the variables age and life zone (Table 2.4a). Additionally, BIC rankings suggest that life zone was a better predictor of soil C stocks than temperature or precipitation alone, and adding age to the variables life zone and temperature in models with those terms improved model fit. After excluding the two youngest pastures, rankings indicated that two other models competed with the age and life zone model (Table 2.4b). The first competing model had only life zone as a predictor variable and the second competing model included an interaction between age and life zone. When ranking models to predict 0-30 cm soil C stocks, the best model included life zone, indicating that the effect of age on soil C stocks was not as strong in 0-30 cm as in the 0-1 m soil layer (Appendix 18). Nevertheless, the life zone and age model strongly competed with the life zone model for 0-30 cm soil C stocks (Appendix 18).

On average, soil C and N stock estimates in pastures adjusted for standardized soil bulk density estimates for mature forests were 24 and 23% higher, respectively, than our original pasture soil C and N stock estimates (Figure 2.2 and Appendix 19). Generally, the smallest increases due to adjusting soil bulk density estimates were found in the Tropical dry forest pastures and the largest increases in the youngest pastures in the Tropical wet forest and Lower Montane rain forest life zone (Appendix 19).

2.3.4 Effects of forest-to-pasture conversion on soil C and N stocks

Average corrected 0-1 m soil C and N stock in pastures ≥8 years were 10 ± 5% (15 ± 7 Mg C/ha) and 12 ± 4% (1.7 ± 0.5 Mg N/ha) higher after forest-to-pasture conversion. However, estimates were highly variable, ranging from -36% (-39 Mg C/ha) to 62% (78 Mg C/ha) for Δ 0-1 m soil C stocks, and -41% (-3.7 Mg N/ha) to 44% (6.0 Mg N/ha) for Δ 0-1 m soil N stocks (Table 2.5). The Δ 0-1 m soil C and N stocks in the two pastures ≤2 years, which were excluded from the comparison of regression lines, were high (C: 49 and 96%; N: 52% for both). Corrected Δ 0-1 m soil C stocks were correlated with Δ 0-1 m soil N stocks in our pastures ($r = 0.92$, $P < 0.01$) (Figure 2.1c).

On average Δ 0-1 m soil C and N stock estimates adjusted for potential tool bias in soil bulk density estimates were 21 Mg C/ha and 1.4 Mg N/ha lower, respectively, than original Δ 0-1 m soil C and N stock estimates (Tables 2.5 and 2.6). Differences between original and adjusted Δ 0-1 m soil C and N stocks varied from -93 to 36 Mg C/ha and -6.5 to 3.0 Mg N/ha compared to original estimates, respectively. On average, adjusted Δ 0-1 m soil C stock were -4 Mg C/ha while adjusted Δ 0-1 m soil N stock indicted no change (Table 2.6 and Figure 2.5). Nevertheless, adjusted Δ 0-1 m soil C and N stocks due to pasture-to-forest conversion varied by pasture from -104 to 145 Mg C/ha and -6.8 to 10.5 Mg N/ha, respectively (Table 2.6).

The direction and relative magnitude of original Δ soil C stocks differed by soil depth for some of our pastures (Table 2.5). While average Δ soil C stocks in the Tropical moist forest and Tropical Premontane rain forest life zone increased in 0-1 m, they decreased in the 0-30 cm soil layer. For two pastures in the Tropical Lower Montane rain forest life zone Δ soil C stocks decreased in the 0-1 m soil layer, while they increased in the 0-30 cm layer. In the Tropical Premontane wet forest-warm life zone, Δ soil C stocks in 0-1 m soils were relatively small compared to 0-30 cm soils.

In Tropical dry forest life zone, negative Δ soil C stocks in the 0-1 m soil layer were relatively large compared to the 0-30 cm soil layer.

The effect of age was not uniform for all life zones and the analysis was sensitive to the exclusion of certain pastures. Generally, Δ 0-1 m soil C stocks in pastures ≥8 years in the Tropical wet forest life zone decreased with pasture age, but changes with pasture age were less profound or not present in other life zones (Figure 2.4ac). Absolute (original and adjusted) Δ 0-1 m soil C stock estimates in pastures ≥8 years were unrelated to age (Table 2.2; Figure 2.4a). There was an interaction effect between age and life zone for absolute original Δ 0-1 m soil N stock estimates ($F_{5,17} = 3.5$, $P = 0.02$; Table 2.2 and Figure 2.4b) while absolute adjusted Δ 0-1 m soil N stocks were unrelated to age (Table 2.2). There was also an interaction between age and life zone for relative Δ 0-1 m soil C and N stocks (C: $F_{5,17} = 2.9$, $P = 0.047$; N: $F_{1,17} = 3.7$, $P = 0.02$; Table 2.2 and Figure 2.4cd). After excluding the oldest pasture (70 years) in the Tropical Premontane rain forest life zone, the interaction effect was insignificant (C: $F_{5,16} = 1.8$, $P = 0.16$; N: $F_{1,16} = 1.1$, $P = 0.4$) and the effect of age became similar for all life zones (C: $F_{1,21} = 9.06$, $P = 0.01$; N: $F_{1,17} = 5.66$, $P = 0.03$). The 70-year-old pasture had higher relative Δ 0-1 m soil C and N stocks than any of the other pastures >54 years old and was the only pasture >54 years old in higher elevation life zones. Within the same life zone the 70-year-old pasture was not an outlier.

Comparisons of regression lines of pastures ≥8 years indicated Δ soil C and N stocks varied by life zone (Table 2.2). All life zones were different from three to five other life zones when comparing Δ soil C stocks in pastures ≥8 years, but we did not conduct this test for 0-1 m soil N stocks due to the interaction between life zone and pasture age (Table 2.5). Original and adjusted soil C stock estimates in most pastures in the Tropical dry forest and Tropical Lower Montane rain forest life zone were lower than in their reference forests. Pastures in all other life zones (with the exception of one pasture in the Tropical moist forest life zone) had higher original soil C stock estimates than their reference forests (Tables 2.5 and 2.6). In contrast, soil C stock estimates adjusted for tool bias were also lower than their reference forests in the Tropical Premontane rain forest life zone (Table 2.6). Original soil N stock estimates were lower than their reference forest in all pastures in the Tropical dry forest life zone and two pastures in the Tropical Lower Montane rain forest life zone; all other pastures had higher soil N stocks than their reference forests (Table 2.5). In contrast, adjusted soil N stock estimates were lower than their reference forest in most pastures in the Tropical dry forest, Tropical Premontane and Lower Montane rain forest life zones and in one pasture in the Tropical moist forest life zone (Table 2.6). In the Tropical wet forest life zone, original soil C stock estimates were 1.5, and original soil N stock estimates 1.4 times higher due to conversion, which was relative high compared to other life zones (Table 2.5).

The "best" BIC-ranked model predicting absolute Δ 0-1 m soil C stocks included the variables age and life zone (Table 2.7a). Additionally, life zone and age predicted Δ 0-1 m soil C stocks better than temperature and precipitation alone. After excluding the two youngest pastures, the age and life zone model strongly competed with the best ranked life zone model in predicting Δ 0-1 m soil C stocks (Table 2.7b). The Δ 0-1 m soil C and N stocks increased with precipitation (C: $r = 0.58$, $P < 0.01$; N: $r = 0.72$, $P < 0.01$; Figures 2.3e-f), and decreased with age (C: $r = -0.65$, $P < 0.01$; N: $r = -0.59$, $P < 0.01$; Appendix 9), confirming the comparison of regression lines and BIC model ranking results.

2.4 Discussion

2.4.1 Soil C and N stocks in pastures

Our estimates of soil C stocks in pastures across a climatic gradient in Costa Rica were similar to other studies in the Neotropics. Powers and Veldkamp's (2005) estimates of corrected 0-30 cm soil C stocks in pastures in the Tropical wet forest and Tropical Premontane wet forest-warm life zone in Costa Rica (51-112 Mg C/ha) were comparable to our pastures (0-30 cm: 80-121 Mg C/ha). Although DeKoning et al. (2003) used forest instead of pasture soils bulk density estimates to estimate soil C stocks, their estimates of 0-50 cm soil C stocks in pastures in Ecuador (59-195 Mg C/ha) were similar to our corrected 0-50 cm soil C stock estimates (54-212 Mg C/ha). Our 0-30 cm soil C stock estimates in pastures in the Tropical moist forest life zone (41-51 Mg C/ha) were less variable but within the range of estimates (32-61 Mg C/ha) from a similar life zone in the Brazilian Amazon (Neill et al. 1997). The 0-1 m soil C stock estimates by Hughes et al. (2000) in the Subtropical rain forest transition to perhumid life zone in Los Tuxtlas, Mexico (154-193 Mg C/ha), were most similar to our pastures in the Tropical wet forest and Tropical Premontane wet forest-warm life zone.

Estimates of N stocks in pastures elsewhere were relatively rare compared to C stocks. However, we would expect our soil N stock estimates to be in a similar range compared to other areas, unless soil C and N were not as highly correlated as in our study. Post et al. (1985) reported that global N storage followed similar patterns as soil C storage. The C:N ratios in our pastures and mature forests in the Tropical wet forest life zone were lower (11.3-18.0) than C:N ratios (30.2 ± 12.8 SD) in forests reported by Post et al. (1985) for this life zone. Our soil C:N ratios in pastures in the Tropical dry (8.0-13.8) and moist forest life zones (7.3-11.2) fell within the same range Post et al. (1985) reported (13.3 ± 16.6 and 14.9 ± 8.6 SD, respectively) for forests in these life zones.

We presented the first estimates of pasture soil C and N stocks in the Tropical Premontane and Lower Montane rain forest life zones in Costa Rica, which were both higher than our estimates for other life zones. Similar estimates were found for Venezuelan forests in the Tropical Lower Montane moist and Tropical Montane wet forest life zones where 0-1 m soil C stocks ranged between 186 and 319 Mg C/ha (Delaney et al. 1997). Our estimates for pastures in the various wet and rain forest life zones were about twice as high in soil C as the global Tropical rain forest life zone estimates, but were common values for soils of volcanic origin (Andisols) (Batjes and Sombroek 1997).

2.4.2 Relationship between life zone and pasture soil C and N stocks

Across all sites, life zones explained substantial variability of our original and adjusted pasture soil C and N stock estimates. Life zones predicted soil C and N stocks better than climate variables such as precipitation and temperature. The high correlations of soil bulk density, % soil C and N, and soil C and N stocks with temperature, precipitation and elevation confirmed the predictive power of life zones because life zones are specific combinations of these variables. Our 0-1 m soil C stocks were correlated with precipitation ($r = 0.91$), temperature ($r = -0.84$), and elevation ($r = 0.70$) to a greater extent than in other studies. Powers and Veldkamp (2005) found that 0-30 cm soil C stocks in pastures were correlated with elevation ($r = 0.64$, $P < 0.001$). In pastures in northwestern Ecuador, elevation and precipitation were correlated with 0-25 cm % soil C ($r = 0.52$ and $r = 0.54$, $p < 0.01$, respectively) and 25-50 cm % soil C ($r = 0.48$ and $r = 0.43$, $p < 0.01$, respectively) (DeKoning et al. 2003). In the Sarapiqui area of Costa Rica, elevation was correlated with 0-30 cm soil C stocks ($r = 0.41$, $P < 0.05$) and % soil C ($r = 0.7$, $P < 0.01$) in forests (Powers and Schlesinger 2002). For mature forest along a similar climatic gradient as our pastures, life zone was a better predictor variable for soil C and N stocks than soil particle size (Kauffman et al. unpublished data).

Life zones may not be the best model to describe soil C and N stocks across the landscape for smaller spatial scales or climatic gradients (e.g., across a selection of the life zones sampled in this study). In mature forests in the Sarapiqui area in Costa Rica covering four life zones, soil C stocks (0-30 cm) were best explained by Al-humus linkages for low elevation soils, by elevation for high elevation soils, by Al-linkages for low elevation residual soils, and by % silt for low elevation alluvial soil (Powers and Schlesinger 2002). Pastures in Ecuador had stronger correlations between

% soil C and most soil minerals than with precipitation or elevation (DeKoning et al. 2003). In some volcanic soils, soil C increased with the presence of non-crystalline minerals, which may have caused soil C stabilization (i.e., protected from decomposition) (Powers and Schlesinger 2002, DeKoning et al. 2003). This mechanism might explain some of our high soil C stocks in volcanic soils as well, because more stable soil C will mineralize at a slower rate and therefore have higher soil C stocks than non-protected soil C (Six et al. 2002).

2.4.3 Relationship between pasture age and soil C and N stocks

We found that pasture age was not as important of a predictor of soil C and N stocks as life zone. Our 0-1 m soil C and N stocks decreased with pasture age, but the losses were small compared to losses or gains due to forest-to-pasture conversion. Adding age to the variables life zone and temperature in our models to predict soil C stocks in pastures improved model fit, but life zone and individual climate variables explained more of the variation in soil C and N stocks than age. Similarly, Powers and Veldkamp (2005) reported that pasture age in combination with elevation best predicted 0-30 cm soil C stocks in pastures in the Sarapiqui area in Costa Rica.

Our ability to measure the effect of pasture age on soil C and N stocks changes was influenced by soil compaction effects, the ages included in our analyses, and soil depth. Correcting soil C and N stocks for soil compaction reduced the effect of pasture age. However, corrected estimates are more appropriate than uncorrected estimates for understanding how land use duration changes soil C and N stocks (Veldkamp 1994). In addition, we would have detected a stronger correlation of soil C stocks with pasture age if our mature forests sites were included as age zero in the analysis, because of the large increase in the soil C stocks immediately following deforestation in many of the life zones. Our results contrasted with findings in the Tropical wet and Premontane wet forest life zones in Costa Rica where soil C stocks in pastures decreased rapidly after deforestation and stabilized after about 5 years (Veldkamp

1994). The number of very young pastures in our study (n = 2 for pastures < 8 years) was limited because deforestation of primary forests has been prohibited in Costa Rica since 1996. Both young pastures in our study contained 96% and 49% higher soil C stocks and 52% higher soil N stocks than their reference forests. Furthermore, the effect of age on soil C stocks (for both original and adjusted estimates) was not as strong in the 0-30 cm soils as it was in the 0-1 m soil, a finding that contradicts much of the literature (e.g., Powers 2004, Veldkamp 1994). These contrasting results may be explained by the differences in soil bulk density estimates between pastures and mature forests that we found throughout the soil profile, while others reported or assumed changes in soil bulk density only occurred in the topsoil (section 2.4.4).

We found that the effect of age differed by life zone for our original 0-1 m soil N stocks, but not for 0-1 m soil C stocks or 0-1 m soil N stock adjusted for tool bias. An interaction between age and life zone could indicate that mechanisms of soil C and N stock changes differ by life zone or that climate-related deforestation patterns in Costa Rica confounded the relationship between age, life zone and soil C and N stocks. Our sampling design (Table 2.1) reflects the deforestation patterns in Costa Rica - the oldest pastures were found in the most habitable driest life zones and the youngest pastures in wetter life zones. Patterns of pasture age varying by life zone could be explained by preferential clearing due to factors such as climate, soil fertility, and distance to existing roads, oldest cities and ports.

The variation within our chronosequences was too great to determine the effect of pasture age on soil C and N stocks with high levels of certainty. This within-chronosequence variability of soil C and N stocks could be a reflection of inherent spatial soil variability or other factors (such as differences in land use management) that explain differences between pastures within chronosequences. Long-term studies that follow individual pastures over time would determine the effect of age more clearly, but these types of studies are virtually nonexistent in the tropics because they are time consuming and require long-term planning as well as funding.

2.4.4 Soil compaction

We found that soil bulk densities in all pastures were higher than in their reference forests at all depths (except for one layer in one pasture), while other studies assumed or found (e.g., in Costa Rica: Powers 2004, Veldkamp 1994) that soil compaction occurred only in the top soil layers. The higher soil bulk densities in pastures versus forests could be explained by several factors, which could not be verified in our study. Soil compaction could have occurred during clearing of forested lands, by cattle trampling, changes in local climate, or pasture management. Sampling errors could have introduced a bias because we used a different soil gouge auger to take soil bulk density samples in mature forests (volume = 23.7 cm^3) than in pastures (volume = 13 cm^3). Our soil bulk density sample volume was low compared to other studies (96.1-656.5 cm3, Constantini 1995; 300 cm^3,Veldkamp 1994; 50-270 cm^3, Folegatti 2001). Regression equations relating soil bulk density with % soil C for the different mature forest data sets sampled with different tools (Appendix 5) indicated that soil bulk density estimates sampled with tool B were relatively low compared to estimates sampled with tool C. Soil bulk density estimates adjusted for this potential tool bias indicated that soil compaction only occurred in 0-30 cm soil layers, but 30-100 cm soil layers decreased in soil bulk density. A decrease in soil bulk density at depth is not commonly found and is difficult to explain at a process level. The adjustment may have introduced another bias. In addition, the space-for-time substitution approach used in this study could have biased the data if reference mature forest were not representative of the forests originally present at the pasture locations.

The original soil bulk density estimates in the mature forest top soils in the Tropical Premontane and Lower Montane rain forest life zones were very low (e.g. 0-10 cm: 0.16 - 0.29 g/cm^3) and also had relatively high soil C concentrations (16 - 28%). The soil bulk density estimates adjusted for tool bias were slightly higher than the original estimates in the first 10 cm soil (0.24 - 0.41 g/cm^3). Alvarado and Forsythe (2005) reported soil bulk density values in Andisols can be as low as 0.30

g/cm^3. Our lowest estimates fall within the range of soil bulk density estimates for Histosols (0.13-0.36 g/cm^3; Lal et al. 2001). The sampled mature forests may have contained relatively low soil bulk densities due to the presence of organic soils.

Soil compaction increases the soil mass at each soil depth layer and introduces a bias when comparing soil C and N stocks in mature forest with pastures. We provided estimates corrected for the additional soil mass to determine impacts of land use change and duration. Comparing sites between forests and pastures based on an equivalent soil depth without correcting the 0-1 m soil C stock estimates for differences in (original) soil bulk density would lead to 9-35% higher estimates for pasture soil C stocks (Appendix 19). Comparing adjusted 0-1 m corrected soil C stock estimates with those not corrected indicated either an overestimation or underestimation of soil C stocks depending on the life zone. Simply replacing soil bulk density values from pastures with original values from reference forests would lead to 7-37% lower estimates of pasture soil C stocks (Appendix 19). Veldkamp (1994) and Amézquita et al. (2005) reported an overestimation of 3% and 11% for 0-50 cm soil C stocks and 2% and 7% for 0-1 m soil C stocks using uncorrected estimates for four pastures in the Tropical (Premontane) wet forest life zones in Costa Rica. Overestimates based on our original data in our study ranged from 12-24% for 0-1 m soil C stock estimates for pastures in similar life zones. Most other studies of tropical pastures did not report the soil C stocks estimates using different methods of calculation; therefore, possible biases are unknown.

2.4.5 Effects of forest-to-pasture conversion on soil C and N stocks

The direction and magnitude of Δ 0-1 m soil C and N stock estimates in pastures differed by life zone with decreases in the Tropical dry forest life zone and Tropical Lower Montane rain life zones and increases in other life zones for our original estimates. Average adjusted soil C and N stock estimates were also lower than their reference forest in the Tropical Premontane rain forest life zone. Regardless of uncertainties in (Δ) 0-1 m soil C and N stock estimates, this indicated that life zone is a good predictor of Δ 0-1 m soil C and N stocks in pastures across a large climatic gradient. In addition, life zone was a better predictor variable than temperature and precipitation. The original 0-1 m soil C and N stock estimates increased due to conversion in all pastures in the Tropical wet forest, Tropical Premontane wet forest-warm, and Tropical Premontane rain forest life zones. In the Tropical wet forest life zone both net soil C and N stock gains due to conversion were relatively high compared to other life zones. All pastures in the Tropical dry forest life zone, and all but one pasture in the Tropical Lower Montane rain forest life zone, had decreased 0-1 m soil C and N stocks due to conversion. Our results were similar to Guo and Gifford (2002) where the majority of the pastures had higher 0-1 m soil C stocks than their reference mature forests. Murty et al. (2002) also found net increases and decreases in soil C and N stocks due to forest-to-pasture conversion with Δ soil C stocks ranging from -50% to 160% and Δ soil N stocks ranging from -50% to 320% . The largest increases were found in Australian fertilized leguminous pastures with no overgrazing and relative low initial soil C and N stocks. Our original and adjusted results in the Tropical moist forest life zone (precipitation: 2317-2467 mm/year) generally supported Guo and Gifford's (2002) finding that 0-1 m soil C stocks increased due to forest-to-pasture conversion when precipitation ranged from 2000-3000 mm/year. However, there was one pasture with lower soil C and N stocks than the reference forest in this life zone.

There are four different patterns we might expect when observing soil C and N stocks over time: (1) a sudden increase followed by a steady decrease, (2) a sudden decrease followed by a steady increase, (3) a steady decrease, or (4) a steady increase. These patterns are generally created by two different mechanisms: (1) changes caused by the disturbance that leads to a large removal or addition of C and N, and (2) changes in the long-term balance between inputs and outputs that leads to steady changes over time.

Although we did not measure inputs and outputs in our pastures, we offer hypotheses to explain the patterns we observed. Inputs to soil C and N stocks in our pastures were decomposing organic matter from forest slash and roots, pasture litter, senesced grassroots, cow dung, and urine. We would expect that decomposing forest roots after forest-to-pasture conversion would lead to inputs of C and N throughout the soil depth profile. In addition, increased soil N stocks could be explained by increased N fixation by free living bacteria associated with planted grasses in some tropical pastures compared to forests (Reis et al., 2001, Piccolo et al. 1996). Increased soil N stocks due to increased N fixation could also lead to increases in soil C stocks. In contrast, decomposition of surface forest slash leads to C and N input to top soils, which can then move down the soil profile over time. Outputs from soil C and N stocks in our pastures were decomposition of soil organic matter which caused soil C to be respired to the atmosphere and N to either be taken up by the vegetation, lost to the atmosphere through denitrification, or leached out of the ecosystem through aquatic pathways. N taken up by vegetation may return to the soil again when the vegetation is eaten by cattle and cattle dung and urine is deposited on the land.

Generally in our pasture chronosequences, we observed either a sudden increase followed by a steady decrease (pattern 1) or a steady decrease (pattern 3), which likely resulted from the shifts in balances between the various pathways of inputs and outputs. In our data set we only have two chronosequences (Tropical wet forest life zone and Tropical Premontane rain forest life zone) that include observations within the first two years following forest-to-pasture conversion. Both of these observations have highly increased soil C and N stocks (throughout the 0-1 m depth profile) compared to reference forests, which could partly be explained by the high input of C and N from decomposing forest slash and roots created by the conversion. However, the increase in soil C and N stocks for these two pastures is higher than the estimated aboveground C and N stocks losses (Chapter 3). Additional increases in soil C and N stocks could have been caused by either increased soil C and N inputs from grass roots, decreased decomposition rate-constants, or increased N inputs (e.g., by N fixation). However, as these processes probably would not explain increases of up to 51 Mg C/ha and 9.7 Mg N/ha (Appendix 32), inadequate reference mature forests would be a more likely explanation. Both of these chronosequences show different patterns after this initial sudden increase. Soil C and N stocks in pastures in the Tropical wet forest life zone decreased with pasture age after the initial increase due to conversion, which may indicate that the pulse of C and N inputs after conversion did not continue and soil C and N stocks returned to original levels. After the initial sudden increase, soil C and N stocks in pastures in the Tropical Premontane rain forest life zone decreased with pasture age and then increased again. For soil C stocks the increase occurred 25 to 45 years after deforestation, but soil N stocks increased after 10 years until 70 years (the age of the oldest pasture). The increase could have been caused by either increased soil C and N inputs from grass roots, decreased decomposition rate-constants, or increased N inputs (e.g., by N fixation), which promoted soil C increases.

Soil C and N stocks in the youngest pastures in the Tropical moist and wet forest, and Premontane wet forest-warm forest life zones were higher than in their reference forests, which may indicate an initial sudden increase due to conversion. In addition, soil C and N stocks decreased over time in these three chronosequences, which could indicate that the pulse of C and N inputs after conversion was not continued. In the Tropical moist forest and Tropical Lower Montane rain forest life zones, soil C and N stocks were eventually lower in pastures than forests, indicating either decreased inputs of C and N, or increased loss rate-constants. Soils C and N stocks in pastures in the Tropical dry forest life zone were all lower than in reference forests and decreased over time for our original estimates, but our adjusted estimates indicated an increase in soil C and N stocks 43 years after deforestation. In this life zone there may have been no initial increase in soil C and N stocks due to conversion. However, we may not have observed an initial increase because the youngest pasture was 29 years old in this life zone. We would expect lower inputs from forest slash in the Tropical dry forest life zone compared to wetter life zones, due to the lower initial forest biomass and due to fire being used as a tool to clear forest slash in this dry ecosystem, thereby reducing the potential input for soil C and N stocks. Fire was often used in other life zones as well, but the amount of biomass consumed by fire generally decreases with fuel moisture content (Kauffman et al. 1993), which was likely lowest in the Tropical dry forest life zone. In addition, fire in these pastures could have caused pyromineralization, which could have promoted soil N uptake by vegetation or losses through gaseous or aquatic pathways. This mechanism would explain a decrease in soil N stocks. A steady decrease in soil C and N stocks over time could also be explained by a decreased input of C and N to the soils from litter and senesced roots, or increased loss rate-constants, but the adjusted estimates indicated that the opposite may be the case.

2.4.6 Study limitations

Interpretations from the space-for-time substitutions in this study depend on the assumption that the original forests at our pasture locations at the time of clearing were in the same condition as our reference mature forests, and that soil C and N stocks in those forests were in a "steady state" prior to deforestation. There is evidence that initial clearing of forests may have occurred preferentially on forest soils with high initial soil C stocks for our agricultural lands in the Tropical wet and Premontane wet forest-warm life zones (Veldkamp et al. 1992, Powers and Veldkamp 2005). Generally, land use history interviews with landowners in this study confirmed this trend. If preferential clearing on more fertile soils applies to this study, we would expect an overestimation of positive Δ soil C and N stocks and an underestimation of negative Δ soil C and N stocks.

Our results could also be confounded by the effects of climate change if soil C and N stocks in forest and pastures have responded differently to climate changes that occurred since deforestation of our pastures. Deforestation in Costa Rican lowlands have already caused regional climate changes in higher elevation areas such as the Monteverde cloud forests (Lawton et al. 2001), which could have changed soil C and N storage in these high elevation regions. The magnitude and direction of future changes in C and N stocks and fluxes related to changes in global temperatures are a matter of debate (Davidson and Janssens 2006). The relationship between climate variables and soil C and N stocks in forests (Kauffman et al. unpublished) and our pastures were similar. Therefore, we expect shifts related to climate change in pastures and forest soil C and N stocks to have been similar.

The use of different soil sampling tools in mature forests and pastures could have introduced a bias in our soil bulk density estimates. This may have affected the Δ soil C and N stock estimates. We did not find literature on the use of gouge augers for soil bulk density measurements, but the effect of sampler size of commonly used small-diameter core samplers was tested in SE Queensland, Australia (Constantini et al.1995). Constantini et al. (1995) found that soil bulk density measurements did not improve with an internal diameter beyond 5.98 cm, which was a smaller diameter than others had reported earlier (Lal et al. 2001). Decreased diameter sizes of augers have been reported to cause both increased and decreased soil bulk density estimates (Constantini et al. 1995). Lower soil bulk density estimates could be attributed to the incomplete filling of the cylinder and/or shattering during penetration (Constantini et al. 1995). Higher soil bulk density estimates could be caused by the increased compaction due to the high area ratio (the amount of soil which is displaced when the sampler is forced into the ground) (Constantini et al. 1995).

We found increased soil bulk densities at depths where commonly no compaction is encountered, and therefore, a sampling bias is a plausible explanation for part of our differences between forest and pasture soil bulk densities. Our estimated differences in soil bulk densities between mature forests and pastures may include a potential sampling bias due to the use of two different tools to estimate soil bulk density in forests and pastures, and/or inadequacy of our mature reference forests. Ideally, field tests should be conducted to test the differences in soil bulk density estimates using the two different tools. In most of Costa Rica the availability of mature forests is limited, and therefore, it may not be possible to find better matching mature reference forests for current pastures.

Soil C and N stocks in pastures could be calculated using mature forest soil bulk density instead of pasture soil bulk density (DeKoning et al. 2003), if we assume that there was no compaction effect due to forest-to-pasture conversion. This would result in lower soil C and N stock estimates in pastures compared to the estimates using pasture soil bulk densities (Appendix 19). Positive Δ 0-1 m soil C and N stock estimates would decrease and negative Δ 0-1 m soil C and N stocks would increase compared to our original estimates (Appendix 19). In comparison to our original estimates, soil N stocks in all pastures ≥8 years in the Tropical moist and the Premontane and Lower Montane rain forest life zones would have decreased instead of increased soil C and N stocks compared to forests (Appendix 19). Although not as pronounced, soil C and N stocks increases would still occur in the Tropical wet and Premontane wet-warm life zones (Appendix 19).

Adjusted soil bulk density estimates of mature forests may be an improvement of our original estimates of (Δ) soil C and N stocks, if we assume that the use of two different sampling tools introduced a sampling bias. This would result in higher soil C and N stock estimates in mature forests and pastures compared to our original estimates (Appendix 19). On average, adjusted Δ 0-1 m soil C and N stock were lower compared to our original estimates. The method to adjust for potential tool bias for forest soil bulk density measurements (section 2.2.5) assumed that the regression equation based on mature forest data sampled with tool C (n = 4) was representative for mature forests sampled with tool B. This assumption may have introduced an uncertainty into the adjusted estimates.

In our calculations of Δ soil C and N stocks we assumed that soil erosion and/or deposition did not occur in our pastures since deforestation. Erosion and deposition could have offset the pasture soil profiles from the mature forest soil profiles. We expect erosional processes to be limited due to the constant groundcover with pasture grasses. Deposition could have occurred, especially, in some of the pastures in the Tropical wet and Premontane wet-warm life zones during flood events.

This indicates that processes of erosion and deposition are another potential source of uncertainty.

The use of non-replicated chronosequences limits the extent to which our findings can be generalized to other pastures within these life zones. Within life zones, edaphic, hydric, and atmospheric conditions can subdivide life zones into different “plant associations” (Holdridge 1967). We careful selected sites that represented “typical” edaphic, hydric and atmospheric conditions, and therefore, this study is limited to what Holdridge (1967) called “the one climatic association”. Rocky outcrops, swamps, and monsoonal areas are examples of sites that should not be classified as the “one climatic association” and therefore our data should not be extrapolated to these other associations.

Despite these limitations, life zone appears to be a good predictor variable and mapping tool for describing soil C and N stocks and their changes due to forest-to-pasture conversion at the regional scale for Costa Rica. In addition, life zone was a good predictor for soil C and N stocks in mature (Kauffman et al., unpublished data), and secondary forests (Cifuentes-Jara 2008), and croplands (Chapter 4) in Costa Rica. Whether life zone would be a good predictor across the (Neo)tropics cannot be evaluated with the data collected in this study, but evidence from other studies on soil C and N stocks (Post et al. 1982 and 1985, Alvarado 2006) suggests this may be the case.

2.4.7 Implications

In contrast to common assumptions, all pastures had higher soil bulk densities than mature forests at all studied depths (down to 1 m). In addition, soil bulk density estimates adjusted for potential tool bias indicated a decrease in soil bulk density at the deepest depths. This indicated that the soil bulk density estimates were an important source of uncertainty of soil C and N stocks due to conversion. The potential tool bias may have changed the inference regarding forest-to-pasture conversions in either soil

C or N sink or sources for the Tropical Premontane rain forest life zone. Therefore, accurate soil bulk density measurements are essential when estimating soil C and N stocks and their changes. To decrease uncertainties in our soil bulk density estimates, field measurements of our soil bulk density should be improved. Efforts to model C and N stock fluxes due to land conversion should account for changes in soil bulk density and should be based on accurate soil bulk density measurements. Using results from studies that did not correct for soil bulk density changes or does not include accurate soil bulk density measurements to model soil C and N stocks and fluxes could introduce substantial biases.

Our study showed that in many pastures soil C and N stocks changed throughout the 0-1 m depth profile, but the effects of conversion differed between the 0-30 cm and 0-1 m soil profiles. This suggests that the common practice of only measuring soil bulk density and/or % soil C to a depth of 30 cm may introduce large errors in C stock flux estimates. Based on the original data in this study between 44 Mg C/ha was lost and 78 Mg C/ha was gained in the 30-100 cm soil layer, representing a -46% to 123% change from the original forest soil C stocks. The potential tool bias may have introduced an uncertainty is these estimates. Regardless of uncertainties in our data, we concur with the recommendations from Nepstad et al. (1994) and Veldkamp et al. (2003) that soil C stocks should be measured to a depth of at least 1 m.

In Chapter 4 we show that current global C stocks and flux estimates (DeFries et al. 2002, Houghton 2003) endorsed by the IPCC (Denman et al. 2007) likely overestimated global C emissions due to forest-to-pasture conversions. They assumed that soil C stocks always decreased after forest-to-pasture conversions and that C stocks and fluxes were similar for all pastures across climatically diverse areas such as Costa Rica (Houghton and Hackler 2001, DeFries et al. 2002, Houghton 2003, Denman et al. 2007). We found that ecosystem C stocks in Costa Rican pastures and croplands were 2-fold larger using our data compared to Houghton and Hackler (2001) based estimates, which may have lead to a 8-19% overestimate of global C fluxes

(Chapter 4). We estimated that 0-1 m soils in six life zones in Costa Rica sequestered 9-34 Tg C due to forest-to-pasture conversion from 1850-1990, while Houghton and Hackler (2001) estimated a loss of 24 Tg soil C (Chapter 4). Therefore, we suggest that including life zone-specific estimates into national- or global-scale C estimates is of global relevance.

Soil C stocks in the pastures in the Tropical Premontane and Lower Montane rain forest life zones in Costa Rica were among the highest of the world; comparable to soil C stocks in the boreal forests (Batjes and Sombroek 1997). The protection of these soils is therefore of high importance because they could potentially serve as a large C source to the atmosphere.

Increased soil N stocks could have led or can still lead to increased C storage if N is a limiting nutrient in the ecosystem (Aber at al. 1998). Increased soil N stocks can also lead to long-term increases in N fluxes if the ecosystem becomes N-saturated (Aber at al. 1998). In addition, N saturation may become more prevalent under the expected increased N deposition rates (Matson et al. 1999). Tropical lowland forests are generally not N-limited, whereas higher elevation forest can be N-limited (Tanner et al. 1998). This probably plays some role in the mechanisms behind the differences in Δ 0-1 m soil C and N stocks among life zones, and it may play a role in future changes in soil C and N stocks in our pastures. Therefore, predictions of how tropical ecosystems might respond to land use conversion, climate change, CO_2 fertilization, or N deposition should incorporate different scenarios depending on the life zone.

2.4.8 Future research

Although changes in soil C and N stocks due to forest-to-pasture conversion provide valuable information for determining if soils behave as net C and N sources or sinks, additional measurements could provide insight into the mechanisms responsible for these changes. Stable C isotopes could be used to determine how forest- and pasture-derived-soil C changes with pasture age (Veldkamp 1994). This would provide essential information to improve our understanding of why the impact of land use change differed by life zone in our study. Data on soil N cycling and its response to land use change and duration in different tropical climatic conditions are needed to quantify the aquatic and gaseous N losses from the different ecosystems. Moreover, it could improve our understanding of how N limitation status and its changes influence C storage and fluxes. The role of N fixation in tropical land uses is poorly understood (Piccolo et al. 1996), although N fixation may play an important role to combat tropical pasture degradation (Cadisch et al. 1994, Thomas 1995). Understanding the role of N in tropical ecosystems has become urgent because N deposition is predicted to increase another two- or threefold especially in the tropics (Matson et al. 1999) and N limitation is more widespread in the tropics than previously assumed (LeBauer and Treseder, 2008). In addition, understanding the role of phosphorous (P) in these systems will help to understand the mechanism for differences in C and N stocks and fluxes across tropical landscapes, because P is a known (co)-limiting factor in some tropical forests (Townsend et al. 2002).

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Table 2.1. Life zone, pasture age, location, elevation, and climate data of 31 sampled pastures arranged in six pasture chronosequences in Costa Rica.

Life zone	Age (yrs)	Latitude	Longitude	Elevation (m)	Temp.** (°C)	Precip.** (mm/year)
Tropical dry forest	29	10°51.44'	85°34.44' W	197	26.5	1589
	43	10°50.35'	85°33.73' W	122	26.9	1589
	62	10°51.41'	85°33.97' W	154	26.7	1589
	>75 (a)*	10°50.72'	85°34.02' W	144	26.8	1512
	>75 (b)*	10°49.44'	85°37.25' W	304	25.8	1533
Tropical moist forest	28 (a)*	9°46.48' N	84°57.77' W	90	27.4	2450
	28 (b)*	9°46.59' N	84°56.32' W	80	27.4	2467
	42	9°46.60' N	84°56.33' W	69	27.5	2392
	>47	9°46.97' N	84°56.22' W	27	27.8	2317
	>69	9°46.90' N	84°56.50' W	32	27.7	2325
Tropical wet forest	2	10°25.60'	84°05.29' W	139	24.9	4083
	8	10°23.50'	84°06.86' W	239	24.4	4275
	16	10°23.76'	84°07.40' W	237	24.4	4153
	18	10°25.53'	84°05.71' W	170	24.7	4070
	35	10°23.54'	84°06.90' W	238	24.4	4083
	> 35	10°23.96'	84°07.68' W	217	24.5	4083
Tropical Premontane wet forest-warm	15	10°27.24'	84°10.56' W	184	24.7	3617
	20	10°27.13'	84°10.57' W	191	24.6	3617
	26	10°23.84'	83°59.18' W	109	25.1	3883
	40	10°26.74'	84°00.42' W	72	25.3	3793
	50	10°27.16'	84°01.02' W	82	25.2	3800
Tropical Premontane rain forest	1	10°15.47'	84°09.72' W	1034	19.9	4883
	10	10°16.56'	84°10.52' W	858	20.8	4950
	25	10°16.02'	84°09.76' W	954	20.3	4933
	45	10°16.22'	84°09.59' W	998	20.1	4933
	70	10°16.34'	84°10.88' W	866	20.8	5126
Tropical Lower Montane rain forest	16	10°22.09'	84°48.59' W	1419	17.8	4517
	28	10°20.92'	84°48.20' W	1547	17.1	4267
	32	10°21.75'	84°49.08' W	1468	17.5	4367
	48	10°21.83'	84°49.16' W	1452	17.5	4317
	54	10°20.63'	84°48.26' W	1595	16.8	4083

*Labels (a) and (b) were used to distinguish between two pastures with the same age within one life zone.

** Temperature (Castro 1992) and precipitation data (Instituto Meteorologico Nacional 1988) are mean annual averages.

Table 2.2. Results for comparisons of regression lines when testing for: (1) interactions between life zones and age, (2) age effect, and (3) life zone effect for various soil response variables per soil layer (cm) in pastures $\geq$8 years in Costa Rica.

Soil Layer	Response variable	(1) Age x Life zone	(2) Age	(3) Life zone
0-10	Bulkdensity	$F_{5,17} = 0.86$, $P = 0.5289$	$F_{1,22} = 2.49$, $P = 0.1291$	$F_{5,23} = 90.56$, $P < 0.0001$
10-20	Bulkdensity	$F_{5,17} = 0.85$, $P = 0.5311$	$F_{1,22} = 0.14$, $P = 0.7134$	$F_{5,23} = 34.85$, $P < 0.0001$
20-30	Bulkdensity	$F_{5,17} = 0.39$, $P = 0.8493$	$F_{1,22} = 0.01$, $P = 0.9442$	$F_{5,23} = 33.03$, $P < 0.0001$
30-50	Bulkdensity	$F_{5,16} = 0.72$, $P = 0.6211$	$F_{1,21} = 0.37$, $P = 0.5489$	$F_{5,22} = 41.98$, $P < 0.0001$
50-100	Bulkdensity	$F_{5,14} = 0.15$, $P = 0.9612$	$F_{1,18} = 0.53$, $P = 0.4773$	$F_{5,19} = 22.77$, $P < 0.0001$
0-10	Ln(%soil C)	$F_{5,17} = 0.74$, $P = 0.6047$	$F_{1,22} = 0.89$, $P = 0.3566$	$F_{5,23} = 170.69$, $P < 0.0001$
10-20	Ln(%soil C)	$F_{5,17} = 0.44$, $P = 0.8118$	$F_{1,22} = 0.86$, $P = 0.3632$	$F_{5,23} = 98.65$, $P < 0.0001$
20-30	Ln(%soil C)	$F_{5,17} = 0.29$, $P = 0.9129$	$F_{1,22} = 0.06$, $P = 0.8141$	$F_{5,23} = 31.68$, $P < 0.0001$
30-50	Ln(%soil C)	$F_{5,16} = 4.08$, $P = 0.0140$	inappropriate test	inappropriate test
50-100	Ln(%soil C)	$F_{5,14} = 0.38$, $P = 0.8216$	$F_{1,18} = 0.98$, $P = 0.3363$	$F_{5,19} = 57.36$, $P < 0.0001$
0-10	Ln(Soil C stock)*	$F_{5,17} = 2.24$, $P = 0.0977$	$F_{1,22} = 0.04$, $P = 0.8461$	$F_{5,23} = 69.67$, $P < 0.0001$
0-30	Ln(Soil C stock)*	$F_{5,17} = 0.69$, $P = 0.6359$	$F_{1,22} = 0.06$, $P = 0.8049$	$F_{5,23} = 69.49$, $P < 0.0001$
0-100	Ln(Soil C stock)*	$F_{5,17} = 2.27$, $P = 0.0941$	$F_{1,22} = 5.70$, $P = 0.0260$	** $F_{5,22} = 280.10$, $P < 0.0001$
0-10	Ln(Adj soil C stock)***	$F_{5,17} = 0.74$, $P = 0.6047$	$F_{1,22} = 0.89$, $P = 0.3566$	$F_{5,23} = 53.05$, $P < 0.0001$
0-30	Ln(Adj soil C stock)***	$F_{5,17} = 2.04$, $P = 0.1246$	$F_{1,22} = 0.43$, $P = 0.5193$	$F_{5,23} = 90.00$, $P < 0.0001$
0-100	Ln(Adj soil C stock)***	$F_{5,17} = 0.94$, $P = 0.4823$	$F_{1,22} = 5.18$, $P = 0.0330$	** $F_{5,22} = 266.49$, $P < 0.0001$
0-10	Ln(Soil N stock)*	$F_{5,17} = 0.77$, $P = 0.5870$	$F_{1,22} = 3.18$, $P = 0.0881$	$F_{5,23} = 17.30$, $P < 0.0001$
0-30	Ln(Soil N stock)*	$F_{5,17} = 0.62$, $P = 0.6871$	$F_{1,22} = 0.98$, $P = 0.3332$	$F_{5,23} = 42.90$, $P < 0.0001$
0-100	Ln(Soil N stock)*	$F_{5,17} = 2.95$, $P = 0.0427$	inappropriate test	inappropriate test
0-10	Ln(Adj soil N stock)***	$F_{5,17} = 0.77$, $P = 0.5870$	$F_{1,22} = 3.18$, $P = 0.0881$	$F_{5,23} = 30.57$, $P < 0.0001$
0-30	Ln(Adj soil N stock)***	$F_{5,17} = 1.11$, $P = 0.3920$	$F_{1,22} = 0.76$, $P = 0.3922$	$F_{5,23} = 78.39$, $P < 0.0001$
0-100	Ln(Adj soil N stock)***	$F_{5,17} = 1.09$, $P = 0.4016$	$F_{1,22} = 0.47$, $P = 0.5024$	$F_{5,23} = 166.57$, $P < 0.0001$
0-10	Δ soil C stock *	$F_{5,17} = 0.54$, $P = 0.7442$	$F_{1,22} = 0.51$, $P = 0.4833$	$F_{5,23} = 19.71$, $P < 0.0001$
0-30	Δ soil C stock *	$F_{5,17} = 1.70$, $P = 0.1892$	$F_{1,22} = 0.53$, $P = 0.4725$	$F_{5,23} = 15.03$, $P < 0.0001$
0-100	Δ soil C stock *	$F_{5,17} = 1.33$, $P = 0.2990$	$F_{1,22} = 1.81$, $P = 0.1927$	$F_{5,23} = 33.6$, $P < 0.0001$
0-100	Δ Adj soil C stock***	$F_{5,17} = 0.28$, $P = 0.9157$	$F_{1,22} = 1.42$, $P = 0.2461$	$F_{5,23} = 33.85$, $P < 0.0001$
0-10	Δ soil N stock *	$F_{5,17} = 0.67$, $P = 0.6485$	$F_{1,22} = 2.38$, $P = 0.1368$	$F_{5,23} = 10.94$, $P < 0.0001$
0-30	Δ soil N stock *	$F_{5,17} = 0.58$, $P = 0.7176$	$F_{1,22} = 0.55$, $P = 0.4676$	$F_{5,23} = 7.87$, $P = 0.0002$
0-100	Δ soil N stock *	$F_{5,17} = 3.48$, $P = 0.0240$	inappropriate test	inappropriate test
0-100	Δ Adj soil N stock***	$F_{5,17} = 0.82$, $P = 0.5528$	$F_{1,22} = 0.02$, $P = 0.8895$	$F_{5,23} = 18.70$, $P < 0.0001$

* Soil C and N stocks corrected for compaction effects following Veldkamp (1994) and Ellert & Bettany (1995). ** We detected an age effect using $P_{\text{critical}} < 0.05$, and therefore, we accounted for the age effect in test 3. *** Soil C and N stock estimates were adjusted for potential tool bias (section 2.2.5).

Table 2.3. Mean soil C and N stocks (Mg/ha) for two profile depths corrected for soil compaction effects in pastures in six chronosequences in Costa Rican and mean, SE and coefficient of variation (CV) soil C and N stocks by life zone.

	Pasture	Corrected soil C stock (Mg C/ha)				Corrected soil N stock (Mg N/ha)			
Life zone	age (yrs)	0-100 cm		0-30 cm		0-100 cm		0-30 cm	
Tropical dry forest	29	81.8		66.1		6.71		5.29	
	43	75.9		52.2		7.09		4.36	
	62	74.3		53.9		6.52		4.66	
	>75 (a)	75.8		59.4		6.71		5.13	
	>75 (b)	70.8		70.8		5.36		5.36	
	average pasture ± SE	75.7 ± 1.8	a	60.5 ± 3.5	a	6.48 ± 0.29		4.96 ± 0.19	a
	CV (%)	5		13		10		9	
Tropical moist forest	28 (a)	86.5		41.0		9.36		4.18	
	28 (b)	90.1		41.5		9.46		3.97	
	42	87.2		49.6		9.35		4.88	
	>47	85.0		47.9		8.71		4.46	
	>69	73.1		41.7		8.34		4.36	
	average pasture ± SE	84.4 ± 2.9	a	44.3 ± 1.8	a	9.04 ± 0.22		4.37 ± 0.15	a
	CV (%)	8		9		5		8	
Tropical wet forest	2	247.3		120.8		16.72		8.10	
	8	204.5		90.8		15.82		6.77	
	16	191.0		89.8		15.86		7.30	
	18	191.6		94.2		14.69		7.00	
	35	170.4		79.9		14.66		6.73	
	>35	181.9		80.0		14.57		6.28	
	average pasture* ± SE	187.8 ± 5.7	b	87.0 ± 2.9	b	15.12 ± 0.30		6.82 ± 0.17	b
	CV (%)	7		8		4		6	
Tropical Premontane wet forest-warm	15	214.2		117.8		18.83		9.89	
	20	197.7		98.2		16.71		8.05	
	26	216.5		100.9		16.54		8.17	
	40	198.2		106.0		18.51		9.47	
	50	194.8		96.2		16.78		8.36	
	average pasture ± SE	204.3 ± 4.6	b	103.8 ± 3.9	cd	17.47 ± 0.49		8.79 ± 0.37	cd
	CV (%)	5		8		6		10	
Tropical Premontane rain forest	1	302.8		127.4		24.25		9.96	
	10	224.5		91.3		17.48		6.91	
	25	214.1		99.3		17.72		7.93	
	45	240.4		86.3		19.25		6.76	
	70	237.8		108.2		21.89		9.81	
	average pasture* ± SE	229.2 ± 6.1	c	96.3 ± 4.8	bc	19.09 ± 1.02		7.85 ± 0.70	bc
	CV (%)	5		10		11		18	
Tropical lower montane rain forest	16	261.9		115.8		23.82		8.62	
	28	301.1		145.8		25.11		12.39	
	32	247.5		151.0		20.10		12.34	
	48	236.5		117.3		19.35		9.45	
	54	263.3		116.2		21.72		9.77	
	average pasture ± SE	262.1 ± 10.9	c	129.2 ± 7.9	d	22.02 ± 1.09		10.52 ± 0.78	d
	CV (%)	9		14		11		17	

* Young pastures (1 and 2 years old) were not included in calculations of mean, SE, and CV.
n.s. means no samples collected due to hard soils.
Means for each life zone followed by the same letter are similar to one another, means for each life zone not followed by a letter indicates mean for this life zone is different from all other life zones ($p_{adjusted}$ <0.1). It was inappropriate to conduct this test for 0.1m soil N stocks.

Table 2.4. A-priori set of linear models predicting 0-1 m soil C stocks (natural log transformed) in pasture chronosequences across six life zones in Costa Rica ranked by Bayesian Information Criterion (BIC) for (a) all pastures, and (b) pastures ≥8 years. Delta BIC is the difference between the BIC scores of the model in question and the "best" (lowest BIC score) model.

a) all 31 pastures included

Model terms	k (# of parameters)	delta BIC
age, life zone	8	0
life zone	7	8.7
*age, life zone, age * life zone*	13	10.5
precipitation	3	36.2
age, precipitation	4	37.6
*age, precipitation, age *precipitation*	5	41.1
*age, temperature, age * temperature*	5	61.4
age, temperature	4	61.7
temperature	3	73.3
age	3	93.2
(null model, intercept only)	2	99.9

b) pastures ≥8 years (two youngest pastures excluded)

Model terms	k (# of parameters)	delta BIC
age, life zone	8	0
*age, life zone, age * life zone*	13	2
life zone	7	3.3
precipitation	3	49
age, precipitation	4	51.4
*age, precipitation, age *precipitation*	5	54.7
*age, temperature, age * temperature*	5	73.7
age, temperature	4	73.8
temperature	3	81.2
age	3	104.1
(null model, intercept only)	2	107.9

Table 2.5. Original mean absolute and relative Δ soil C and N stock estimates by pasture (and two profile depths for C) in six chronosequences in Costa Rica, and mean (± SE) Δ soil C and N stocks by life zone.

		Δ Soil C stocks				Δ Soil N stocks 0-1 m	
	Pasture	0-1 m		0-30 cm			
Life zone	age (yrs)	total (Mg C/ha)	relative (%)	total (Mg C/ha)	relative (%)	total (Mg N/ha)	relative (%)
Tropical	29	-28.1	-26	-6.4	-8.9	-2.34	-26
dry forest	43	-34.1	-31	-20.4	-28	-1.96	-22
	62	-35.7	-32	-18.6	-26	-2.54	-28
	>75 (a)	-34.1	-31	-13.2	-18	-2.34	-26
	>75 (b)	-39.2	-36	-1.1	-1.5	-3.70	-41
average difference ± SE		-34.3 ± 1.8	-31 ± 1.6	-12.0 ± 3.6 b	-16 ± 5.0 b	-2.58 ± 0.3	-28 ± 3.3
Tropical	28 (a)	8.3	11	-12.8	-24	1.34	17
moist forest	28 (b)	11.9	15	-11.5	-21	1.44	18
	42	9.0	11	-2.6	-4.9	1.33	17
	>47	6.8	9	-6.1	-11	0.69	9
	>69	-5.1	-6	-12.4	-23	0.32	4
average difference ± SE		6.2 ± 2.9 bd	8 ± 3.8 ac	-9.1 ± 2.0 b	-17 ± 3.7 b	1.02 ± 0.2	13 ± 2.8
Tropical	2	121.0	96	53.2	79	5.72	52
wet forest	8	78.2	62	23.6	35	4.83	44
	16	64.7	51	24.3	36	4.87	44
	18	65.3	52	26.6	39.4	3.70	34
	35	44.1	35	12.3	18	3.67	33
	>35	55.6	44	13.2	20	3.57	33
average difference *± SE		61.6 ± 5.7 a	49 ± 4.5	20.0 ± 3.0 ac	30 ± 4.4 a	4.13 ± 0.3	38 ± 2.7
Tropical	15	51.5	32	41.6	55	5.10	37
Premontane	20	34.9	21	22.1	29	2.98	22
wet forest-	26	53.8	33	24.8	32	2.82	21
warm	40	35.4	22	29.8	39	4.78	35
	50	32.1	20	20.0	26	3.05	22
average difference ± SE		41.5 ± 4.6 ac	26 ± 2.8 b	27.6 ± 3.9 a	36 ± 5.1 a	3.75 ± 0.5	27 ± 3.6
Tropical	1	99.0	49	20.5	19.1	8.35	52
Premontane	10	20.7	10	-12.5	-12	1.57	10
rain forest	25	10.3	5	-5.8	-5.4	1.81	11
	45	36.7	18	-8.7	-8.1	3.35	21
	70	34.0	17	3.5	3.3	5.99	38
average difference *± SE		25.4 ± 6.1 bc	12 ± 3.0 ab	-5.9 ± 3.4 bd	-5 ± 3.2 bc	3.18 ± 1.0	20 ± 6.4
Tropical	16	-9.2	-3	8.1	6.2	2.99	14
lower montane	28	30.0	11	20.5	16	4.29	21
rain forest	32	-23.6	-9	33.2	25.4	-0.72	-3
	48	-34.6	-13	-1.0	-0.8	-1.48	-7
	54	-7.7	-3	-8.0	-6.2	0.90	4
average difference ± SE		-9.0 ± 10.9 d	-3 ± 4.0 c	10.5 ± 7.4 cd	8 ± 5.7 c	1.20 ± 1.1	6 ± 5.2

* Young pastures (1 and 2 years old) were not included in calculations of mean and SE. Means for each life zone followed by the same letter are similar to one another, means for each life zone not followed by a letter indicates mean for this life zone is different from all other life zones ($p_{adjusted}$ <0.1).

Table 2.6. Mean absolute and relative Δ soil C and N stock estimates adjusted for tool bias by pasture in six chronosequences in Costa Rica, and mean (± SE) Δ soil C and N stocks by life zone.

	Pasture	Δ Soil C stocks 0-1 m		Δ Soil N stocks 0-1 m	
Life zone	age (yrs)	total (Mg C/ha)	relative (%)	total (Mg N/ha)	relative (%)
Tropical dry forest	29	-47.7	-36	-3.99	-36
	43	-47.5	-36	-2.72	-25
	62	-53.8	-40	-4.01	-36
	>75 (a)	-51.5	-39	-3.72	-34
	>75 (b)	-57.9	-43	-5.33	-48
average difference ± SE		-51.6 ± 2.0	-39 ± 1.5	-3.95 ± 0.4	-36 ± 3.8
Tropical moist forest	28 (a)	1.7	2	0.58	5
	28 (b)	13.9	14	1.42	13
	42	-0.1	0	0.26	2
	>47	0.8	1	0.14	1
	>69	-13.7	-14	-0.41	-4
average difference ± SE		0.5 ± 4.4	1 ± 4.3	0.40 ± 0.3	4 ± 2.8
Tropical wet forest	2	144.5	72	4.58	26
	8	62.9	31	2.53	14
	16	44.0	22	2.86	16
	18	48.5	24	1.53	9
	35	35.6	18	2.96	17
	>35	46.4	23	2.17	12
average difference *± SE		47.5 ± 4.4	24 ± 2.2	2.41 ± 0.3	14 ± 1.5
Tropical Premontane wet forest-warm	15	45.4	23	5.22	32
	20	35.9	18	3.22	19
	26	56.5	28	2.78	17
	40	24.6	12	4.68	28
	50	30.0	15	3.03	18
average difference ± SE		38.5 ± 5.7	19 ± 2.8	3.78 ± 0.5	23 ± 3.0
Tropical Premontane rain forest	1	126.3	35	10.53	38
	10	-58.6	-16	-4.74	-17
	25	-65.4	-18	-3.59	-13
	45	-27.3	-8	-1.99	-7
	70	-59.3	-17	-0.56	-2
average difference *± SE		-52.6 ± 8.6	-15 ± 2.4	-2.72 ± 0.9	-10 ± 3.3
Tropical lower montane rain forest	16	-70.4	-18	-4.86	-16
	28	-10.2	-3	1.37	5
	32	-104.3	-27	-6.87	-23
	48	-104.2	-27	-6.78	-22
	54	-58.0	-15	-2.79	-9
average difference ± SE		-69.4 ± 17.4	-18 ± 4.4	-3.99 ± 1.5	-13 ± 5.1

* Young pastures (1 and 2 years old) were not included in calculations of mean and SE.

Table 2.7. A-priori set of linear models predicting Δ 0-1 m soil C stocks in pasture chronosequences across six life zones in Costa Rica ranked by Bayesian Information Criterion (BIC) for (a) all pastures, and (b) pastures ≥8 years. Delta BIC is the difference between the BIC scores of the model in question and the “best” (lowest BIC score) model.

a) all 31 pastures included

Model terms	k (# of parameters)	delta BIC
age, life zone	8	0
life zone	7	4.3
*age, life zone, age * life zone*	13	12.2
age, precipitation	4	18.2
age	3	20.1
*age, precipitation, age *precipitation*	5	21.6
age, temperature	4	22.9
precipitation	3	24.7
*age, temperature, age * temperature*	5	24.8
(null model, intercept only)	2	33.9
temperature	3	37.3

b) pastures ≥ 8 years (two youngest pastures excluded)

Model terms	k (# of parameters)	delta BIC
life zone	7	0
age, life zone	8	1.1
*age, life zone, age * life zone*	13	8.3
age, precipitation	4	34.2
precipitation	3	35.6
*age, precipitation, age *precipitation*	5	37.1
age	3	37.5
*age, temperature, age * temperature*	5	40
age, temperature	4	40.2
(null model, intercept only)	2	44.5
temperature	3	47.9

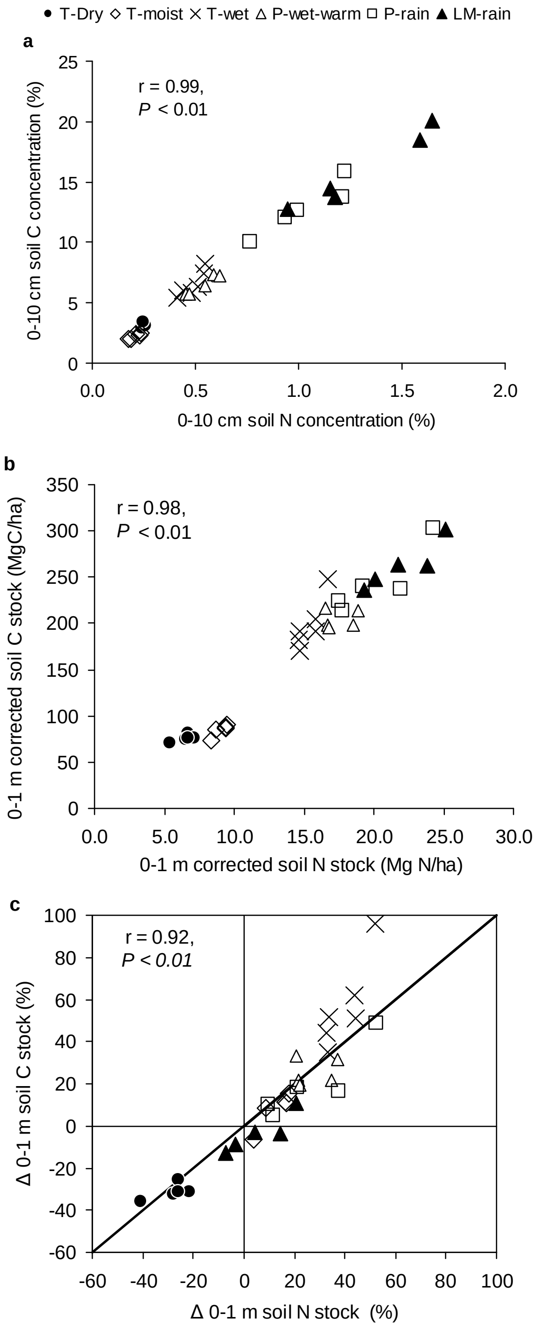

Figure 2.1. Correlations between (a) 0-10 cm % soil C and N, (b) 0-1 m corrected soil C and N stocks, and (c) relative Δ 0-1 m corrected soil C and N stocks in 31 pastures labeled by life zones in Costa Rica. Life zones: T-dry = Tropical dry forest; T-moist = Tropical moist forest; T- wet = Tropical wet forest; P-wet-warm = Tropical Premontane wet forest-warm; P-rain = Tropical Premontane rain forest; LM-rain = Tropical Lower Montane rain forest.

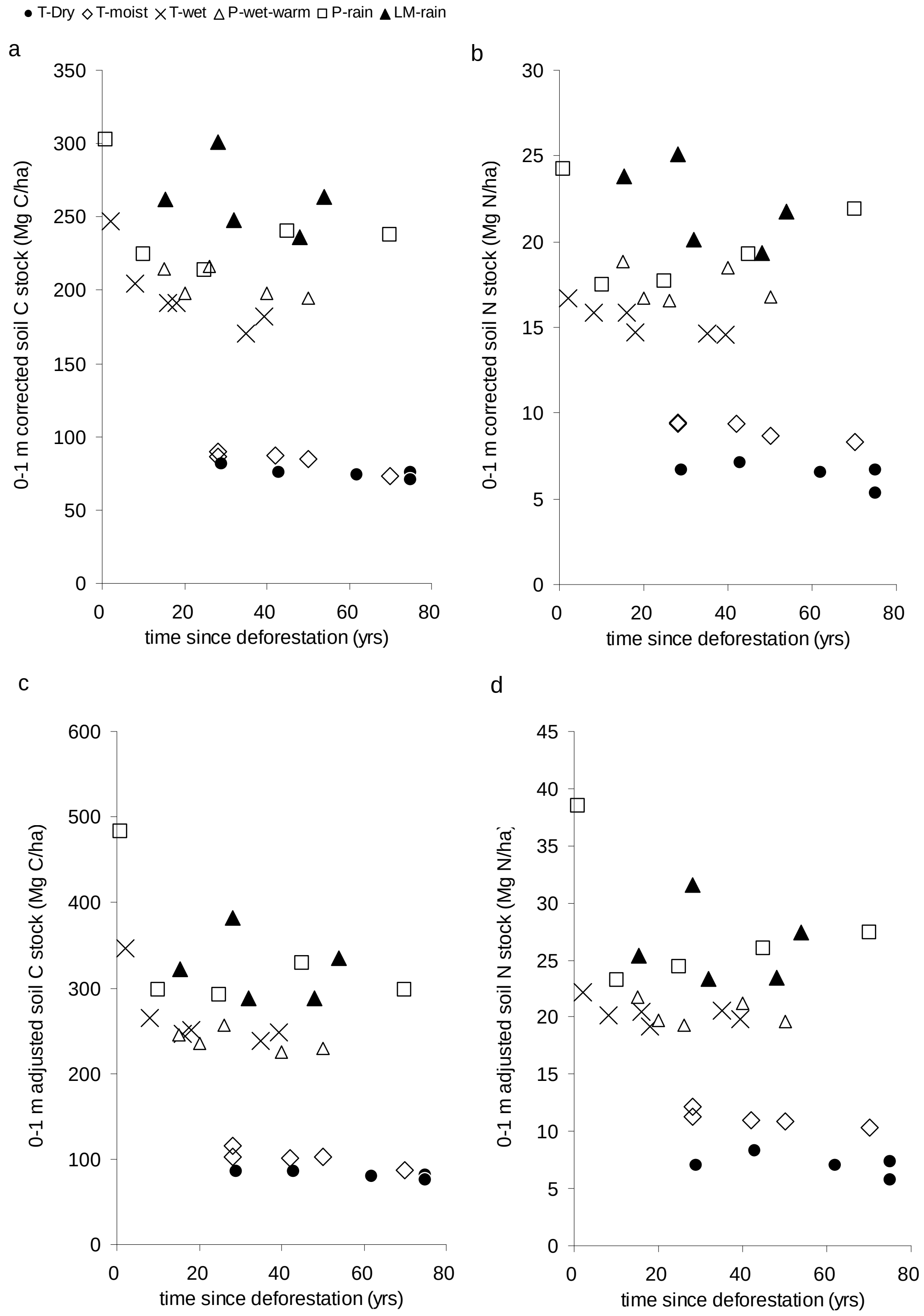

Figure 2.2. (a) Corrected soil C and (b) N stock estimates, (c) adjusted soil C and (d) N stock estimates in pastures by pasture age in six life zones in Costa Rica. Life zones: T-dry = Tropical dry forest; T-moist = Tropical moist forest; T- wet = Tropical wet forest; P-wet-warm = Tropical Premontane wet forest-warm; P-rain = Tropical Premontane rain forest; LM-rain = Tropical Lower Montane rain forest.

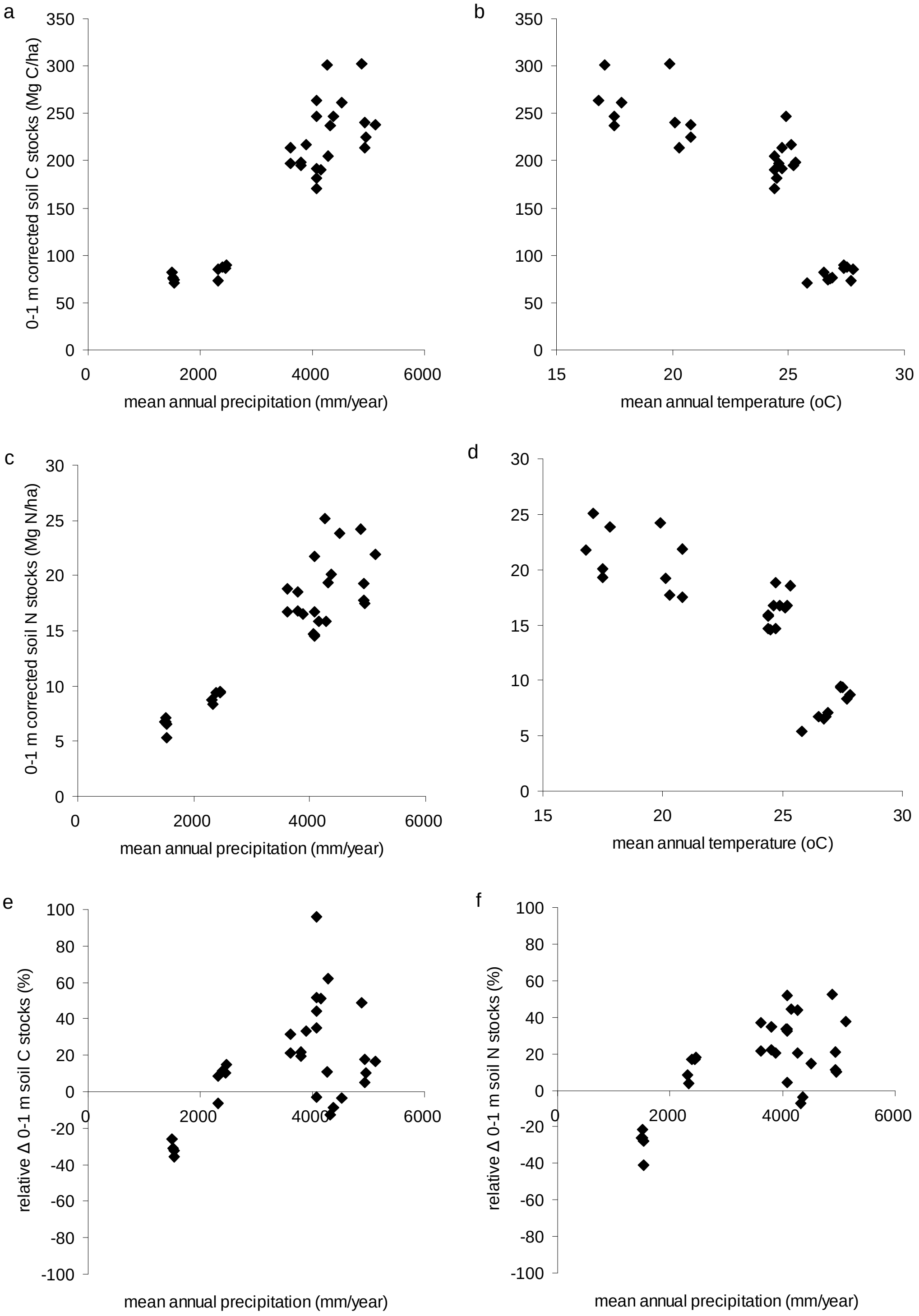

Figure 2.3. Relationships between (a-b) corrected soil C and (c-d) N stocks in pastures (Mg/ha) and (e) relative Δ soil C and (f) N stocks (%) in 31 Costa Rican pastures with mean annual precipitation (mm/year) and temperature (^{o}C).

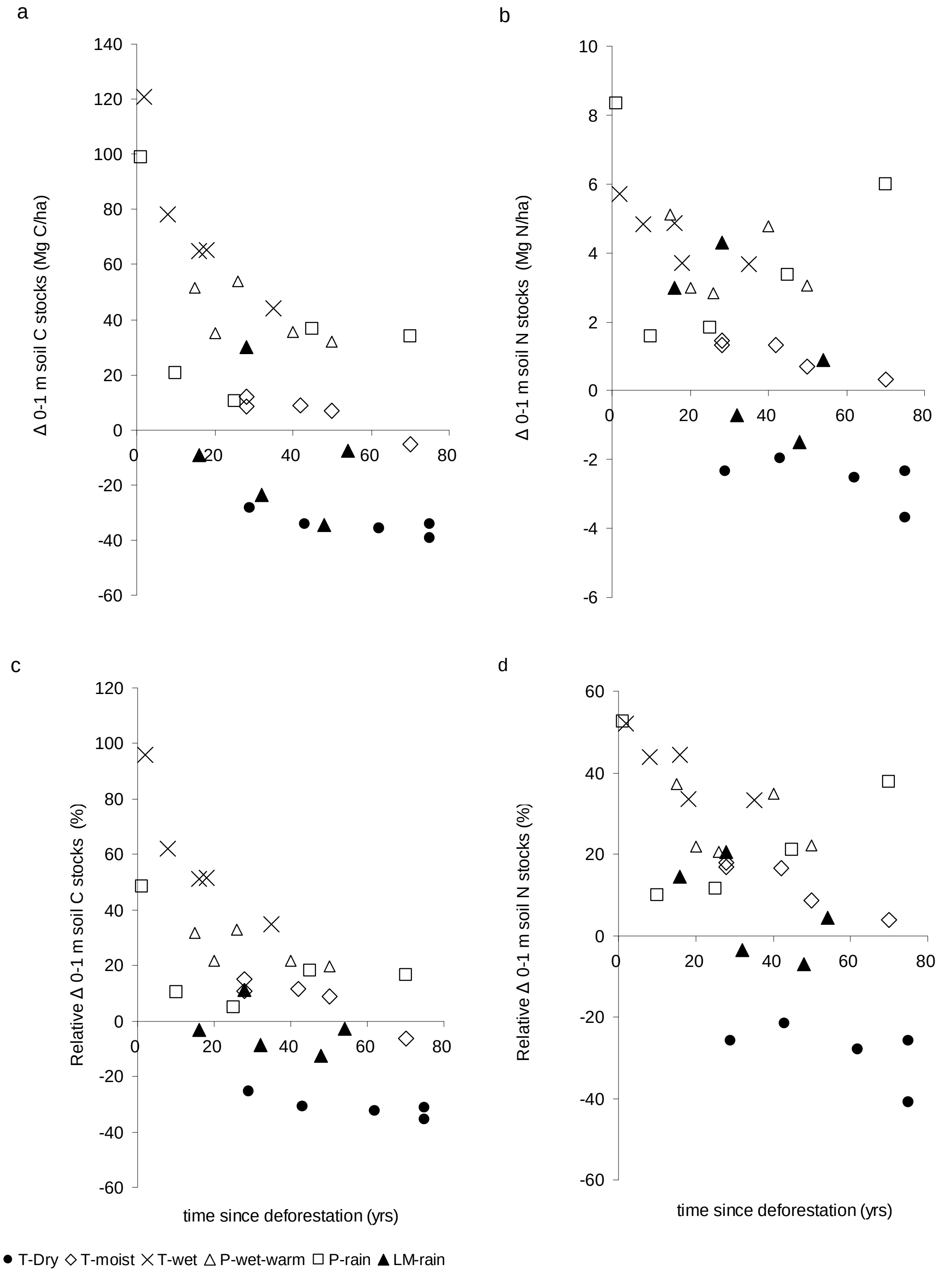

Figure 2.4. Absolute (a and c) and relative (b and d) Δ 0-1 m soil C and N stocks by pasture age in six life zones in Costa Rica. Life zones: T-dry = Tropical dry forest; T-moist = Tropical moist forest; T- wet = Tropical wet forest; P-wet-warm = Tropical Premontane wet forest-warm; P-rain = Tropical Premontane rain forest; T-lm-rain = Tropical Lower Montane rain forest.

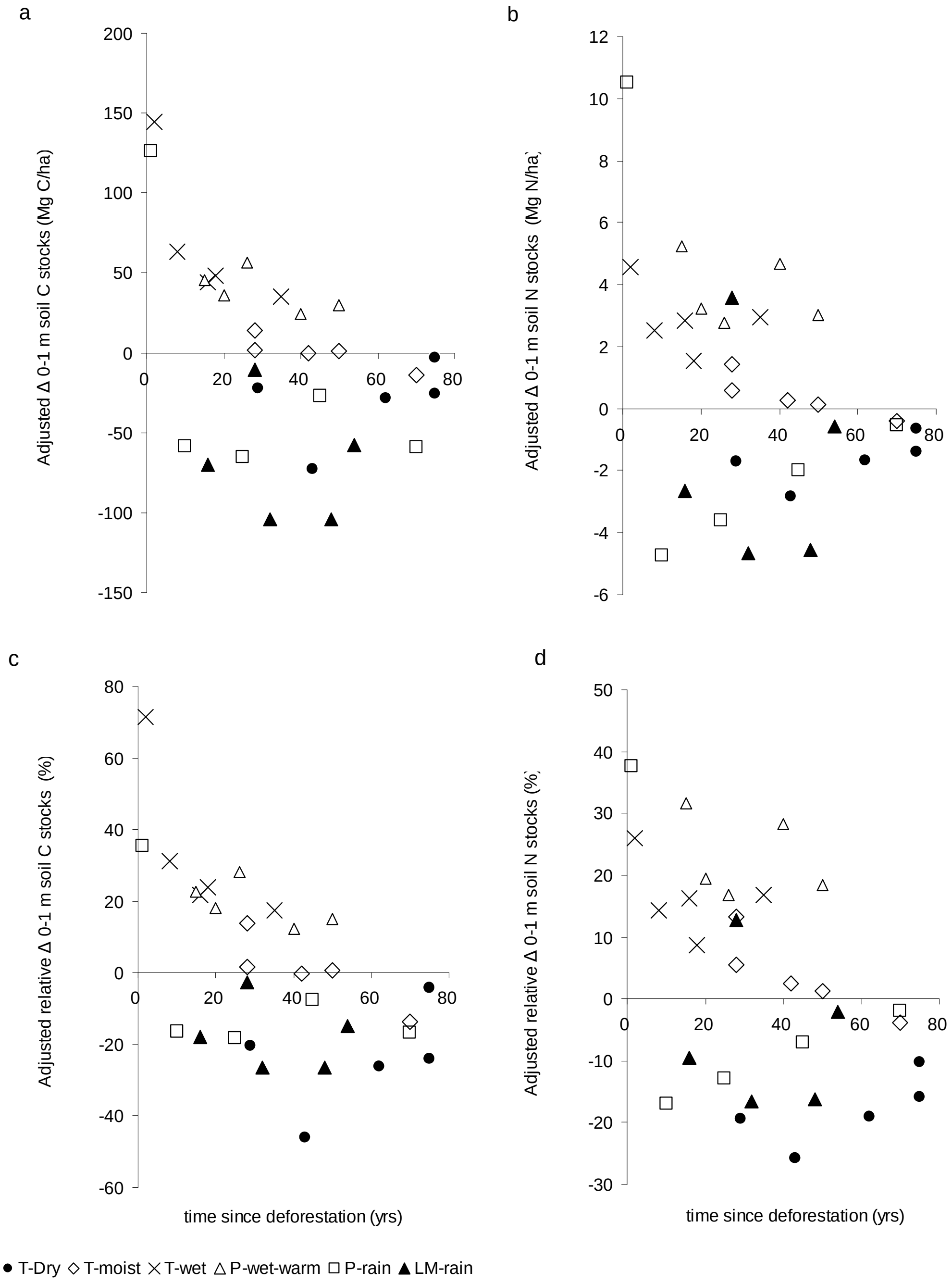

Figure 2.5. Absolute (a and c) and relative (b and d) adjusted Δ 0-1 m soil C and N stocks by pasture age in six life zones in Costa Rica. Life zones: T-dry = Tropical dry forest; T-moist = Tropical moist forest; T- wet = Tropical wet forest; P-wet-warm = Tropical Premontane wet forest-warm; P-rain = Tropical Premontane rain forest; LM-rain = Tropical Lower Montane rain forest.

CHAPTER 3

ABOVEGROUND AND ECOSYSTEM CARBON AND NITROGEN STOCKS AFTER FOREST-TO-PASTURE CONVERSION IN SIX PASTURE CHRONOSEQUENCES ALONG A BIOCLIMATIC GRADIENT IN COSTA RICA

Chapter 3 Aboveground and ecosystem carbon and nitrogen stocks after forest-to-pasture conversion in six pasture chronosequences along a bioclimatic gradient in Costa Rica

Abstract

In the 1980s and 1990s, forest-to-pasture conversions in the tropics contributed to ~20% of global atmospheric carbon (C) emissions and uncertainties of these estimates were highest of all fluxes in the global carbon C budget. In addition, land conversion may affect C storage indirectly due to changes in soil nitrogen (N). C and N in forest vegetation are lost from the ecosystem when forests are converted to pasture, but the extent of aboveground C and N loss and the fate of C and N stocks in soils are uncertain. Life zone and pasture age may influence the variability in C and N stocks. Our objectives were to: (1) quantify aboveground and ecosystem C and N stocks in pastures of a wide age range across a broad climatic gradient, (2) quantify net changes in aboveground and ecosystem C and N stocks due to forest-to-pasture conversion, and (3) determine how aboveground and ecosystem C and N stocks and associated net changes varied with pasture age and life zone. We measured ecosystem C and N stocks in 31 Costa Rican pastures representing chronosequences within six different life zones from the Tropical dry forest to Tropical Lower Montane rain forest life zones. Ecosystem C and N stocks were on average 38 ± 4% (-119 ± 13 Mg C/ha) lower and 6 ± 4% (1.03 ± 0.53 Mg N/ha) higher, respectively, in pastures compared to their reference mature forests. However, changes in ecosystem C and N stocks due to forest-to-pasture conversion varied by life zone ranging from -66% to 8% (-259 to 26 Mg C/ha) and -53% to 43% (-6.12 to 7.48 Mg N/ha), respectively. High spatial soil variability, potential inadequate reference mature forests, and the use of different sampling tools to estimate soil bulk density in mature forests and pastures contributed to uncertainties in ecosystem C and N stock changes due to forest-to-pasture conversion. Variability in ecosystem C and N stocks and the changes due to forest-to-pasture conversion were related to life zone and pasture age; generally life zone explained more variation than pasture age. Generally, ecosystem C and N stocks increased with precipitation and decreased with temperature and pasture age, although, ecosystem C and N stocks increased with pasture age in the Tropical Premontane rain forest life zone. Ecosystem C stocks changes increased with initial forest C stocks and precipitation and decreased with age, while ecosystem N stock changes increased with temperature and decreased with age. In 20% of the pastures, large remnant trees were responsible for exceptional high aboveground C and N stocks, which caused high variability within life zones. We suggest that potential biases and uncertainties of global C stocks and flux estimates could be reduced if the variability in ecosystem C stocks and changes related to life zone and large remnant trees are incorporated when making these estimates.

3.1 Introduction

Knowledge about carbon (C) and nitrogen (N) cycling and related uncertainties is essential to our understanding of ecosystems and the biosphere. Human activities, such as fossil fuel burning, mining, land use change and agriculture, have altered C and N cycles since the beginning of the Industrial Revolution (Solomon et al. 2007). In the 1980s and 1990s land use change, primarily tropical forest-to-pasture conversion, contributed to ~20% of the global atmospheric C emissions (Denman et al. 2007). Moreover, these tropical C flux estimates had the highest uncertainty of all the fluxes in the global C budget (Denman et al. 2007). Tropical land use change is also a large source of another important greenhouse gas, nitrous oxide (N_2O), which is released during forest biomass burning, cattle raising, and use of N fertilizers (Denman et al. 2007). The impacts of forest-to-pasture conversion on the N cycle are also highly uncertain (Neill et al. 2005).

An improved understanding of global C and N cycling and its response to land use change is needed to include N feedbacks into climate-C cycle models (Thornton et al. 2007). The coupled climate-C cycle models used in the Intergovernmental Panel on Climate Change's (IPCC) most recent assessment do not include N feedbacks (Denman et al. 2007). Nevertheless, N is the primary limiting nutrient in terrestrial ecosystems at mid and high latitudes, as well as an important co-limiting nutrient for tropical plant growth, and hence, for terrestrial CO_2 uptake (Reich et al. 2006, Thornton et al. 2007).

Forest ecosystems contain the majority of the terrestrial C stocks but 40-50% of the world's terrestrial lands are used for agricultural purposes, 70% of which is permanently used as pasture (Smith et al. 2007). Therefore, ecosystem C and N stocks in pastures and their changes due to forest-to-pasture conversion are a significant part of the global C and N stock and flux estimates. Nevertheless, aboveground and ecosystem C and N stocks in tropical agricultural lands have rarely been measured

(Guild et al 1998, Kauffman et al. 1998, Hughes et al. 2000 and 2002, Jaramillo et al. 2003).

Although, forest C is lost when clearing trees for pasture, the extent and rate of C lost with vegetation change are highly variable (Houghton 2007). Climate and time since deforestation (pasture age) may play important roles in controlling the variability in aboveground C and N stocks among pastures. Aboveground C stocks in mature (Brown and Lugo 1982, Kauffman et al. unpublished data) and secondary forests (Cifuentes Jara 2008) differ by life zone and other climate variables. Especially when all forest trees are not cleared during pasture conversion, aboveground C and N stocks in pastures may depend on the initial forest C and N stocks, and thus on life zones. Aboveground C and N stocks may decline rapidly immediately after deforestation followed by a slow decrease over time (Kauffman et al. 2003). Nevertheless, the IPCC’s latest estimate assumed that C stocks in the vegetation of all Neotropical pastures were 10 Mg C/ha within 10 years after deforestation (Houghton and Hackler 2001, Houghton 2003, Denman et al. 2007), introducing a possible bias into the global C budget.

The fate of soil C and N stocks in response to land use change is uncertain as well (Guo and Gifford 2002, Murty et al. 2002). This uncertainty may play an important role at the ecosystem level, because globally, soils contain larger C and N stocks than vegetation (Chapin et al. 2002). Both losses and gains in soil C and N stocks due forest-to-pasture conversion have been reported; two global reviews found that on average either: (1) soil C stocks increased (Guo and Gifford 2002), or (2) soil C and N stocks remained the same (Murty et al. 2002). Guo and Gifford (2002) found that sites with precipitation between 2000-3000 mm/year had increased soil C stocks after conversion; whereas sites with higher or lower precipitation had both increased and decreased soil C stocks suggesting that soil C changes are related to climate. Nevertheless, the IPCC’s latest estimate assumed that all tropical soil C stocks decreased after forest-to-pasture conversions (Houghton and Hackler 2001, Houghton 2003, Denman et al. 2007), introducing another possible bias into the global C budget.

Life zone-based estimates of ecosystem C and N stock changes may reduce possible biases and uncertainties in global C flux models substantially and aid the development of coupled climate-C-N models. Houghton et al. (1991) indicated that life zone based estimates of croplands and pastures in Latin America increased the estimates of ecosystem C flux between 1850 and 1990 by 15% compared to their reference estimate. However, no life zone based estimate for C stocks in pasture vegetation was used, probably due to a lack of data. In addition, they still assumed all soil C stocks decreased due to forest-to-pasture conversion regardless of life zone (Houghton et al. 1991).

In this study we determined if tropical aboveground and ecosystem C and N stocks and associated net changes were related to life zone and land use duration in Costa Rica. Our objectives were to: (1) quantify aboveground and ecosystem C and N stocks in pastures of a wide age range across a broad climatic gradient, (2) quantify net changes in aboveground and ecosystem C and N stocks due to forest-to-pasture conversion, and (3) determine how aboveground and ecosystem C and N stocks and associated net changes varied with pasture age and life zone. More specifically, we addressed the following research questions: (1) Are life zone and other climate variables good predictors of aboveground and ecosystem C and N stocks in pastures and their net changes due to pasture-to-forest conversion?; (2) Do aboveground and ecosystem C and N stocks in pastures change with pasture age?; and (3) Does the effect of pasture age on aboveground and ecosystem C and N stocks differ by life zone?

3.2 Methods

3.2.1 Study areas

Our research was conducted in Costa Rica because it has an extremely high biotic and physical diversity in a relatively small area (51,100 km^2). Costa Rica is bordered by the Atlantic and the Pacific oceans, and is dissected by volcanic mountain ranges from northwest to southeast. Across all sampled pastures, mean annual precipitation ranged from 1512-5126 mm/year and mean annual temperature ranged from 16.8-27.8 ^oC (Table 2.1). There are 23 different life zones in Costa Rica including 11 transition life zones (Bolaños and Watson 1993). Transition life zones are transitions between two major life zones, similar to ecotones. For example, the Tropical Premontane wet forest-warm is the transition life zone between the Tropical Premontane wet forest and Tropical wet forest life zones. Deforestation in Costa Rica started in the Tropical dry and moist forest life zones, and later in the Tropical wet and Tropical Premontane moist and wet forest life zones; by 1983, only the less accessible areas in the very wet life zones retained relatively undisturbed forest (Sader and Joyce 1988). In 2002, pastures made up about 46% of Costa Rica and 90% of all agricultural land use types (FAO 2008). More details on life zones and soils in Costa Rica and estimation of climate variables were described chapter 2.

3.2.2 Site selection

We stratified pasture sites by six dominant life zones in Costa Rica (Table 2.1). Within each of these life zones, we sampled one chronosequence, consisting of five or six pastures of various ages. The sites for each chronosequence were selected based upon their proximity to mature forest sites sampled in a companion study (Kauffman et al. unpublished) (Appendix 1). We used these mature forests as reference sites to infer impacts of forest-to-pasture conversion. We avoided areas of anomalous soils, rock outcrops, and riparian zones. At each site, geographic coordinates and elevations (Table 2.1) were derived from global positioning system (GPS) readings.

Our pasture chronosequences represented the broadest age range (time since deforestation) within the sampled area that we could find with our time and resource constraints. We determined pasture age by interviews with landowners and other local residents and once with aerial photographs. Chronosequences are space-for-time substitutions and a critical assumption of this approach is that the conditions for all pastures within a chronosequence were initially the same, and thus, differences between pastures of different ages were due to pasture age alone. Assumptions critical to determine net changes due to forest-to-pasture conversion were that our reference forests were in equilibrium and that forest conditions at the pasture sites prior to conversion were similar among sites within each life zone. These assumptions were impossible to verify, but we carefully selected sites to minimize confounding factors.

Pasture management differed by site and we made no attempts to account for these differences. All the pastures were owned by small to large beef cattle ranchers or dairy farmers, and had been actively grazed since pasture establishment. Prior to pasture establishment, many of the pastures were initially cultivated with rice or corn for 1-2 years following forest clearing. In drier areas, slashed forests were burned before pastures were established, and then burned periodically as part of their maintenance. Pasture owners indicated that environmental and health concerns had reduced the use of fire in recent years. We sampled all pastures from January to March 2002.

3.2.3 Aboveground biomass and C and N stocks

Our plot design for quantifying biomass, C, and N stocks in pastures (Appendix 2) was similar to Hughes et al. (2000) and Kauffman et al. (2003). We determined total aboveground biomass (TAGB) of all trees, palms, vines, snags ≥10 cm dbh (diameter at breast height at 1.3 m aboveground), and stumps ≥10 cm diameter in 50- x 100-m macro plots established near the center of each pasture. We measured dbh of smaller (< 10 cm dbh) trees, palms, vines, dead snags, and stumps 0-10 cm dbh within three 1- x 100-m nested subplots 25 m apart in the macro plot. We calculated biomass of downed woody debris using planar intersect techniques (Van Wagner 1968, Brown and Roussopoulous 1974, Table 3.1). We measured diameter of woody debris ≥2.5 cm diameter that intersected one of the three 100-m or two 50-m sampling planes located along macro plot edges and mid-line (Appendix 2). We classified woody debris ≥7.5 cm diameter into sound and rotten classes. Pieces that were soft and fell apart when poking into them were considered rotten. We recorded percent slope of all sampling planes for use in the biomass estimate equation (Table 3.1). Mean specific gravity estimates for downed wood collected in the companion mature forest study (Kauffman et al. unpublished) were used for downed wood in pastures. We estimated biomass of all trees, palms, vines, and snags using allometric relations of diameter and/or height (Table 3.1). We sampled surface layer biomass consisting of litter (fallen leaves, fruits, seeds, bark fragments) and wood <2.5 cm diameter, grasses, and other vegetation <1.3 m in height by collecting all materials in eight 50- x 50-cm micro plots. We placed all micro plots systematically: four at the corners of the macro plot, three at the midpoints of the macro plot outline, and one in the middle of the macro plot (Appendix 2). Fresh weight was determined for all surface layer (grass/litter) samples and subsamples were then oven-dried for 2-3 days at 65 ºC to determine dry weight. To determine C and N concentrations of the pasture surface layer, samples were ground to pass through a 40-mesh screen (0.5 mm) using a cyclotec sample mill (Tecator Inc., Herdon, Virginia), and total C and N analyses were conducted by induction furnace method (Nelson and Sommers 1996) using a Carlo-Erba NA series 1500 NCS analyzer (Fisons Instruments, Danvers, Massachusetts) at Oregon State University. We used C and N concentration estimates from the mature forest data (Kauffman et al., unpublished) for trees, palms, vines, and downed wood in pastures.

3.2.4 Soil and ecosystem C and N stocks

We collected five soil cores to 0-1 m in depth at five locations spaced 25 m apart along a 100-m transect in the middle of the macro plot. Soil cores were partitioned into 5 depth layers and soil samples (n = 25) were collected for each layer to determine soil bulk density, and soil C and N concentrations, which were used to calculate soil C and N stocks. Soil samples were sieved to remove particles >2 mm in diameter, and ground to allow passage through a 60-mesh screen (250-µm pore size). Total C and N concentrations in the soils were determined using the same methods as for our litter/grass samples. Generally, soil C and N stocks were calculated by multiplying soil C and N concentrations with soil bulk density estimates, the length of the soil layer, and a unit conversion factor (Chapter 2). We applied a correction for soil bulk density differences between mature reference forests and pastures (i.e., soil compaction; referred to as corrected soil C and N estimates, Chapter 2). Most mature forests that served as reference forests for the pastures were sampled using another gouge auger (tool B: volume = 23.7 cm^3, width between vertical cutting edges = 3.45 cm) than the gouge auger used to sample pasture soils (tool C: volume = 13 cm^3, width between vertical cutting edges = 2.4 cm). Two reference forests were sampled with the same gouge auger as was used to sample pasture soils (tool C). To adjust for this potential tool bias, we also calculated adjusted soil C and N stocks. We standardized (i.e., adjusted) all reference forest soil bulk densities by estimating soil bulk densities based on forest soil C concentrations using a regression equation of forest data sampled with tool C. Additional information on soil sampling and adjustments of soil C and N stock estimates were described in Chapter 2.

We calculated ecosystem C and N stocks by summing aboveground C or N stocks and 0-1 m soil C or N stocks. In this dissertation we specifically state if estimates were adjusted and in all other cases statements refer to our original estimates. Adjusted ecosystem C and N stocks are the sum of aboveground C or N stocks and soil C or N stock estimates adjusted for potential tool bias. We assumed that the differences in C and N stocks between pastures and mature forests (Δ C and N stocks) were due to the conversions from forest-to-pasture. Our original Δ ecosystem C and N stocks were calculated by subtracting ecosystem C and N stock estimates of reference mature forests from estimates of pastures. Adjusted Δ ecosystem C and N stocks were defined as ecosystem C and N stock estimates adjusted for potential tool bias from pastures minus adjusted estimates from reference mature forests.

3.2.5 Statistical analyses

We determined Pearson coefficients of correlation (*r*) between response variables (aboveground and ecosystem C and N stocks, absolute and relative aboveground and ecosystem C and N stock difference between pastures and forests [Δ aboveground and ecosystem C and N stocks], %C and N and C:N ratio for grass/litter) and explanatory variables (pasture age, elevation, temperature, and precipitation) for our 31 pastures. We compared six regression lines that described the change of response variables with pasture age for the different life zones for each response variable. Regression line comparisons tested whether the: (1) slopes of the regression lines were similar to each other (homogeneity of slopes); (2) response variable correlated with pasture age (slope $\neq 0$); and (3) chronosequences (and thus life zones) were different from each other, while accounting for the effect of pasture age (unequal intercepts). If the slopes of the regression lines differed among life zones (test 1), we did not conduct test 2 and 3 because of the age by life zone interaction. If we detected an age effect (test 2), then we conducted test 3, which was similar to an analysis of covariance with pasture age as a covariate. If we failed to detect an age effect (test 2), then test 3 resembled an analysis of variance. If we detected an effect of life zone in test 2 or 3, we conducted pair wise multiple comparisons with Tukey-Kramer adjustments to test for differences among life zones. We only corrected for age in the multi comparison test for Δ ecosystem C stocks. We natural log-transformed aboveground and ecosystem C stocks to correct for unequal variance and we backtransformed those results; hence, we reported differences between median life zone estimates (Ramsey and Shafer 2002). All statistical tests were conducted in PROC CORR and PROC MIXED using SAS[1] software v 9.1 for Windows (SAS Institute 2002-2003).

Although the ranges of pasture age for the different chronosequences were not identical, they all overlapped substantially (Table 2.1), and therefore, we assumed that our comparison of regression lines was an appropriate procedure. Insufficient sites were available for years immediately after deforestation, therefore only pastures ≥8 years were used to test for age effects in the comparison of regression lines. We could not determine the exact age of five pastures due to constraints in time and resources (Table 2.1). Therefore, the following nominal ages were used for those five pastures in the analyses: >75 years = 75 years, >47 years = 50 years, >69 = 70 years, >35 years = 40 years. We report results on the sensitivity of our regression analyses by using the ages: >75 years (site a) = 100 years, >75 years (site b) = 150 years >47 years = 50 years, >69 = 80 years, >35 years = 50 years.

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3.3 Results

3.3.1 Aboveground C and N stocks in pastures

Aboveground C and N stock estimates in pastures were highly variable mostly due to the presence of large remnant trees and to a lesser extent downed and standing dead wood. Aboveground C stocks ranged from 1-111 Mg C/ha and aboveground N stocks from 0.046-0.886 Mg N/ha (Tables 3.2 and 3.3, Appendices 20-22). The youngest pastures (1 and 2 years) contained among the highest aboveground C and N stocks for all pastures, although there were four older pastures with similar values (Tables 3.2 and 3.3, Appendices 20-22). Aboveground C stocks in our pastures ≥8 years averaged 24 ± 5.8 Mg C/ha. Trees and downed wood stored ≤1 Mg C/ha in 29% and 45% of the pastures, respectively, including all pastures in the Tropical dry forest life zone (Table 3.2). In all pastures, the combined tree, shrub, palm, and vine (labeled as tree/shrub) C and N stock estimates ranged from 0-105 Mg C/ha and 0-0.71 Mg N/ha, respectively (Tables 3.2 and 3.3). Trees >10 cm dbh comprised from 0-100% of tree/shrub biomass (Appendix 23). In five of the six pastures that contained the highest C and N stocks, the majority of aboveground C was stored in 5 trees >30 cm dbh/ha, whereas in the one remaining pasture the majority of the C was stored in 19 trees 10-30 cm dbh/ha. In all pastures, palms comprised 0-15% of tree/shrub biomass, and vines 0-3% of tree/shrub biomass (Appendix 23). Downed wood C and N stock estimates ranged from 0-31 Mg C/ha and 0-0.23 Mg N/ha, respectively, and standing dead material ranged from 0-23 Mg C/ha and 0-0.49 Mg N/ha (Tables 3.2 and 3.3). Grass/litter estimates ranged from 1.1-7.8 Mg C/ha and 0.04-0.24 Mg N/ha (Tables 3.2 and 3.3) and variation in these estimates were probably related to the time between our sampling date and the last grazing event.

In pastures ≥8 years, the effect of age on total aboveground C and N stocks differed by life zone (C: $F_{5,17} = 2.3$, $P = 0.09$; N: $F_{5,17} = 2.5$, $P = 0.07$), and therefore, no life zone comparisons were conducted (Appendix 24). When all 31 pastures were combined, aboveground C and N stocks declined with pasture age (C: $r = -0.51$, $P < 0.01$; N: $r = -0.55$, $P < 0.01$) and increased with precipitation (C: $r = 0.44$, $P = 0.01$; N: $r = 0.46$, $P = 0.01$; Figure 3.1a; Appendix 25). The maxima in aboveground C and N stocks were dissimilar among life zones, but the minima were similar; the highest values in C and N stocks in pastures ≥8 years were found in the Tropical Premontane wet forest-T-basal forest and Tropical Premontane rain forest life zones (Tables 3.2 and 3.3; Appendix 24). Sensitivity tests of our regression analyses using other nominal ages changed results to some degree; it slightly changed correlations between aboveground C (r = -0.46, $P = 0.01$) and N stocks (r = -0.49, $P < 0.01$) and pasture age, but it did not change the results from comparison of regression lines for aboveground C and N stocks. This indicated that effect of age on total aboveground C and N stocks differed by life zone regardless of uncertainty in the ages of the oldest pastures.

3.3.2 C and N concentrations and ratios in pasture litter/grass

In general, litter C:N ratios in mature forests were higher than C:N ratios in pasture grass/litter, except for three pastures in the Tropical dry forest life zone and one of three pastures in the Tropical Lower Montane rain forest life zone (Appendix 26). The %C in grass/litter samples ranged from 34.7-47.4%, %N from 0.74-2.09 %, and mean C:N ratios from 22.7-57.1 (Appendix 27). Mean % C in grass/litter in pastures ≥8 years was not related to pasture age or life zone (Table 3.4). In contrast, mean %N in grass/litter and grass/litter C:N ratios differed with life zone ($F_{5,22} = 9.68$, $P < 0.01$; $F_{5,22} = 13.6$, $P < 0.01$, respectively). Mean % N in grass/litter were lower, and grass/litter C:N ratios were higher in pastures ≥8 years in the Tropical dry forest life zone than in all other life zones, which were similar to one another (Appendix 27). C:N ratios and %N in litter/grass were correlated with elevation (C:N ratio: $r = 0.43$, $P = 0.02$; %N: $r = 0.51$, $P < 0.01$), temperature (C:N ratio: $r = 0.51$, $P < 0.01$; %N: $r = -0.58$, $P < 0.01$), and precipitation (C:N ratio: $r = -0.73$, $P < 0.01$; %N: $r = 0.74$, $P <$

0.01); but we found no correlations between %C in litter/grass and elevation, age, and climate variables (Appendix 25 and 28).

3.3.3 Effects of forest-to-pasture conversion on aboveground C and N stocks

The total aboveground C and N stocks in pastures were all lower than mature reference forests (Table 3.5). Total aboveground C and N stocks in pastures were on average 83% (-139 Mg C/ha) and 78% (-1.05 Mg N/ha) lower than mature forests, respectively, ranging from -24% to -99 % (-34 to -237 Mg C/ha) and -25% to -97% (-0.3 to -1.78 Mg N/ha), respectively (Table 3.5; Figure 3.3a-b; Appendix 29a-b). Absolute Δ aboveground C and N stocks in pastures were dependent on the initial forest stocks. Absolute Δ aboveground C and N stocks in pastures ≥8 years had a stronger relationship with life zone (C: $F_{5,22} = 24.1$, $P < 0.01$; N: $F_{5,22} = 23.7$, $P < 0.01$) than relative differences (C: $F_{5,23} = 2.8$, $P = 0.04$; N: $F_{5,22} = 3.8$, $P = 0.01$; Table 3.4). Hence, absolute mean Δ aboveground C and N stocks in pastures ≥8 years were highest in the Tropical Lower Montane rainforest life zone (-231 Mg C/ha and -1.7 Mg N/ha) where forest aboveground C and N stocks were the highest of all life zones (Table 3.5). Similarly, absolute mean Δ aboveground C and N stocks varied more by pasture age (C: $F_{1,22} = 3.1$, $P = 0.09$; N: $F_{1,22} = 4.6$, $P = 0.04$) than relative differences (C: $F_{1,22} = 2.3$, $P = 0.15$; N: $F_{1,22} = 3.6$, $P = 0.07$). Sensitivity of our regression analyses using other nominal ages changed our results for absolute Δ aboveground C and N stocks: the age effects disappeared (C: $F_{1,22} = 1.49$, $P = 0.23$; N: $F_{1,22} = 2.19$, $P = 0.15$).

Pearson coefficients of correlation indicated that absolute Δ aboveground C and N stocks decreased with elevation (C: $r = -0.72$, $P < 0.01$; N: $r = -0.70$, $P < 0.01$) and precipitation (C: $r = -0.58$, $P < 0.01$; N: $r = -0.52$, $P < 0.01$), and increased with temperature (C: $r = 0.73$, $P < 0.01$; N: $r = 0.69$, $P < 0.01$) (Figure 3.1 b-c, Appendix 25). Relative Δ aboveground C stocks only weakly increased with precipitation ($r = 0.31$, $P = 0.09$) and relative Δ aboveground N stocks were not correlated with any of the climate variables (Appendix 25). The effects of age on absolute Δ aboveground C and N stocks were masked by the effect of climate (Appendix 25), and relative differences decreased with pasture age (C: $r = -0.62$, $P < 0.01$; N: $r = -0.58$, $P < 0.01$).

3.3.4 Ecosystem C and N stocks in pastures

Soil C and N stocks comprised the majority of pasture ecosystem C and N stocks because aboveground C comprised on average 11% (ranging from 1-36%), and aboveground N comprised on average 2% (ranging from 0.2-4.7%) of the ecosystem (Tables 3.2 and 3.3; Figure 3.4). Original ecosystem C and N stock estimates in pastures were highly variable, ranging from 73-406 Mg C/ha, and 5.4-25.4 Mg N/ha, respectively (Tables 3.2 and 3.3, Appendix 24 c-d). The pastures with the highest aboveground C and N stocks also contained the highest soil C and N stocks (Appendix 30). Ecosystem C and N stock estimates in pastures adjusted for potential soil sampling tool bias were higher than our original estimates and ranged from 78-586 Mg C/ha, and 5.8-39.4 Mg N/ha, respectively (Appendix 31).

Median ecosystem C and N stock estimates in pastures ≥8 years differed by life zone (C: $F_{5,22} = 109.8$, $P < 0.01$; N: $F_{5,23} = 158.6$, $P < 0.01$). Median ecosystem C stocks in pastures ≥8 years formed three different groups: 1) the Tropical dry and moist forest life zones had the lowest estimates, 2) the Tropical wet forest life zone estimates were about twice as high as the first group, and 3) the estimates for the three other life zones were another 33% higher than group 2 (Table 3.2). In contrast, median ecosystem N stocks in pastures ≥8 years formed five groups: median ecosystem N stocks in Tropical dry, moist, and wet forest life zones were different from the other life zones, and the other three life zones formed two partially overlapping groups (Table 3.3). Estimates in the Tropical Premontane rain forest life zone were similar to estimates in the Tropical Premontane wet forest-warm and Tropical Lower Montane rain forest life zones, while the two latter life zones differed from each other (Table 3.3). Median ecosystem N stocks in the Tropical moist forest life zone were 29%

higher than in the Tropical dry forest life zone. The estimate in the Tropical wet forest life zone was another 67% higher than the Tropical moist forest, and the estimate in the Tropical Lower Montane rain forest was another 27% higher than the Tropical wet forest (Table 3.3). Ecosystem C and N stocks decreased with temperature (C: $r = -0.73$, $P < 0.01$; N: $r = -0.83$, $P < 0.01$) and increased with precipitation (C: $r = 0.87$, $P < 0.01$; N: $r = 0.90$, $P < 0.01$; Table 3.3 and Figures 3.2a-b).

In pastures ≥8 years, ecosystem C stocks differed by pasture age ($F_{1,17} = 10.98$, $P < 0.01$). In contrast, the age effect on ecosystem N stocks was marginally related to life zone ($F_{5,17} = 2.2$, $P = 0.10$) because the pastures in the Tropical Premontane rain forest life zone increased with pasture age, while pastures in other life zones did not change or decreased with age (Table 3.4, Appendix 24). When all pasture were combined ecosystem C and N stock estimates decreased with age (C: $r = -0.57$; $P < 0.01$; N: $r = -0.45$; $P = 0.01$; Appendix 23). Sensitivity tests of our regression analyses using other nominal ages changed some of our results. It slightly changed correlations between ecosystem C ($r = -0.56$, $P < 0.01$) and N ($r = -0.50$, $P < 0.01$) stocks and pasture age. It did not change the comparison of regression lines for ecosystem C stocks, but for ecosystem N stocks we now detected an interaction effect between life zone and age ($F_{5,17} = 2.58$, $P = 0.065$).

3.3.5 Effects of forest-to-pasture conversion on ecosystem C and N stocks

At the ecosystem level losses due to forest-to-pasture conversion were more apparent for C than N stocks. Original ecosystem C stock estimates were on average -38 ± 4% (-119 ± 13 Mg C/ha) lower in pastures than mature reference forests (Table 3.6). In contrast, original ecosystem N stock estimates were on average 6 ± 4% (1.03 ± 0.53 Mg N/ha) higher in pastures than forests (Table 3.6). Absolute and relative original Δ ecosystem C and N stock estimates were highly variable, ranging from -66 to 8% (-259 to 26 Mg C/ha) and -53% to 43% (-6.12 to 7.48 Mg N/ha) in pastures compared to mature forests (Table 3.6; Figures 3.3 c-d and 3.4; Appendix 29c-d). The Δ ecosystem

C and N stock estimates adjusted for soil sampling tool bias were lower than our original estimates with average losses for both ecosystem C and N stocks of -143 Mg C/ha and -1.1 Mg N/ha, respectively (Appendix 32). Absolute and relative adjusted Δ ecosystem C and N stock estimates were highly variable and ranged from -342 to 51 Mg C/ha (-64% to 13%) and -8.7 to 9.7 Mg N/ha (-51% to 33%), respectively.

The original Δ ecosystem C stocks in pastures were dependent on pasture age, life zone, and initial forest C stocks. Absolute and relative Δ ecosystem C stocks in pastures ≥8 years were related to pastures age ($F_{1,22} = 3.6$, $P = 0.07$; $F_{1,22} = 4.5$, $P = 0.05$), respectively, and life zone ($F_{5,22} = 25.2$, $P < 0.01$; $F_{5,22} = 11.7$, $P < 0.01$), respectively. Sensitivity tests of our regression analyses using other nominal ages did not substantially change our results for absolute Δ ecosystem C stocks. Mean absolute Δ ecosystem C stocks were highest (-238 ± 10 Mg C/ha) in the Tropical Lower Montane rain forest life zone (Table 3.6; Figure 3.3c). Mean absolute Δ ecosystem C stocks were lowest but highly variable (-49 ± 24 Mg C/ha) in the Tropical Premontane wet forest-warm life zone, and thus, not different (-118 ± 2 Mg C/ha) from the Tropical dry forest life zone mean (Table 3.6, Figure 3.3 c). Mean absolute Δ ecosystem C stocks in other life zones were similar to each other ranging between -110 ± 5 and -135 ± 17 Mg C/ha (Table 3.6). In contrast, mean relative Δ ecosystem C stock was lowest in the Tropical Premontane wet forest-warm (-16%) while the mean in the remaining life zones differed from none to two out of five life zones (Table 3.6, Appendix 29c).

The Δ ecosystem N stocks were not dependent on forest N stocks, and there was an interaction between life zone and age on both absolute and relative Δ ecosystem N stocks ($F_{5,17} = 2.3$, $P = 0.09$; $F_{5,17} = 2.4$, $P = 0.08$, respectively). Sensitivity tests of our regression analyses using other nominal ages did not substantially change our results for absolute Δ ecosystem N stocks. All pastures in the Tropical dry forest life zone had lower ecosystem N stocks than their reference mature forests, while all pastures in the Tropical wet forest, Tropical Premontane rain forest and Tropical Premontane wet forest-warm life zones had higher ecosystem N stocks than forests (Table 3.6, Figure 3.3d). The Δ ecosystem N stocks in the Tropical Lower Montane rain forest life zone were highly variable, ranging from -3.4 ± 0.3 (-34 ± 3 %) to 3.5 ± 0.6 Mg N/ha (14 ± 4 %) (Table 3.6, Figure 3.3d, Appendix 29d). In contrast, pastures in the Tropical moist forest life zone had similar ecosystem N stocks as their reference forests (Table 3.6, Figure 3.3d, Appendix 27d).

With all pastures combined, absolute Δ ecosystem C stocks decreased with pasture age (r = -0.36, P = 0.05) and elevation (r = -0.67; P < 0.01) and increased with temperature (r = 0.58; P < 0.01). Relative Δ ecosystem C stocks decreased with age (r = -0.65, P < 0.01) and increased with precipitation (r = 0.58; P < 0.01; Figures 3.2 c, Appendix 25). In contrast to Δ ecosystem C stocks, the correlation with age, elevation, and climate variables were similar for absolute and relative Δ ecosystem N stocks. Absolute and relative Δ ecosystem N stocks decreased with age (r = -0.52, P < 0.01 and r = -0.63, P < 0.01, respectively) and increased with precipitation (r = 0.65, P < 0.01 and r = 0.71, P < 0.01, respectively; Figure 3.2d, Appendix 25).

3.4 Discussion

3.4.1 Aboveground C and N stocks

Our study documented exceptionally high C and N stocks in some of the pastures, which caused relatively small differences between those pastures and their reference forests. In about 80% of our pastures, aboveground C and N stocks were 75-99% and 62-97% lower, respectively, than mature forests, which was similar to findings from other Neotropical pastures (Kauffman et. al. 1993, 1998 and 2003; Guild et al. 1998; Hughes et al. 2000 and 2002; Jaramillo et al. 2003). The other 20% of our pastures contained 24-62% and 25-58% less aboveground C and N stocks than their reference mature forests, respectively. This 20% included our 1- and 2-year-old pastures, which contained aboveground C and N stocks equivalent to ~50% of mature forest stocks. These findings were similar to slashed primary forests and a 1-year-old shifting cultivation site in the Tropical moist forest life zone in the Amazon basin (Kauffman et al. 1995, Guild et al. 1998, Hughes et al. 2002). Besides our two pastures ≤2 years, four pastures located in Tropical Premontane wet forest-warm and Tropical Premontane rain forest life zones contained high C and N stocks ranging from 81-111 Mg C/ha and 0.686-0.886 Mg N/ha, which has not been documented elsewhere in Neotropical pastures ≥2 years old.

Large (remnant) trees and to a lesser extent downed wood were responsible for the high aboveground C and N stocks we documented. Large remnant trees and downed wood were particularly abundant in the pastures ≤2 years, and in pastures in the Tropical Premontane rain forest life zone where C and N stocks in both components decreased with pasture age. In addition, large trees were also abundant in two pastures in the Tropical Premontane wet forest-warm life zone. The C and N stocks in downed wood in our study were equal to or smaller than other findings in very young pastures in the Amazon Basin, while our highest C and N stocks in large trees have not been documented elsewhere in Neotropical pastures (Guild et al. 1998; Kauffman et al. 1998 and 2003, Hughes et al. 2000 and 2002, Jamarillo et al. 2003).

The socio-economic and cultural background of individual land owners and managers were probably important drivers affecting the amount of large forest remnant trees in pastures, and hence aboveground pasture C and N stocks. Farmers leave trees in pastures for the provision of shade, timber, and fence posts as well as aesthetic and wildlife purposes (Harvey and Haber 1999).

We did not find decreasing aboveground C and N stocks with pasture age in the majority of our chronosequences. Forest legacy components in pastures should decrease with pasture age due to natural and anthropogenic losses of remnant trees and decomposition of downed wood. Unless the rate of re-growth and invasion of vegetation is higher than the removal rate by grazers and humans, pasture aboveground C and N stocks should have decreased with pasture age. Although pasture age probably played some role in the amount of vegetation in pastures, the high level of variation in legacy components among pastures within life zones prevented us from detecting an age effect in most life zones.

We showed that not accounting for forest legacy components in pastures can lead to underestimation of aboveground C stocks in Neotropical pastures, hence, it may have lead to overestimation of C fluxes due to forest-to-pasture conversion when using Houghton and Hackler's (2001) widely used model. On average our pastures ≥8 years contained 24 ± 5.8 Mg C/ha aboveground C stocks, which is 2.4 times higher than what Houghton and Hackler's (2001) assume. If we exclude the 4 pastures ≥2 years with exceptional high C and N stocks, the remaining pastures contained on average 13 ± 2 Mg C/ha. This indicates that Houghton and Hackler's (2001) assumption of 10 Mg C/ha in their model is reasonable for pastures without large trees or downed wood.

Absolute aboveground C and N stock losses due to forest-to pasture conversion differed by life zone and were dependent on initial forest C and N stocks. Although some tropical C flux models (e.g., Achard et al. 2004) assumed aboveground C stocks to be dependent on initial forest C stocks, most tropical C flux models (Achard et al. 2004, Houghton 2003, Houghton and Hackler 2001) do not account for all climate-related variability in C fluxes. In addition, if forest C stocks estimates are highly uncertain, then C flux estimates may also be uncertain. Furthermore, current tropical C flux models do not account for the existence of pastures with large remnant trees (Achard et al. 2004, Houghton 2003, Houghton and Hackler 2001). Our study suggests that life zones could be used to predict maximum aboveground C and N stocks in pastures and C and N stock differences between pastures and forests. Therefore, we recommend that future C flux models should account for C stock variability related to life zones. Life zones were good predictors for ecosystem C and N stocks in croplands (Chapter 4), as well as mature (Kauffman unpublished) and secondary forests (Cifuentes Jara 2008).

3.4.2 Ecosystem C and N stocks

Ecosystem C and N stock estimates varied by life zone among our pastures and included higher estimates than reported elsewhere for the Neotropics (Guild et al 1998, Hughes et al. 2000 and 2002, Jaramillo et al. 2003, Kauffman et al. 1998). Aboveground C and N stocks comprised only a fraction of the ecosystem C and N stocks in pastures with the exception of 20% of our pastures with high C stocks in large remnant trees and downed wood. These forest legacy components and the relatively high soil C and N stocks in the wettest life zones were the driving factors of the highest ecosystem C and N stocks in our pastures. In our study, minimum ecosystem C losses due to forest-to-pasture conversion were lower than findings from other Neotropical pastures because of the presence of these high C stocks in forest legacy components in some of our pastures (Hughes et al. 2002 and 2002, Jaramillo et al. 2003, Kauffman et. al. 1998).

The original Δ ecosystem N stocks due to forest-to-pasture conversion in our study differed from the few other studies in the Neotropics, which reported both ecosystem C and N losses due to forest-to-pasture conversion (Hughes et al. 2000 and 2002, Jaramillo et al. 2003, Kauffman et. al. 1998). Our original estimates indicated that pastures had on average 4% higher ecosystem N stocks and 39% lower ecosystem C stocks than their reference mature forests. Our estimates adjusted for potential sampling tool bias indicated that pastures had on average 38% and 6% lower ecosystem C and N stocks, respectively, than their reference mature forests. This difference between ecosystem C and N stock changes could occur because unlike C, the vast majority of forest ecosystem N is naturally stored in the soils and not in the vegetation. In our study, the absolute aboveground N stock losses were smaller than the absolute soil N stocks gains in some of the pastures (Figure 3.4b and Appendices 31-32). Both soil N stock gains and losses after forest-to-pasture conversions have been commonly found in other studies (Murty et al. 2002).

Ecosystem C and N stocks and their changes were related to life zone and pasture age. Pasture age was negatively correlated with ecosystem C stocks and its changes. For ecosystem N stocks and its changes there were interactions between the age and life zone effects, although not statistically significant for ecosystem N stocks. The ecosystem N stocks and its changes in the Tropical Premontane rain forest life zone increased with pasture age, while soil N stocks and its changes in other life zones decreased or did not vary with pasture age. The high variability within some life zones probably reduced our ability to detect N changes related to pasture age.

Part of the variation in Δ ecosystem C and N stocks were driven by variation in Δ soil C and N stocks. Differences in C and N stocks inputs and decomposition may explain the variation in Δ soil C and N stocks and we proposed three different mechanisms based on the net balance between inputs and outputs (Chapter 2). All pastures in the Tropical dry forest and Tropical Premontane rain forest life zone had lower C and N stocks in the litter layer than mature forests, which may have resulted in lower soil C and N inputs. The C and N stocks in the litter layers in pastures in the Tropical moist and wet forest, Tropical Lower Montane rain forest life zones did not substantially differ from the mature forest litter layers, which may have resulted in similar inputs for soil C and N stocks in the pastures and forests. The C and N stocks in the litter layers in pastures in the Tropical Premontane wet forest-warm life zone had substantially higher C and N stocks than the mature forest litter layers, which may have resulted in higher inputs for soil C and N stocks in the pastures and forests. We would need data on differences in decomposition rates and N fixation rates in our pastures versus mature forests to evaluate the mechanisms we proposed in Chapter 2 for our sites.

3.4.3 Study limitations

Adjusted soil bulk density estimates of mature forests may be an improvement of our original estimates of (Δ) soil and ecosystem C and N stocks, if we assume that the use of two different sampling tools introduced a sampling bias. This would result in higher soil and ecosystem C and N stock estimates in mature forests and pastures compared to our original estimates. In contrast to our original estimates, adjusted ecosystem N stocks were on average lower in pastures than forests. Nevertheless, adjusted Δ ecosystem C and N stocks due to pasture-to-forest conversion varied widely by pasture including both net increases and decreases.

Interpretations from the space-for-time substitutions in this study depend on the partly untestable assumption that the original forests at our pasture locations at the time of clearing were in the same condition as our reference mature forests, and that ecosystem C and N stocks in those forests were in a "steady state" prior to deforestation. There is evidence from the Guapiles area of Costa Rica that forests on more fertile soils were preferentially cleared (Veldkamp et al. 1992). Therefore, initial clearing of forests may have occurred preferentially on forest soils with high initial C stocks for our pastures in the Tropical wet and Premontane wet forest-T-basal life zones (Powers and Veldkamp 2005). Generally, land use history interviews with landowners in this study confirmed this trend. The preferential clearing of forests with high initial soil C and N stocks could explain the increased soil and ecosystem C and N stocks in our pastures compared to our mature reference forests.

Due to high within chronosequence variability the effect of pasture age was not always clear. Long term studies that follow sites over time after deforestation would be a better way to determine the effect of pasture age on ecosystem C and N stocks. Measurements before and after deforestation over a long period of time would also address potential biases due to inadequate reference mature forests. This type of study is virtually non-existent in the tropics because they are time consuming and require long term planning a well as funding.

Differences in temperature and elevation between pastures and reference mature forest may have confounded the relationship between temperature and elevation and Δ ecosystem C and N stocks. Generally, these differences occurred because there were no mature forests present at the exact same elevation as the pastures. The Δ ecosystem C stocks increased with temperature differences (r =0.59, $P < 0.01$) between pastures and forests, whereas Δ ecosystem N stocks increased with elevation differences ($r = 0.56$, $P < 0.01$) between pastures and forests. The Δ aboveground C and N stocks increased with temperature differences between pastures and forests (r =0.48, $P < 0.01$, r =0.47, $P < 0.01$, respectively). When excluding pastures in the Tropical Lower Montane rain forest life zone, the direction of the relationship between Δ aboveground C and N stocks and temperature differences between pastures and forests reverses ($r = -0.45$, $P = 0.02$, $r = -0.44$, $P = 0.02$, respectively). This indicates that the confounding effect of temperature varied by life zone. A correction for these confounding factors may not decrease the uncertainty of our findings because of uncertainties in the climatic data and the inherently high variability in soil and aboveground C and N stocks in forests.

The use of non-replicated chronosequences limits the extent to which our finding can be generalized to other pastures within these life zones, especially our findings on the highly variable forest legacy components (trees and downed wood) in pastures. Within life zones edaphic, hydric, and atmospheric conditions can subdivide life zones into different “plant associations” (Holdridge 1967). We careful selected sites that represented “typical” edaphic, hydric and atmospheric conditions, and therefore this study is limited to what Holdridge (1967) called “the one climatic association”. Rocky outcrops, swamps, and monsoonal areas are examples of sites that should not be classified as the “one climatic association” and therefore our data should not be extrapolated to these other associations.

A larger sample size or a different technique that accounts for high variability in legacy components in pastures might have increased our ability to detect age and life zone effects on aboveground C and N stocks. The plot design we used to estimate tree biomass in pastures was chosen for its efficiency and to keep methods consistent with reference mature forest data. A point quarter sampling approach or remote sensing techniques could be used to determine how common large (remnant) trees are in all pastures across large areas.

Despite these limitations, life zone appears to be a good predictor variable and mapping tool for describing ecosystem C and N stocks at the regional scale for Costa Rica. This was also confirmed by data from mature (Kauffman et al., unpublished data) and secondary forests (Cifuentes Jara 2008), as well as croplands (Chapter 4). Whether life zone would be a good predictor across the whole (Neo)tropics cannot be evaluated with the data collected in this study, but evidence from other studies on soil C and N stocks (Post et al. 1982 and 1985, Alvarado 2006) suggests this may be the case.

3.4.4 Implications and future research

Our study and its companion studies (Kauffman et al. unpublished data, Cifuentes Jara 2008) suggested that the Life Zone system (Holdridge 1947 and 1967) is a useful classification system and mapping tool to estimate regional (in our case Costa Rica) and perhaps global ecosystem C and N stocks and fluxes. Based on our study, incorporating ecosystem C and N stock variability related to life zone into regional and global models is more important than including variability related to pasture age. Most C flux models already account for variability with pasture age to some extent because they often include different rates of C recovery and loss for various time intervals (e.g., Houghton and Hackler 2001). Accounting for the variability in ecosystem C stocks related to climatic differences within the tropics in pan-tropical and global C flux models is also important (Chapter 4).

Ecosystem N stocks increased after forest-to-pasture conversion in some of our pastures due to increased soil N stocks. Although uncertainties exist in our data, soil N increases have been reported elsewhere. The long-term implications of increased N storage are under debate, but it may lead to increased C and N fluxes (Aber et al. 1998) especially given the increased N deposition rates expected in the tropics (Matson et al. 1999). The role of phosphorous, often a limiting nutrient in tropical ecosystems (Townsend et al. 2002), and data on N cycling in our pastures and forests are needed to better understand the mechanisms behind the ecosystem C and N stocks and changes documented in our study.

Reforestation of pastures could potentially resequester large aboveground C stocks that were lost due to forest-to-pasture conversion. The global importance of reforestation has been recognized because of the worldwide extent of (pasture) land that could be reforested (Brown and Lugo 1990, Silver et al. 2000, Wright and Mueller-Landau 2006). Cifuentes Jara (2008) predicted that secondary forests along a similar climatic gradient as our pastures could attain ecosystem C levels similar to that of mature forests in 44-105 years. Ecosystem C stocks in secondary forests differed by life zone and rates of ecosystem C sequestration were highest in life zones with intermediate levels of precipitation and lowest in the Tropical dry forest and Premontane rain forest life zones.

Protecting remaining forest in the Tropical Premontane and Lower Montane rain forest life zones is essential for reducing future C emissions. Our study determined that the potential C loss if converted to pasture is highest in these wettest life zones. Protection could conserve more aboveground C per hectare in the wettest life zones (averaging 160 and 231 Mg C/ha in Tropical Premontane and Lower Montane rain forest life zones) than could be maximally sequestered by reforestation of the drier life zones (on average 86 and 125 Mg C /ha in the Tropical dry and moist forest life zones using mature forest estimates). These wetter life zones have relative large forested areas which may be available for protection (Sánchez-Azofeifa et al. 2001).

We suggest that the extent of remnant trees in pastures and possibly other land uses across large areas should be evaluated with a different technique than our plot-level estimates, because these remnant trees caused exceptionally high aboveground C and N stocks in 14% of our pastures ≥8 years. While this type of information was only documented for a few pastures (Guild et al. 1998; Kauffman et al. 1998 and 2003, Hughes et al. 2000 and 2002, Jamarillo et al. 2003), we suggest data are needed to evaluate whether presence of large remnant trees should be included in pan-tropical or global C stocks and flux estimates. Harvey and Haber (1999) surveyed a 400-ha area nearby our pastures in the Tropical Lower Montane rain forest life zone and on average found 25 remnant trees per hectare with a mean dbh of 38.9 cm and 10 m height, which amounts to 6.5 Mg biomass/ha using our biomass equations. This estimate is 18-58% of the tree/shrub biomass that we documented in pastures in similar life zones, which suggests that our plot-level estimates of remnant trees should not be extrapolated to other areas.

Our study highlights the importance of remnant trees for local C storage, even though the presence of these trees at a global scale remains equivocal. Our results suggested that large remnant trees in pastures in the Tropical Premontane rain forest and Premontane wet forest-warm life zones could conserve the same amount of C on a per-hectare basis as protecting tropical dry forest. In addition, remnant trees may play an important role in C storage in secondary forests (Cifuentes Jara unpublished data). Besides C storage, large remnant trees in pastures provide benefits to many organisms and humans and therefore protection of these trees has great ecological value (Harvey and Haber 1999). We suggest that landowners be encouraged to retain large trees to the extent possible with pasture management goals.

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Table 3.1. Equations to determine height and aboveground biomass of Costa Rican mature forest and pasture components in different life zones and literature references.

Component Class	Biomass equations	Reference
Tree Height (m)		
Tropical dry forest	8.5513 ln(dbh) – 13.384	Kauffman et al. unpublished
Tropical moist forest	9.8279 ln(dbh) – 11.775	Kauffman et al. unpublished
Tropical wet forest	13.185 ln(dbh) – 20.407	Kauffman et al. unpublished
Tropical Premontane wet forest	10.601 ln(dbh) – 13.493	Kauffman et al. unpublished
Tropical Premont. & Lower Mont. Rain	12.032 ln(dbh) – 16.612	Kauffman et al. unpublished
Tree biomass (Mg)		Kauffman et al. unpublished
0-10 cm dbh	[0.1295exp(2.3734 ln (dbh)] x 10-3	Kauffman et al. unpublished
10-30 cm dbh	[0.0292(dbh2*H) + 2.444] x 10-3	Kauffman et al. unpublished
> 30 cm dbh	[0.0295(dbh2*H) – 184.91] x 10-3	Kauffman et al. unpublished
Palm biomass (Mg)		
0-10 cm dbh	[(exp(0.9285 ln(dbh)2 + 5.7236)) x 1.05] x 10-6	Cummings et al. 2002
> 10 cm dbh	[7.7(stem ht) + 4.5] x 10-3	Frangi and Lugo 1985
Liana biomass (Mg)		
Tropical dry and moist forest	[exp(0.07 +2.17(lndbh))] x 10-3	Gerwin and Farias 2000
Tropical wet and rain forest	[10 0.12 + 0.91(log10(BA))] x 10-3	Putz 1983
Dead wood (Mg)		
Standing	Π(dbh/2)2 H(sg) x 10-6	
Downed wood	(sg x ((Π2 x Σ(d2) x C)/8L)) x 102	Van Wagner 1968, Brown and Roussopoulous 1974

Definitions and units used in equations: Biomass is expressed in Mg on a dry weight basis. dbh = diameter (cm) at 1.3 m height; d = diameter of downed wood at the point where the particle crosses the transect; H = height (m); BA = basal area (cm2); sg = specific gravity(g/cm3); C = slope correction factor √(1+(%slope/100)2); L = transect length (cm).

Table 3.2. Aboveground C stocks by component and ecosystem C stocks (Mg C/ha) in pastures arranged in six chronosequences in Costa Rica, and mean ± SE reference mature forest and pasture C stocks by life zone, and median (95% confidence interval) pasture C stocks by life zone.

Life zone	Age (yrs)	Trees/ shrubs	Standing dead	Grass/litter mean	SE	Downed wood mean	SE	Total aboveground	Total ecosystem
Tropical dry forest	forest (n=2)	64.2 ± 0.5	2.0 ± 0.7	6.2	± 0.1	13.9	± 2.5	86.3 ± 3.7	196.3 ± 25.1
	29	0.3	0.0	3.5	± 0.5	0.3	± 0.2	4.1	86.0
	43	0.0	0.0	4.7	± 0.6	0.0	± 0.0	4.7	80.6
	62	1.1	1.3	4.8	± 0.5	0.0	± 0.0	7.2	81.5
	>75 (a)	0.7	0.0	3.7	± 0.4	0.0	± 0.0	4.4	80.2
	>75 (b)	0.0	0.0	2.7	± 0.6	0.0	± 0.0	2.7	73.5
	mean pasture ± SE	0.4 ± 0.2	0.3 ± 0.3	3.9	± 0.4	0.1	± 0.1	4.6 ± 0.7	80.3 ± 2.0
	median pasture (95% CI)							4 (2-11)	80 (72-90) a
Tropical moist forest	forest (n=3)	109.3 ± 1.7	1.5 ± 0.4	4.2	± 0.0	10.2	± 0.6	125.1 ± 2.4	203.4 ± 6.6
	28 (a)	15.7	0.0	4.3	± 0.6	0.3	± 0.1	20.2	106.8
	28 (b)	2.5	0.0	7.0	± 1.4	0.6	± 0.4	10.1	100.2
	42	2.7	0.1	4.3	± 0.5	2.2	± 1.3	9.2	96.4
	>47	2.2	0.0	2.0	± 0.9	0.0	± 0.0	4.2	89.2
	>69	0.0	0.0	2.9	± 0.6	0.0	± 0.0	2.9	76.0
	mean pasture ± SE	4.6 ± 2.8	0.0 ± 0.0	4.1	± 0.8	0.6	± 0.4	9.3 ± 3.1	93.7 ± 5.3
	median pasture (95% CI)							7 (3.19)	93 (83-104) a
Tropical wet forest	forest (n=3)	153.2 ± 15.7	4.5 ± 1.4	2.1	± 0.1	27.7	± 5.4	187.4 ± 12.4	313.7 ± 25.0
	2	64.6	2.7	7.8	± 1.2	19.0	± 4.8	94.1	341.4
	8	5.5	0.7	2.5	± 0.5	1.7	± 0.8	10.4	214.8
	16	2.4	0.3	1.1	± 0.1	3.1	± 1.6	6.9	197.9
	18	10.5	0.2	4.9	± 0.6	0.2	± 0.1	16.0	207.5
	35	9.4	0.6	4.2	± 0.7	6.2	± 3.2	20.3	190.7
	> 35	5.4	0.1	1.8	± 0.3	0.7	± 0.6	8.0	189.9
	mean pasture ± SE	6.6 ± 1.5*	0.4 ± 0.1*	2.9*	± 0.7*	2.4*	± 1.1*	12.3 ± 2.5*	200.2 ± 4.8*
	median pasture (95% CI)							11 (5-29)*	200 (178-224)
Tropical Premontane wet forest-warm	forest (n=2)	117.9 ± 6.6	8.0 ± 3.3	2.7	± 0.2	16.4	± 3.6	144.9 ± 0.5	307.7 ± 36.3
	15	54.1	23.2	6.9	± 0.7	16.7	± 9.9	100.9	315.2
	20	0.0	0.0	6.1	± 0.8	0.7	± 0.4	6.8	204.5
	26	20.6	0.6	7.0	± 0.6	8.7	± 2.7	36.9	253.4
	40	105.4	0.0	3.6	± 0.3	1.8	± 1.1	110.8	309.0
	50	0.5	0.0	7.1	± 1.3	0.0	± 0.0	7.6	202.4
	mean pasture ± SE	36.1 ± 19.9	4.8 ± 4.6	6.1	± 0.7	5.6	± 3.2	52.6 ± 22.5	256.9 ± 24.3
	median pasture (95% CI)							29 (12-73)	252 (225-283) b
Tropical Premontane rain forest	forest (n=3)	172.4 ± 2.7	9.5 ± 1.5	4.0	± 0.6	26.0	± 2.0	211.9 ± 1.4	415.6 ± 8.7
	1	57.6	10.7	3.7	± 0.3	30.8	± 9.0	102.8	405.6
	10	53.7	2.6	3.3	± 0.6	21.3	± 4.9	80.8	305.3
	25	76.1	7.6	3.0	± 0.3	11.5	± 4.6	98.2	312.3
	45	11.4	1.2	3.0	± 0.3	10.4	± 6.0	25.9	266.4
	70	0.0	0.0	1.1	± 0.1	0.3	± 0.2	1.4	239.1
	mean pasture ± SE	35.3 ± 17.8*	2.8 ± 1.7*	2.6*	± 0.5*	10.9*	± 4.3*	51.6 ± 22.8*	280.8 ± 17.2*
	median pasture (95% CI)							23 (8-65)*	279 (246-317) b
Tropical Lower Montan rain forest	forest (n=2)	223.0 ± 13.4	2.7 ± 0.6	3.8	± 0.6	21.9	± 1.6	251.4 ± 15.5	522.5 ± 57.6
	16	12.1	2.3	4.7	± 0.5	2.9	± 1.9	22.0	283.9
	28	5.7	1.0	7.8	± 0.8	3.0	± 1.4	17.6	318.6
	32	5.9	3.6	2.2	± 0.2	2.5	± 1.5	14.1	261.6
	48	21.0	0.2	3.3	± 0.5	2.8	± 1.9	27.3	263.8
	54	11.4	0.8	3.8	± 0.4	7.0	± 6.0	23.0	286.3
	mean pasture ± SE	11.2 ± 2.8	1.6 ± 0.6	4.3	± 1.0	3.6	± 0.8	20.8 ± 2.3	282.9 ± 10.3
	median pasture (95% CI)							20 (8-51)	282 (252-316) b

Labels (a) and (b) were used to distinguish between two pastures with the same age within one life zone. **Young pastures (1 and 2 years old) were not included in calculations of mean and SE and median (95% confidence interval). Median ecosystem C stocks in pastures by life zone followed by the same letter are similar to one another; median not followed by a letter indicates median for this life zone is different from all other life zones ($P_{\text{adjusted}} < 0.1$).

Table 3.3. Aboveground N stocks by component and ecosystem N stocks (Mg N/ha) in pastures arranged in six chronosequences in Costa Rica, and mean ± SE reference mature forest and pasture N stocks by life zone, and median (95% confidence interval) pasture N stocks by life zone.

Life zone	Age	Trees/	Standing	Grass/litter			Downed wood			Total	Total	
	(yrs)	shrubs	dead	mean		SE	mean		SE	aboveground	ecosystem	
Tropical dry forest	forest (n=2)	0.497 ± 0.004	0.015 ± 0.005	0.142	±	0.001	0.118	±	0.022	0.771 ± 0.022	9.824 ± 1.831	
	29	0.002	0.000	0.062	±	0.0092	0.002	±	0.0019	0.067	6.775	
	43	0.000	0.000	0.085	±	0.0108	0.000	±	0.0000	0.085	7.173	
	62	0.007	0.010	0.100	±	0.0113	0.000	±	0.0004	0.117	6.632	
	>75 (a)	0.005	0.000	0.084	±	0.0083	0.000	±	0.0002	0.088	6.801	
	>75 (b)	0.000	0.000	0.069	±	0.0141	0.000	±	0.0000	0.069	5.426	
	mean pasture ± SE	0.003 ± 0.001	0.002 ± 0.002	0.080	±	0.001	0.001	±	0.000	0.003 ± 0.001	6.561 ± 0.298	
	median pasture (95% CI)									0.08 (0.05-0.15)	7 (6-7)	
Tropical moist forest	forest (n=3)	0.886 ± 0.011	0.011 ± 0.003	0.115	±	0.001	0.091	±	0.003	1.103 ± 0.015	9.123 ± 0.330	
	28 (a)	0.117	0.000	0.141	±	0.0193	0.003	±	0.0012	0.261	9.623	
	28 (b)	0.019	0.000	0.188	±	0.0372	0.007	±	0.0041	0.213	9.674	
	42	0.020	0.000	0.157	±	0.0200	0.023	±	0.0130	0.200	9.553	
	>47	0.016	0.000	0.067	±	0.0314	0.000	±	0.0000	0.083	8.792	
	>69	0.000	0.000	0.102	±	0.0218	0.000	±	0.0000	0.102	8.439	
	mean pasture ± SE	0.034 ± 0.021	0.000 ± 0.000	0.131	±	0.004	0.007	±	0.004	0.172 ± 0.034	9.216 ± 0.252	
	median pasture (95% CI)									0.16 (0.09-0.29)	9 (9-10)	
Tropical wet forest	forest (n=3)	1.131 ± 0.093	0.033 ± 0.010	0.060	±	0.002	0.230	±	0.043	1.454 ± 0.072	12.446 ± 0.619	
	2	0.415	0.020	0.243	±	0.0372	0.148	±	0.0372	0.826	17.541	
	8	0.035	0.005	0.077	±	0.0150	0.018	±	0.0076	0.135	15.956	
	16	0.015	0.003	0.038	±	0.0033	0.027	±	0.0139	0.082	15.945	
	18	0.068	0.002	0.159	±	0.0188	0.002	±	0.0007	0.231	14.919	
	35	0.060	0.004	0.163	±	0.0282	0.047	±	0.0234	0.274	14.933	
	> 35	0.035	0.001	0.050	±	0.0068	0.005	±	0.0048	0.090	14.656	
	mean pasture ± SE	0.043 ± 0.009*	0.003 ± 0.001*	0.097*	±	0.004*	0.019*	±	0.008*	0.162 ± 0.038*	15.282 ± 0.277*	
	median pasture (95% CI)									0.14 (0.08-0.27)*	15 (5-17)*	
Tropical Premontane wet forest-warm	forest (n=2)	0.928 ± 0.003	0.059 ± 0.024	0.072	±	0.006	0.130	±	0.031	1.189 ± 0.059	14.917 ± 4.783	
	15	0.366	0.171	0.212	±	0.0228	0.136	±	0.0830	0.886	19.714	
	20	0.000	0.000	0.177	±	0.0227	0.007	±	0.0050	0.184	16.896	
	26	0.139	0.004	0.234	±	0.0208	0.073	±	0.0214	0.451	16.995	
	40	0.712	0.000	0.098	±	0.0078	0.014	±	0.0084	0.824	19.331	
	50	0.003	0.000	0.230	±	0.0431	0.000	±	0.0000	0.234	17.012	
	mean pasture ± SE	0.244 ± 0.135	0.0035 ± 0.034	0.191	±	0.006	0.046	±	0.026	0.516 ± 0.146	17.990 ± 0.629	
	median pasture (95% CI)									0.43 (0.23-0.78)	18 (14-19)	a
Tropical Premontane rain forest	forest (n=3)	1.215 ± 0.026	0.070 ± 0.011	0.120	±	0.019	0.227	±	0.017	1.631 ± 0.021	17.536 ± 0.774	
	1	0.371	0.079	0.147	±	0.0119	0.233	±	0.0673	0.830	25.081	
	10	0.346	0.019	0.122	±	0.0206	0.200	±	0.0552	0.686	18.165	
	25	0.490	0.056	0.132	±	0.0140	0.099	±	0.0416	0.778	18.497	
	45	0.073	0.009	0.086	±	0.0099	0.086	±	0.0506	0.254	19.508	
	70	0.000	0.000	0.044	±	0.0059	0.002	±	0.0013	0.046	21.939	
	mean pasture ± SE	0.277 ± 0.115*	0.021 ± 0.012*	0.106*	±	0.002*	0.097*	±	0.041*	0.441 ± 0.174*	19.527 ± 0.853*	
	median pasture (95% CI)									0.28 (0.14-0.55)*	19 (18-21)*	ab
Tropical Lower Montane rain forest	forest (n=2)	1.579 ± 0.039	0.020 ± 0.004	0.145	±	0.022	0.201	±	0.017	1.945 ± 0.064	22.768 ± 3.019	
	16	0.075	0.017	0.199	±	0.0195	0.029	±	0.0208	0.321	24.136	
	28	0.036	0.008	0.241	±	0.0261	0.025	±	0.0105	0.310	25.422	
	32	0.036	0.027	0.081	±	0.0075	0.019	±	0.0117	0.163	20.263	
	48	0.131	0.002	0.124	±	0.0176	0.021	±	0.0138	0.278	19.623	
	54	0.071	0.006	0.155	±	0.0169	0.077	±	0.0689	0.309	22.033	
	mean pasture ± SE	0.070 ± 0.017	0.012 ± 0.005	0.160	±	0.003	0.034	±	0.011	0.276 ± 0.029	22.296 ± 1.107	
	median pasture (95% CI)									0.27 (0.15-0.49)	22 (21-24)	b

Labels (a) and (b) were used to distinguish between two pastures with the same age within one life zone. **Young pastures (1 and 2 years old) were not included in calculations of mean and SE and median (95% confidence interval). Median ecosystem N stocks in pastures by life zone followed by the same letter are similar to one another; median not followed by a letter indicates median for this life zone is different from all other life zones ($P_{\text{adjusted}} < 0.1$).

Table 3.4. Results for comparisons of regression lines when testing for: (1) interactions between life zones and age, (2) age effect, and (3) life zone effect for various response variables in pastures ≥8 years in Costa Rica.

Response variable	(1) Age x Life zone	(2) Age		(3) Life zone
Ln(aboveground C)	$F_{5,17} = 2.29$, $P = 0.09$	inappropriate test		inappropriate test
Ln(aboveground N)	$F_{5,17} = 2.51$, $P = 0.07$	inappropriate test		inappropriate test
Ln(ecosystem C)	$F_{5,17} = 0.44$, $P = 0.82$	$F_{1,22} = 10.98$, $P < 0.01$	*	$F_{5,22} = 109.84$, $P < 0.01$
Ln(ecosystem N)	$F_{5,17} = 2.20$, $P = 0.10$	$F_{1,22} = 1.68$, $P = 0.21$		$F_{5,23} = 158.60$, $P < 0.01$
Δ Aboveground C	$F_{5,17} = 1.07$, $P = 0.41$	$F_{1,22} = 3.09$, $P = 0.09$	*	$F_{5,22} = 24.13$, $P < 0.01$
Δ Aboveground N	$F_{5,17} = 1.40$, $P = 0.28$	$F_{1,22} = 4.56$, $P = 0.04$	*	$F_{5,22} = 23.73$, $P < 0.01$
Relative Δ aboveground C	$F_{5,17} = 0.53$, $P = 0.75$	$F_{1,22} = 2.26$, $P = 0.15$		$F_{5,23} = 2.84$, $P = 0.04$
Relative Δ aboveground N	$F_{5,17} = 0.85$, $P = 0.53$	$F_{1,22} = 3.58$, $P = 0.07$	*	$F_{5,22} = 3.82$, $P = 0.01$
Δ Ecosystem C	$F_{5,17} = 0.61$, $P = 0.69$	$F_{1,22} = 3.61$, $P = 0.07$	*	$F_{5,22} = 25.22$, $P < 0.01$
Δ Ecosystem N	$F_{5,17} = 2.33$, $P = 0.09$	inappropriate test		inappropriate test
Relative Δ ecosystem C	$F_{5,17} = 0.40$, $P = 0.84$	$F_{1,22} = 4.46$, $P = 0.05$	*	$F_{5,22} = 11.68$, $P < 0.01$
Relative Δ ecosystem N	$F_{5,17} = 2.42$, $P = 0.08$	inappropriate test		inappropriate test
C:N ratio grass/litter	$F_{5,14} = 1.70$, $P = 0.20$	$F_{1,19} = 2.61$, $P = 0.12$		$F_{5,20} = 11.95$ $P < 0.01$
%C grass/litter	$F_{5,14} = 0.69$, $P = 0.64$	$F_{1,19} = 0.01$, $P = 0.94$		$F_{5,20} = 0.80$, $P = 0.56$
%N grass/litter	$F_{5,14} = 0.97$, $P = 0.47$	$F_{1,19} = 0.55$, $P = 0.47$		$F_{5,20} = 7.98$, $P < 0.01$

* We detected an age effect using $P_{\text{critical}} < 0.1$, and therefore, we accounted for the age effect in test 3.

Table 3.5. Absolute and relative Δ aboveground C and N stock estimates in six pasture chronosequences in Costa Rica and mean ± SE estimates by life zones.

	Pasture	Δ Aboveground C stock				Δ Aboveground C stock			
Life zone	age (yrs)	total (Mg C/ha)		relative (%)		total (Mg N/ha)		relative (%)	
Tropical	29	-82.1		-95		-0.70		-91	
dry forest	43	-81.6		-95		-0.69		-89	
	62	-79.1		-92		-0.65		-85	
	>75 (a)*	-81.9		-95		-0.68		-89	
	>75 (b)*	-83.6		-97		-0.70		-91	
mean difference ± SE		-81.7 ± 0.73	a	-95 ± 0.8	a	-0.69 ± 0.01	ad	-89 ± 1.2	b
Tropical	28 (a)*	-104.9		-84		-0.84		-76	
moist forest	28 (b)*	-115.1		-92		-0.89		-81	
	42	-115.9		-93		-0.90		-82	
	>47	-121.0		-97		-1.02		-92	
	>69	-122.2		-98		-1.00		-91	
mean difference ± SE		-115.8 ± 3.06	ab	-93 ± 2.4	ab	-0.93 ± 0.03	ab	-84 ± 3.1	b
Tropical	2	-93.3		-50		-0.63		-43	
wet forest	8	-177.1		-94		-1.32		-91	
	16	-180.5		-96		-1.37		-94	
	18	-171.5		-91		-1.22		-84	
	35	-167.1		-89		-1.18		-81	
	>35	-179.4		-96		-1.36		-94	
mean difference ± SE**		-175.1 ± 2.54	c	-93 ± 1.4	a	-1.29 ± 0.04	c	-89 ± 2.6	b
Tropical	15	-44.0		-30		-0.30		-25	
Premontane	20	-138.2		-95		-1.00		-85	
wet forest	26	-108.1		-75		-0.74		-62	
transition to	40	-34.1		-24		-0.36		-31	
basal	50	-137.4		-95		-0.95		-80	
mean difference ± SE		-92.4 ± 22.47	a	-64 ± 15.5	b	-0.67 ± 0.15	a	-57 ± 12.3	a
Tropical	1	-109.1		-51		-0.80		-49	
Premontane	10	-131.0		-62		-0.94		-58	
rain forest	25	-113.6		-54		-0.85		-52	
	45	-186.0		-88		-1.38		-84	
	70	-210.5		-99		-1.59		-97	
mean difference ± SE**		-160.3 ± 22.75	bc	-76 ± 10.7	ab	-1.19 ± 0.17	bc	-73 ± 10.7	ab
Tropical	16	-229.4		-91		-1.62		-84	
Lower Montane	28	-233.8		-93		-1.64		-84	
rain forest	32	-237.3		-94		-1.78		-92	
	48	-224.1		-89		-1.67		-86	
	54	-228.4		-91		-1.64		-84	
mean difference ± SE		-230.6 ± 2.28		-92 ± 0.9	ab	-1.67 ± 0.03		-86 ± 1.5	b

*Labels (a) and (b) were used to distinguish between two pastures with the same age within one life zone.

**Young pastures (1 and 2 years old) were not included in calculations of mean and SE.

Pasture means by life zone followed by the same letter are similar to one another; means not followed by a letter indicates mean for this life zone is different from all other life zones ($P_{\text{adjusted}} < 0.1$).

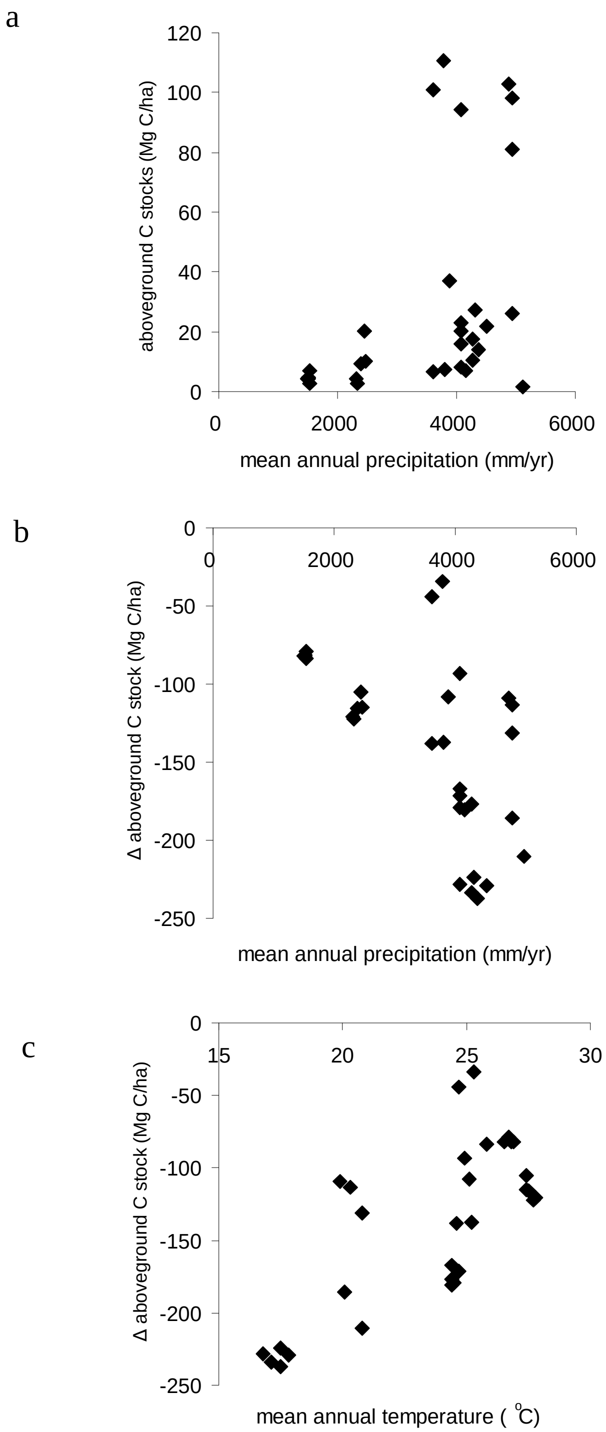
Table 3.6. Absolute and relative Δ ecosystem C and N stock estimates in six pasture chronosequences in Costa Rica and mean ± SE estimates by life zones.

Life zone	Pasture age (yrs)	Δ Ecosystem C stock		Δ Ecosystem N stock	
		total (Mg C/ha)	relative (%)	total (Mg N/ha)	relative (%)
Tropical dry forest	29	-111.8	-57	-3.19	-32
	43	-117.2	-59	-2.79	-28
	62	-116.3	-59	-3.33	-33
	>75 (a)*	-117.6	-59	-3.16	-32
	>75 (b)*	-124.3	-63	-4.54	-46
	mean ± SE	-117.5 ± 2.0 ab	-59 ± 1.0 a	-3.40 ± 0.3	-34 ± 3.0
Tropical moist forest	28 (a)*	-97.2	-48	0.46	5
	28 (b)*	-103.7	-51	0.51	6
	42	-107.5	-53	0.39	4
	>47	-114.7	-56	-0.38	-4
	>69	-127.9	-63	-0.73	-8
	mean ± SE	-110.2 ± 5.3 b	-54 ± 2.6 a	0.05 ± 0.3	1 ± 2.8
Tropical wet forest	2	25.8	8	4.92	39
	8	-100.7	-32	3.34	26
	16	-117.7	-37	3.33	26
	18	-108.0	-34	2.30	18
	35	-124.9	-40	2.31	18
	>35	-125.7	-40	2.04	16
	mean ± SE**	-115.4 ± 4.8 b	-37 ± 1.5 ab	2.66 ± 0.3	21 ± 2.2
Tropical Premontane wet forest-warm	15	9.0	3	5.17	36
	20	-101.7	-33	2.35	16
	26	-52.8	-17	2.45	17
	40	2.8	1	4.79	33
	50	-103.7	-34	2.47	17
	mean ± SE	-49.3 ± 24.3 a	-16 ± 7.9	3.45 ± 0.6	24 ± 4.3
Tropical Premontane rain forest	1	-10.6	-3	7.48	43
	10	-110.9	-27	0.56	3
	25	-103.9	-25	0.90	5
	45	-149.9	-36	1.91	11
	70	-177.1	-43	4.34	25
	mean ± SE**	-135.4 ± 17.2 b	-33 ± 4.1 b	1.93 ± 0.9	11 ± 4.8
Tropical lower montane rain forest	16	-236.9	-45	1.46	6
	28	-202.2	-39	2.75	12
	32	-259.2	-50	-2.41	-11
	48	-257.0	-49	-3.05	-13
	54	-234.5	-45	-0.64	-3
	mean difference ± SE	-238.0 ± 10.3	-46 ± 2.0 ab	-0.38 ± 1.1	-2 ± 4.9

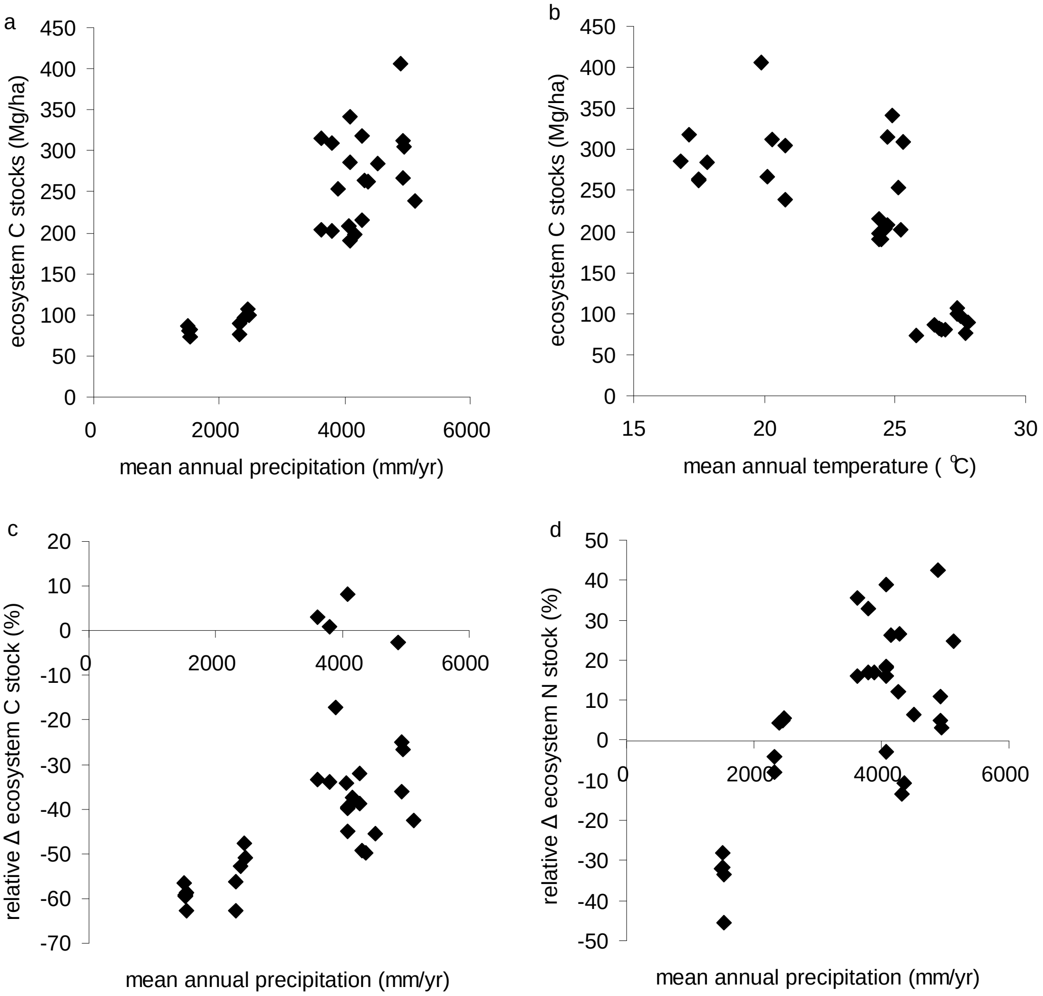
*Labels (a) and (b) were used to distinguish between two pastures with the same age within one life zone.

**Young pastures (1 and 2 years old) were not included in calculations of mean and SE.

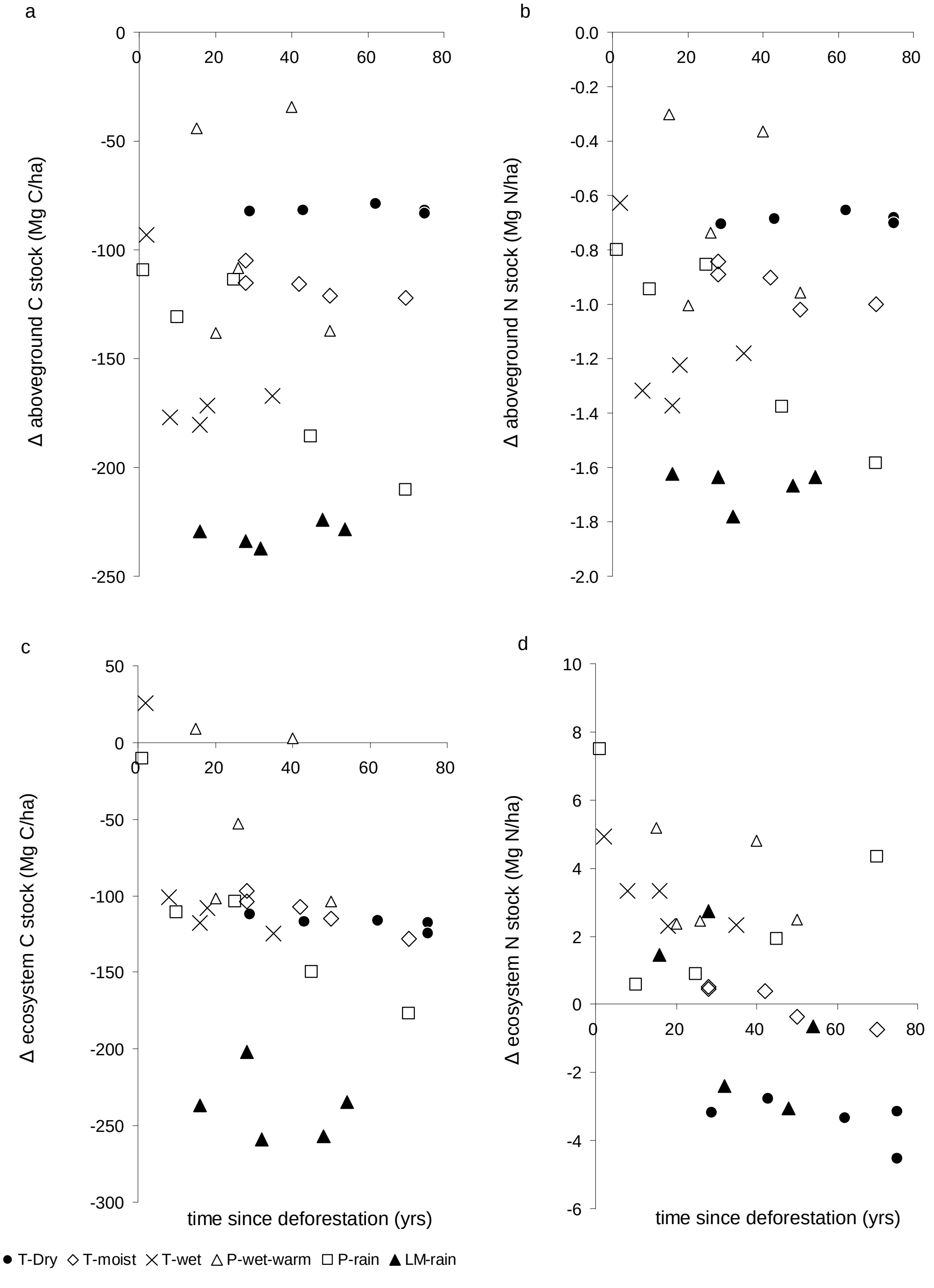
Pasture means for Δ ecosystem C stocks by life zone followed by the same letter are similar to one another; means not followed by a label indicates mean for this life zone is different from all other life zones ($P_{\text{adjusted}} < 0.1$).



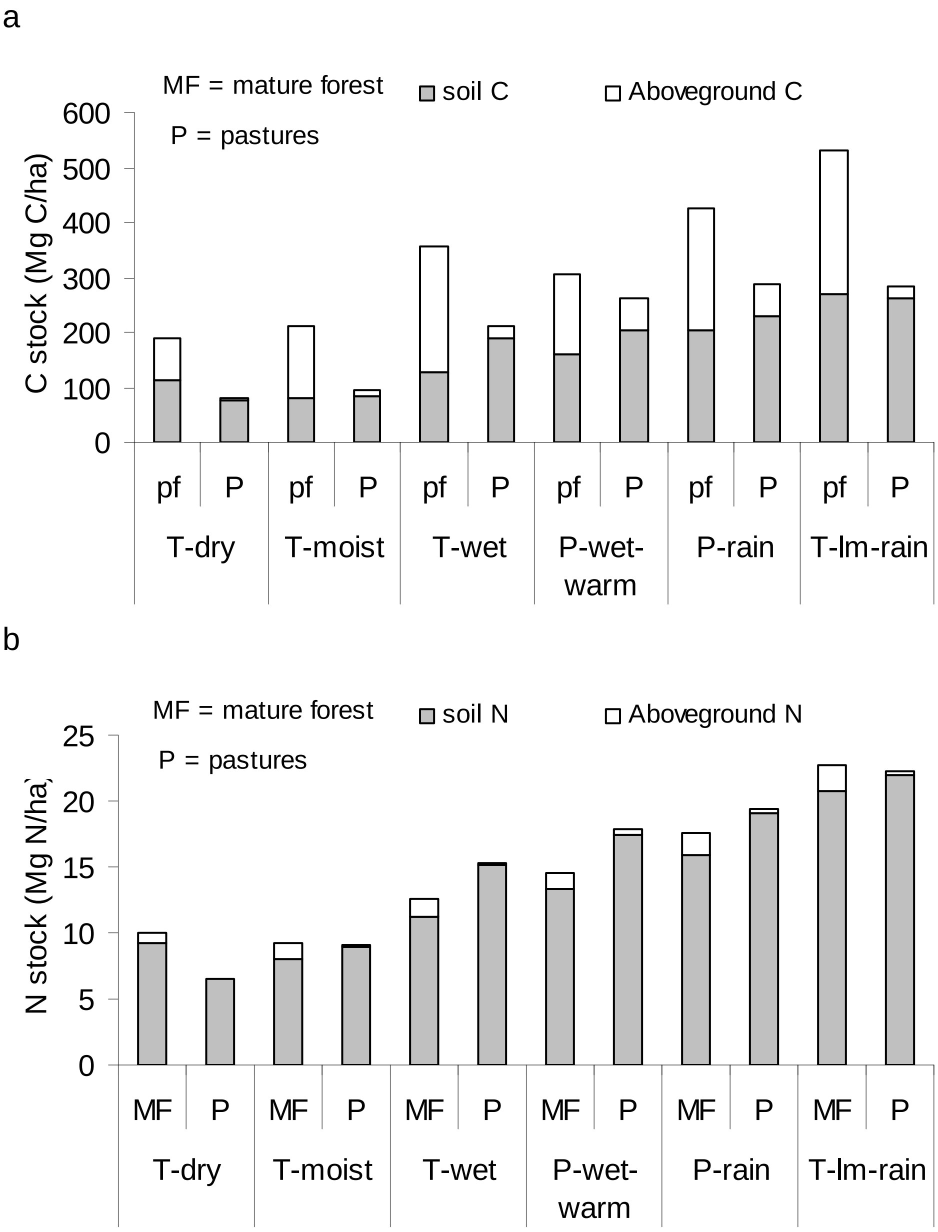
Figures 3.1. Relationships between (a) aboveground C stocks and mean annual precipitation, (b) Δ aboveground C stocks and mean annual precipitation, and (c) Δ aboveground C stocks and mean annual temperature in 31 Costa Rican pastures.



Figures 3.2. Relationships of (a and b) ecosystem C stocks and (c and d) relative Δ ecosystem C and N stock (% of forest) with mean annual precipitation and temperature in 31 Costa Rican pastures.



Figures 3.3. Δ Aboveground (a and b) and Δ ecosystem C and N stocks (c and d) in six pasture chroquences by life zones in Costa Rica. T-dry = Tropical dry forest; T-moist = Tropical moist forest; T- wet = Tropical wet forest; P-wet-warm = Tropical Premontane wet forest-warm; P-rain = Tropical Premontane rain forest; LM-rain = Tropical Lower Montane rain forest.



Figures 3.4. Mean ecosystem (aboveground and soil) (a) C and (b) N stock estimates (Mg /ha) in pastures ≥8 years and mature forests in six life zones in Costa Rica. T-dry = Tropical dry forest; T-moist = Tropical moist forest; T- wet = Tropical wet forest; P-wet-warm = Tropical Premontane wet forest-warm; P-rain = Tropical Premontane rain forest; T-lm-rain = Tropical Lower Montane rain forest.

CHAPTER 4

LIFE ZONE BASED ESTIMATES OF ECOSYSTEM C STOCK CHANGES DUE TO FOREST-TO-AGRICULTURAL CONVERSION IN COSTA RICA

Abstract

Conversion of tropical forest to agriculture has been estimated to contribute ~20% of the global carbon (C) emissions. Global and pan-tropical C flux estimates assume C is lost from both vegetation and soils due to conversion and that the amount of C stored in agricultural lands is fairly uniform across the tropics. If C stocks in agricultural lands are not homogenous and if soil C does not always decrease following conversion, then global C stock and flux estimates may contain large errors given that agricultural lands comprise 40% to 50% of the world's land area. Our objectives were to determine: (1) if ecosystem C stocks and net changes due to forest-to-agricultural conversion differ among agricultural land use types in Costa Rica; (2) how life zones affect estimates of ecosystem C stocks and net changes due to forest-to-agricultural conversion in Costa Rica, and (3) if using life zone-specific estimates reduces potential biases and uncertainty of regional and global C flux estimates for forest-to-agricultural conversions. We sampled 62 agricultural sites in Costa Rica stratified by land use and life zone and compared them to mature forest data. Ecosystem C stocks varied more by life zone than by land use. On average, aboveground (-86% ± 2%) and ecosystem (-38% ± 3%) C stocks decreased, and soil C stocks increased (10% ± 5%) due to forest-to-agricultural conversion. Soil C stock changes due to conversion were highly variable and increased or decreased depending on the site. Our Costa Rican agricultural ecosystem C stock estimates were 2-fold greater and our estimates of ecosystem C changes due to forest-to-agricultural conversions were 8-19% less than the Intergovernmental Panel on Climate Change-endorsed estimates. Applying the 19% overestimate at a global scale would reduce the estimated annual global C flux due to land use change by 0.4 Pg C/year. High spatial soil variability, potential inadequate reference mature forests, and the use of different sampling tools to estimate soil bulk density in mature forests and agricultural lands contributed to uncertainties in our estimates of ecosystem C and N stock changes due to forest-to-agricultural conversion. Our results suggest that incorporating variability among life zones in

estimates of ecosystem C stocks and changes due to conversion is more important than incorporating agricultural land use types when estimating ecosystem C stocks in tropical agricultural landscapes at regional scales.

Chapter 4 Life zone based estimates of ecosystem C stock changes due to forest-to-agricultural conversion at the scale of Costa Rica

4.1 Introduction

Estimates of carbon (C) emissions from land use change in the tropics range from 0.5-3.0 Pg C/year and this flux is the largest uncertainty in the global C budget (Denman et al. 2007, Houghton 2007). Despite the fact that agriculture is the most abundant land use in the tropics, estimates of ecosystem C stocks are not well documented in these systems. C stock and flux estimates can be considered at three different scales: local, regional, and global. The Intergovernmental Panel on Climate Change (IPCC)-endorsed estimates (Denman et al. 2007) from Houghton (2003) summed nine C flux estimates from different regions to calculate global C fluxes. They tracked, with an annual time step, changes in aboveground and belowground C in different ecosystems following changes in land use. The estimate for Latin America includes conversions from mature forest to pasture, cropland, shifting cultivation, logged forest, and forest plantation (Houghton and Hackler 2001). Land areas in this region were divided into regional vegetation types to determine C stocks in disturbed and undisturbed vegetation (Houghton and Hackler 2001). For each land use conversion they assumed that C fluxes were similar within each of the regional vegetation types. All of Costa Rica was classified as Tropical seasonal forest (Houghton et al. 1991), yet, Costa Rica contains 23 different life zones (*sensu* Holdridge 1947) including transition life zones (Bolaños and Watson 1993). Life zones can profoundly affect net C stock changes due to conversion (Chapters 2 and 3) and ignoring life zone differences could substantially bias estimates of C emissions over regional or even global scales.

Efforts to reduce the uncertainty in C flux models have focused on improving estimates of deforestation rates and C stocks present in the original forests (Achard et al. 2004, Houghton 2005). Fewer efforts have focused on the uncertainties in C stocks of the agricultural lands to which most forests were converted. We investigated C stocks in agricultural lands and compared them to mature forests within the dominant life zones and land uses in Costa Rica.

In 2002, pastures made up about 46% of Costa Rica (FAO 2008) and 70% of world's agricultural lands (Smith et al. 2007), and are therefore, the single most important agricultural land use. In 2002, bananas and coffee beans were the most important agricultural exports for Costa Rica and plantations for these products covered about 1% and 2% of Costa Rica, respectively; sugarcane plantations covered about 1% (FAO 2008). Rice paddies and oil palm plantations (not covered in our study) also cover about 1% of Costa Rica each; and all other crops were less abundant (FAO 2008).

Our objectives were to: (1) quantify ecosystem C stocks in the major Costa Rican cropland types, (2) quantify net changes in ecosystem C stocks due to forest-to-cropland conversion, (3) determine how ecosystem C stocks and associated net changes varied by land use and life zone, and (4) determine how life zones based estimates affect estimates of C stocks and their changes due to forest-to-agricultural conversion at the scale of Costa Rica. Our research was driven by the following research questions: (1) How do ecosystem C stocks and their net changes due to forest-to-agricultural conversion differ among life zone and agricultural land use type in Costa Rica?; and (2) Can the use of life zones reduce potential biases and uncertainty of regional and global C flux estimates for forest-to-agricultural conversions?

4.2 Methods

4.2.1 Study areas

Our research was conducted in Costa Rica because it has an extremely high biotic and physical diversity in a relatively small area (51,100 km^2). Costa Rica is bordered by the Atlantic and the Pacific oceans, and is dissected by volcanic mountain ranges from northwest to southeast. Mean annual precipitation ranges from 1512-5126 mm/year and mean annual temperature ranges from 16.8-27.8 ^{o}C among agricultural lands we sampled (Table 2.1 and Appendix 33). Methods for estimating climate variables were described Chapters 2 and 3. There are 23 different life zones in Costa Rica including 11 transition life zones (Bolaños and Watson 1993). Transition life zones are transitions between two major life zones, similar to ecotones.

4.2.2 Site selection

We sampled 62 agricultural sites, including four different land use types (pastures, banana, coffee, and sugarcane plantations). Cattle pastures (n = 29) were sampled in chronosequences of pasture age ≥8 years (i.e., time since deforestation) within six dominant life zones of Costa Rica covering a large climatic gradient (Table 2.1). The location for each chronosequence was chosen for proximity to mature forest sites from a companion study (Kauffman et al. unpublished data) to infer impacts of forest-to-pasture conversion in each life zone (Chapters 2 and 3). We sampled banana (n = 11), coffee (n = 10) and sugarcane plantations (n = 10) across a rainfall gradient in life zones where they are common land uses (Appendix 33). The coffee plantations included four sun-grown, four shade-grown, and two young organic plantations. Sugarcane plantations represented various harvest management scenarios (e.g., harvest with or without the use of fire). More details on pasture management and land use duration are described in Chapter 2.

4.2.3 Aboveground vegetation and soil sampling and analyses

Our ecosystem C stock estimates were the sum of total aboveground C stocks and 0-1 m soil C stocks. Generally, we assumed that the differences in C stocks between agricultural lands and mature forests (Δ C stocks) were due to the conversions from forest-to-agriculture. Root biomass was not estimated nor included in our ecosystem stock estimates. However, we did not exclude fine roots from soil samples. Live fences (containing trees) were present in or around some of the agricultural lands and these fences were not included in the C stock estimates. There were no trees in banana and sugarcane plantations. Trees were present in pastures and most coffee plantations and were included in C stock estimates.

Methods used to sample, calculate and analyze ecosystem C stocks in pastures were described in Chapter 2 and 3. In coffee plantations, height and diameter at breast height (dbh) of all trees >10 cm dbh were measured in 25- x 50-m macro plots (Appendix 34). We measured all trees <5 m in height with a meter stick, and estimated height of trees >5 m with an inclinometer. The mass of smaller (<10 cm dbh) trees, palms, vines, dead snags, and stumps 0-10 cm dbh were measured within nested subplots at each sampled site (Appendix 34). Trees were identified as *Cordia alliodora*, *Eucalyptus deglupta, Erythrina poeppigiana*, *Inga spp,* or labeled 'other species'. We estimated tree biomass for *Erythrina poeppigiana* and other species with the biomass equation for trees in pastures and primary forests (Table 3.1). The biomass equations for *Cordia alliodora*, *Eucalyptus deglupta*, and *Inga* spp. were from studies in coffee plantations in Nicaragua (Segura et al. 2006) and *Eucalyptus saligna* plantations mixed with *Albizia* in Hawaii (Kaye et al. 2000) (Table 4.1).

We measured coffee plants in 10-m sections of four different coffee plant rows at random locations in each of the 25- x 50-m macro plots (Appendix 34). We counted the number of plants in these four sections and calculated the number of plants per hectare using equation 4.1 (Table 4.1). For coffee plantations El Rodeo and Juan Vinas 1 and 2, we measured both the maximum height per plant and the stem diameter at 15 cm above the ground for all stems of each plant. In the other plantations we measured the height of all coffee plant stems. Biomass of the coffee plants were calculated using equations 4.2 or 4.3 (Table 4.1).

We destructively sampled standing sugarcane biomass in 8 micro plots that were 1 m x the width of a sugarcane row. These samples were taken immediately prior to harvest. We weighed the fresh sugarcane in the micro plots in the field. Subsamples (divided into stem, brown, and green leaves) of sugarcane were oven-dried for 3 days at 65 ^{o}C to determine dry weight. We calculated the aboveground biomass in sugarcane plantations by averaging the sugarcane biomass at harvest and surface layer biomass after harvest.

We used estimates of mean annual number of banana plants per hectare made by plantation managers for our sites in banana plantations. We assumed the mean biomass of each banana plant was 7.36 kg organic matter (Yamaguchi and Araki 2004), and calculated aboveground banana biomass by multiplying the number of plants per hectare by 7.36 kg.

No downed wood was present in banana and sugarcane plantations, which may be due to its removal before the crops were initially planted. In one banana plantation we encountered a large piece of remnant downed wood, but given the rarity of this material in banana plantations, its biomass was not included in the aboveground biomass estimate. We calculated biomass of woody debris in coffee plantations using planar intersect techniques (Van Wagner 1968, Brown and Roussopoulous 1974) by recording measurements along 16, 15-m sampling planes stratified throughout each 25- x 50-m macroplot in a manner as described for downed wood in pastures (Chapter 3). The mean specific gravity of downed wood in coffee plantations was assumed to be 0.4, 0.35, and 0.3 g/m^3 for 2.5-7.5 cm in diameter (d), d ≥7.5 cm sound, and d ≥7.5 cm rotten classes, respectively.

The surface layers in banana, coffee, and sugarcane plantations were destructively sampled using methods developed for forest and pasture surface layers (Chapter 3). In banana plantations, we increased the microplot size to 1- x 1-m due to the large size of leaves. We sampled the surface layer in sugarcane plantations directly after harvest.

We calculated C stocks of the vegetation (coffee plants, trees, sugarcane, banana plants, surface layer) by multiplying vegetation biomass estimates by the average C concentration. Samples from the stem, branches and leaves of four random coffee plants (from four different plantations) were analyzed to determine total C concentration. We assumed the average C concentration for trees in coffee plantations was the same as for individual trees in Costa Rican mature forests (Kauffman et al. unpublished data). We analyzed samples of the sugarcane stems, and brown, and green leaves from nine sugarcane plantations for total C concentration. We calculated the average C concentration for a whole sugarcane stalk by multiplying the C concentration with the relative weight of the three cane stalk components. We collected samples of banana plant pseudostem and leaves from three different banana plantations to determine total C concentrations. In all coffee plantations, seven banana plantations, and four sugarcane plantations we analyzed the surface layer to determine average total C concentration. All total C concentration analyses were conducted by induction furnace method (Nelson and Summers 1996).

In coffee plantations, we collected 1-m deep soil cores along plot edges, at 0, 25, and 50 m along one edge and 0 and 25 m along the other edge. In the other land uses, soil samples were taken at similar location as in pastures (Chapter 2, Appendix 34). Soil bulk density, soil C concentration and soil C stocks methods were the same as described in Chapter 2.

Most mature forests that served as reference forests for the agricultural lands were sampled using other gouge augers (tool A [AMS soil core sampler with slide hammer and a retaining liner]: volume ≥ 48.7 cm^3, diameter core head = 5.08 cm ; tool B [JMC 51-792-8285]: volume = 23.7 cm^3, width between vertical cutting edges = 3.45 cm) than the gouge auger used to sample agricultural soils (tool C [gouge auger for hard soils made by Eijkelkamp]: volume = 13 cm^3, width between vertical cutting edges = 2.4 cm). Three reference forests were sampled with the same gouge auger as the one used to sample agricultural soils (tool C).

We used the relationship between soil bulk density and % soil C (Périé and Ouimet 2008) to investigate the impacts of the different sampling tools on the soil bulk density estimates, assuming that our sampling methods did not influence our % soil C estimates. We made scatter plots of the relationship between all soil bulk density and % soil C estimates stratified by tool for all mature forest data from

Kauffman et al. (unpublished) (Appendix 5). We calculated different regression lines for each mature forest data set sampled with a different tool (Appendix 5). If the regression equations were different for each sampling tool then there may have been a sampling tool bias, although, other factors that may have influenced the regression line could not be excluded.

We standardized all soil bulk density estimates by calculating soil bulk density estimates of all mature reference forests sampled with tools A and B with the regression equation based on mature forest data sampled with tool C (Appendix 5). These adjusted forest soil bulk density estimates were used to calculate adjusted (Δ) soil and ecosystem C and N stocks in forests and agricultural lands. In this dissertation we specifically state if estimates were adjusted and in all other cases statements refer to our original estimates.

We calculated Pearson coefficients of correlation (*r*) to determine the relationship between climate and response variables. Due to uneven sample sizes per life zone and land use, and differences in land use histories we did not conduct analysis of variance or multiple comparisons to test for differences among life zones and land uses.

4.2.4 Calculations to scale up from sites to Costa Rica

To determine the impact of life zone-specific estimates of ecosystem C stocks and their changes due to conversion at the scale of Costa Rica, we compared modeled estimates using our data for eight life zones with modeled estimates using Houghton's (2003) assumptions. We estimated the agricultural land areas by life zone in Costa Rica, by assuming that all non-forest cover was used as agricultural land (Table 4.2). Forest cover by life zone was obtained by overlaying the most recent forest cover (Calvo-Alvarado and Sánchez Azofeifa 2006) and the Holdridge life zone (Bolaños and Watson 1993) maps for Costa Rica in a Geographic Information System (Vicente Watson, Tropical Science Center, Costa Rica, March 2008). Houghton and Hackler

(2001) applied different estimates for pastures and croplands; therefore, we also distinguished between these two land use types in our analysis. We assumed that in each life zone 90% of all agricultural land was used as pasture, and 10% as cropland, except in three life zones for which we only had C stocks estimates for one of the land uses. Our estimates of land area by land use in Costa Rica were generally similar to FAO (2008) estimates from the last decade. We multiplied area of pasture and cropland per life zone in Costa Rica by mean (Δ) C stock estimates for all pastures and croplands based on our data and Houghton's (2003) (Table 4.2). For mean estimates based on our pasture data we only included pastures ≥8 years because we only sampled younger pastures for two life zones. For mean estimates based on Houghton (2003) we used estimates for pastures and croplands 20 year after conversion (Houghton and Hackler 2001). Houghton and Hackler's (2001) "aboveground" C stock estimates include root biomass, which means we expect our aboveground and ecosystem C stocks estimates to be more conservative, and our estimates of Δ aboveground and ecosystem C stocks (difference between agricultural lands and mature forests) to be higher. Due to potential biases in our data set associated with inadequate reference mature forests, we adjusted our estimates of Δ C stocks for our country-scale estimates as described in section 4.3.3. We conducted a sensitivity analysis to determine the impact of these changes to exclude our potential biases and outliers for the country-scale estimates.

4.3 Results and discussion

4.3.1 C stocks in agricultural sites

Ecosystem C stocks varied more by life zone than by land use (Figure 4.1) with estimates ranging from 61-655 Mg C/ha among all sites. Differences in ecosystem C stocks among life zones were dependent on the degree of climatic difference among life zones (Table 2.1 and Appendix 33). The range of ecosystem C stocks among agricultural land use types overlapped with each other and variability was high within pastures, sugarcane and coffee plantations (Figure 4.1, Appendix 35). Mean soil C stocks and associated variability were greatest in the Tropical Premontane wet forest life zone (Figure 4.1). Generally for banana plantations, ecosystem C stocks were lower compared to most other agricultural sites (Figure 4.1, Appendix 35). In addition, the variability among life zones was low for this land use (Figure 4.1, Appendix 35), probably because these banana plantations occurred within relatively small temperature, precipitation, and elevation ranges (Figures 4.2, Appendix 33). Ecosystem C stocks across all agricultural sites increased with mean annual precipitation ($r = 0.57$, $P < 0.01$) and elevation ($r = 0.62$, $P < 0.01$), and decreased with mean annual temperature ($r = -0.77$, $P < 0.01$, Figure 4.2), which supports the strong relationship between life zone and ecosystem C stocks in these sites, because life zones are specific combinations of these three variables.

It is possible that ecosystem C stocks were more similar among land uses than we reported because we excluded root biomass. However, root biomass is often a fraction of aboveground biomass (0.24 ± 0.14, Cairns et al. 1997; 0.19-0.48, Dossa et al. 2008). Our average aboveground vegetation in all agricultural lands comprised only a small fraction of ecosystem C stocks (mean ± SE: 0.1 ± 0.01) compared to soil C stocks. Therefore, we would not expect our main findings to change substantially if we had included root biomass.

Where comparative data were available, our aboveground and ecosystem C stocks estimates were consistent with findings in other studies. Published data on aboveground and ecosystem C stocks in agricultural lands were less abundant than soil C stock data especially for croplands. Our aboveground and ecosystem C stock data in pastures were generally consistent with data collected elsewhere with the exception of the high C stocks due to large remnant trees in some of our pastures (Chapter 3). Data on soil C stocks in 0-30 cm soils in banana plantations in the Sarapiqui area in Costa Rica (Powers 2004) were similar to our estimates. Soil C stocks up to 1-m depth in two sugarcane plantation in Tropical Lower Montane Ecuador (Rhoades et al. 2000) were in the same range as our study. Our aboveground C stocks in coffee plantations were similar to findings in southern Costa Rica (Polzot 2004).

We found that remnant trees in pastures can increase ecosystem C stocks substantially (Chapter 3), and the same may be true for croplands that contain large remnant trees. Our pastures with large remnant large forest trees contained higher aboveground C stocks than coffee plantations mixed with trees (Chapter 3, Table 3.2, Table 4.3 and Appendix 35). However, this might be different in countries where other types of shaded coffee plantations are prevalent. For example, in Mexico the majority of coffee plants are grown under natural forest cover (Moguel and Toledo 1999). Therefore, those plantations might store more C aboveground (Peeters et al. 2003) than we found in Costa Rica. Our shaded coffee plantations contained higher aboveground C stocks than sun-grown plantations, but the ecosystem C stocks were not always higher in shaded plantations due to soil C stock differences (Table 4.3 and Appendix 35).

4.3.2 C stocks changes due to forest-to-agriculture conversion

We found that the change of aboveground, soil, and ecosystem C stocks due to forest-to-agricultural conversion differed by life zone (Figure 4.3). On average, aboveground (-86 ± 2%) and ecosystem (-38 ± 3%) C stocks decreased, and soil C stocks increased (10 ± 5%) due to forest-to-agricultural conversion. Aboveground and ecosystem C stocks in agricultural lands were on average 147 ± 7 and 131 ± 12 Mg C/ha lower, respectively, than mature forests while soil C stocks were 14 ± 9 Mg C/ha higher than mature forests. Soil C stocks corrected for compaction effects in agricultural lands increased with mature forest stocks ($r = 0.66$, $P < 0.01$; Figure 4.4b). The variability in Δ soil C stocks increased with mature forest stocks (Figure 4.4a). Estimates ranged from -123 to 302 Mg C/ha and included both positive and negative differences for all land uses. Mean Δ soil C stocks in croplands (13 ± 17 Mg C/ha) had a higher uncertainty than mean Δ soil C stocks in pastures ≥8 years (15 ± 7 Mg C/ha). This higher uncertainty in croplands may be due to higher variation of land use management among and within croplands compared to pastures, and to higher uncertainty in the adequacy of reference forests sites for croplands versus pastures.

4.3.3 Uncertainties in our site-level estimates

Much of the uncertainty of our conversion data is related to the methodology and the inherently high spatial variability in soil C stocks. Interpretations from the space-for-time substitutions in this study depend on the assumption that the original forests at our agricultural locations at the time of clearing were in the same conditions as our reference mature forests, and that ecosystem C stocks in those forests were in a "steady state" prior to deforestation. We carefully selected our pasture sites to address this issue, but there is evidence that initial clearing of forests may have occurred preferentially on forest soils with high initial C stocks for our agricultural lands in the Tropical wet and Premontane wet forest-warm life zones (Veldkamp et al. 1992, Powers and Veldkamp 2005). For many of the croplands there are no mature forests in the same life zone or in the vicinity of these croplands. In addition, cropland sites were not primarily selected based on their proximity to reference mature forest; rather we sought to capture the climatic variation that existed across the important growing areas for these crops in Costa Rica.

The selection of our reference forests sites for our croplands may have introduced some biases into our study. Our first potential bias was that we may have overestimated positive Δ soil C stocks and underestimated negative Δ aboveground C stocks in banana plantations in the Tropical moist forest life zone (Table 4.3, Figure 4.1). These banana plantations were located on the Caribbean side of the country, which has higher year-round productivity due to a lack of a distinct dry season compared to the Pacific side, where the reference forests (and pastures) were located. Instead of using these potential biased estimates, we excluded Δ C stocks for crops in the Tropical moist forest life zone in our analysis of Δ C stocks at the scale of Costa

Rica to minimize the effect of our potential bias on the comparison with Houghton and Hackler’s assumptions (Table 4.2).

A second potential bias is that our reference mature forests for sugarcane plantations in the Tropical moist forest-warm life zone occurred in the Tropical dry forest life zone, although, they were located within 8 km of each other (Table 4.3, Figure 4.1). However, these sugarcane and forest sites are not very different in climatic terms. Another difference between these sugarcane plantations and forests is that the plantations are on a low terrace with recent alluvial soils, while the forest soils are older (Vicente Watson personal communication). Forests that were replaced by these sugarcane plantations may have had higher ecosystem C stocks than their reference forests. Therefore, negative Δ soil and Δ ecosystem C stocks may have been overestimated and Δ aboveground C stocks could have been underestimated in these same sites. Therefore, we excluded this life zone from our country-scale estimates of Δ C stocks.

The two highest soil C stock estimates for coffee plantations were potential outliers and these coffee plantations probably replaced forests with relatively high soil C stocks compared to the reference forests we sampled (Table 4.3, Figure 4.4). Therefore, Δ soil C stocks may have been overestimated for these sites. Relatively high C stocks in forest soils usually coincides with high aboveground C stocks (Kauffman et al. unpublished data), which would indicate that Δ aboveground C stocks may have been underestimated at these sites. Our Δ ecosystem C stock estimates may be more robust than Δ soil and Δ aboveground stocks because of the opposite direction of bias in the Δ soil and Δ aboveground stock estimates. To account for this potential bias, we excluded these two coffee plantations when estimating mean Δ C stocks in croplands in the Tropical Premontane wet forest life zone (Table 4.2).

Sampling tool bias may have occurred because we used different soil gouge augers to take soil bulk density samples in mature forests than agricultural lands. Our soil bulk density sample volume for tools B and C were low compared to other studies (96.1-656.5 cm3, Constantini 1995; 300 cm^3, Veldkamp 1994; 50-270 cm^3, Folegatti

2001). Regression equations relating soil bulk density with % soil C for the different mature forest data sets sampled with different tools (Appendix 5) indicated that soil bulk density estimates sampled with tool B were relatively low compared to estimates sampled with tools A and C. The impacts of adjusted soil bulk density estimates on pasture data were described in Chapters 2 and 3. The adjustment of forest soil bulk density estimates generally increased (corrected) soil and ecosystem C stock estimates in croplands and reference mature forests (Appendix 36). The adjusted Δ soil and Δ ecosystem C stock estimates in croplands were on average 5 Mg C/ha lower than our original estimates. Nevertheless, individual adjusted estimates were between 67 Mg C/ha lower and 122 Mg C/ha higher than our original estimates (Table 4.3, Appendix 36). The adjusted estimates may have excluded sampling tool bias, but it has introduced an uncertainty because adjusted soil bulk densities are based on a regression equation instead of actual measurements.

Most other studies reporting impacts of forest-to-agricultural conversion on soil C stocks have also used space-for-time methodologies (Guo and Gifford 2002, Murty et al. 2002). Our pasture results were similar to studies covering sites across the globe. Murty et al (2002) found on average no change in soil C stocks due to forest-to-pasture conversion while soil C stocks decreased or increased depending on the site, and Guo and Gifford (2002) reported an average 8% increase in soil C stocks. Contrary to our study, Guo and Gifford (2002) found an average 42% loss, and Murty et al. (2002) reported a 30% loss in soil C stocks due to forest-to-crop conversion. However, in addition to the differences in the geographical ranges, the majority of the studies in these reviews contained only data on topsoils (Guo and Gifford 2002, Murty et al. 2002), which could explain the differences with our results. For some of our life zones Δ soil C stocks changed signs when comparing 0-30 cm Δ soil C stocks to 0-1 m Δ soil C stocks in pastures (Chapter 2).

4.3.4 Implications for Costa Rican and global C stocks and fluxes

Despite the limitations and potential biases in our study, our results provided insights about uncertainties in the impacts of land use change on C stocks. Until better data are available we suggest that some of the assumptions made by Houghton (2003) and others be revised. One of their model assumptions is that soil C stocks always decrease after forest-to-agricultural conversion. Our data and two global reviews (Guo and Gifford, Murty et al. 2002) suggest that in the most cases, soil C increases, especially in forest-to-pastures conversion. There is evidence in our study and Guo and Gifford's (2002) that Δ soil C stocks is related to climate. Hence, the uncertainty in the model assumption about Δ soil C stocks can be tied to another assumption-C stocks and their changes are similar throughout most of the tropics. Variation in C stocks in mature (Kauffman et al. unpublished) and secondary forest (Cifuentes 2008) and agricultural lands (this study) in Costa Rica are related to the climate variability within the tropics. Therefore, we suggest modeling C stocks and their changes by life zone (a bioclimatic classification system).

We modeled C stock estimates and their changes by life zone and compared those estimates with modeled estimates based on Houghton and Hackler (2001) for the eight life zones sampled in our study. When ecosystem C stocks for all pastures and croplands were averaged and multiplied by the land area of pasture and cropland per life zone in Costa Rica, our ecosystem C stock estimates are twice those when Houghton & Hackler's (2001) assumptions are applied (Appendix 37). Our soil C stock estimates would also be twice those when Houghton & Hackler's (2001) assumptions are applied (Appendix 38), because soil C stocks made up the majority of ecosystem C stocks. Furthermore, ecosystem C stocks changes due to conversion were 1.2 times lower, and soil C stock changes 3.4 times lower using our assumptions compared to Houghton & Hackler's (2001) assumptions (Appendices 39 and 40). This potentially leads to an overestimate of 48 Tg C for forest-to-agriculture conversion effects from seven life zones in Costa Rica using Houghton and Hackler (2001) assumptions (Figure 4.5). Applying this overestimation factor to larger scales and assuming C stocks in other forests and agricultural lands were similar to our study, the overestimate would be 4 Pg C for all 1,520,000 km^2 tropical seasonal forest cleared in Latin America between 1850 and 1990 (Houghton and Hackler 2001) and 20 Pg C for all 7,300,000 km^2 tropical forest cleared globally for agricultural purposes over the same time period (Houghton 1999). Houghton (2003) estimated that the global C flux was 2.2 Pg/year, assuming a 19% overestimate equates to a 0.4 Pg/year overestimate compared to our more conservative estimate. Because this is a substantial overestimate, we suggest including life zone in future modeling efforts.

Sensitivity analysis indicated that potential biases and outliers in our data set can change our results. Our results changed substantially when we used Δ soil and ecosystem C stock estimates adjusted for potential tool bias (Appendix 41). The Δ ecosystem C stock estimate for our study at the scale of all seven life zones in Costa Rica decreased from -48 Tg C (Figure 4.5) to -19 Tg C, which indicated a 8% instead of a 19% overestimate. Our results did not substantially change when we used our likely overestimated Δ soil stocks for banana plantations in the Tropical moist forest life zone compared to the exclusion of croplands in this life zone. However, our results did change when we included the two exceptional high Δ soil C stocks estimates of two coffee plantations in the Tropical Premontane wet forest life zone. The Δ ecosystem C stock estimate for our study at the scale of all seven life zones in Costa Rica increased from -48 Tg C (Figure 4.5) to -59 Tg C. We documented highly variable soil C stock estimates (especially in croplands), and therefore, we expect that exclusion of other individual sites may change our results as well. We therefore suggest that future research efforts be directed towards reduction of uncertainties in soil C stocks and their changes due to land use conversion.

We found strong evidence that ecosystem C stocks in agricultural lands differ by life zone, but our results did not show that ecosystem C stocks differed widely by agricultural land use. One approach for reducing uncertainty in global C flux estimates would be to use remote sensing to stratify the landscape by land use type, but our study suggests that it is more important to stratify by life zone than agricultural land use type.

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Table 4.1. Equations to determine number of coffee plant and tree biomass, and their literature references and model statistics.

Component	Equation #	Equations	n	R^2	MSE	Reference
Number of coffee plants/ha	4.1	p/40*100*100/s				This study
Coffee plant	4.2	$10^{-1.181 + 1.991 * \log(d_{15})}$	96	0.93	0.03	Segura et al. 2006
	4.3	$10^{-0.779 + 2.338 * \log(h)}$	96	0.82	0.07	Segura et al. 2006
Trees in coffee plantations:						
Inga (punctata)	4.4	$10^{-0.559 + 2.067 * \log(dbh)}$	7	0.97	0.02	Segura et al. 2006
Cordia alliodora	4.5	$10^{-0.755 + 2.072 * \log(dbh)}$	10	0.95	0.01	Segura et al. 2006
Eucalyptus (Saligna)						
Wood	4.6	$0.0062 * dbh^{3.3178}$	35	0.997		Kaye et al. 2000
Crown	4.7	$0.0082 * dbh^{2.2095}$	35	0.997		Kaye et al. 2000

n = sample size, R^2 = adjusted coefficient of determination, MSE = mean squared error, p = number of plants measured in 40 m coffee plant row length, s = spacing between coffee plant rows (m), d_{15} = stem diameter at 15 cm above ground, dbh = diameter at breast height in cm (1.3 m height above ground), h = height in m.

Table 4.2. Estimates of agricultural land area, ecosystem and soil C stock estimates and their changes (Δ) due to forest-to-agriculture conversion for the eight life zones sampled in our study.

	ha				Mg C/ha							
	Area				Pasture ≥ 8 years				Cropland			
		Non-forested			C stock		Δ C stock		C stock		Δ C stock	
Life zone	Costa Rica	in 2005	Pasture*	Cropland*	Ecosystem	Soil	Ecosystem	Soil	Ecosystem	Soil	Ecosystem	Soil
Tropical dry forest	116,140	69,853	69,853	0	80	76	-117	-34				
Tropical moist forest ***	714,962	451,953	406,758	45,195	94	84	-110	6	142	134	***	***
Tropical wet forest	832,934	356,948	321,253	35,695	200	188	-115	62	134	125	-182	-3
Premontane moist forest-warm**	471,897	291,098	261,988	29,110	80	76	**	**	153	133	**	**
Premontane wet forest-warm	706,880	488,898	440,009	48,890	257	204	-49	42	157	148	-172	-43
Premontane wet forest ****	429,002	296,013	0	296,013					312	289	-194	-14
Premontane rain forest	437,216	112,508	101,257	11,251	281	229	-135	25	235	220	-182	16
Lower Montane rain forest	334,869	27,046	27,046	0	283	262	-238	-9				
Total included for C stocks	4,043,900	2,094,318	1,628,164	466,153								
Total included for Δ C stocks	3,572,003	1,803,219	1,366,176	391,848								

* We assumed 90% of agricultural land is in pasture ≥ 8 years and 10% in croplands within each life zone, unless we report no C stock and Δ C stock data for pastures or croplands. ** We assumed that soil C stocks in pastures in the Tropical Premontane moist forest-warm life zone is similar to pastures in the Tropical dry forest life zone, which is a conservative estimate. *** We excluded Δ soil C stocks in croplands in the Tropical moist forest life zone due to a lack of reference mature forest data. **** We excluded two coffee plantations with exceptional high Δ soil C stocks when calculating mean Δ ecosystem and soil C for the Tropical Premontane wet forest life zone.

Tabe 4.3. Aboveground and soil C stock estimates in croplands and differences (Δ) between cropland and mature forest stocks by life zone in Costa Rica.

Land use	Life zone	Site #	Aboveground C	Soil C	Corrected soil C	Δ Aboveground C	Δ Soil C	Δ Ecosystem C	n*
Banana	Tropical moist forest	224	8	120	107	-115 **	14 **	-101	5
		225	9	133	121	-114 **	28 **	-86	5
		226	7	131	138	-115 **	45 **	-71	5
		227	7	165	170	-116 **	77 **	-39	5
	Tropical Premontane wet forest-warm	222	8	140	141	-130	-51	-180	3
		230	7	139	139	-131	-53	-184	3
		229	9	147	150	-129	-42	-171	3
		221	11	161	164	-127	-28	-155	3
	Tropical wet forest	220	10	171	128	-178	0	-178	3
		228	8	129	101	-179	-27	-206	3
		223	8	181	146	-180	18	-162	3
Coffee	Tropical Premontane wet forest	218	22	293	288	-122	105	-17	1
		219	17	406	468	-128	285	157	1
		216	10	357	272	-211	1	-210	3
		217	58	597	573	-163	302	139	3
		211	28	197	149	-193	-123	-315	3
		212	7	294	277	-214	6	-208	3
		210	4	210	166	-217	-105	-323	3
		213	26	264	221	-195	-50	-245	3
	Tropical Premontane rain forest	214	16	233	195	-196	-9	-205	2
		215	13	310	245	-198	40	-158	2
Sugarcane	Tropical Premontane moist forest-warm	201	22	127	122	-42 ***	-18 ***	-60	3
		202	17	136	128	-47 ***	-13 ***	-60	3
		200	22	154	143	-42 ***	3 ***	-39	3
		203	16	134	141	-48 ***	1 ***	-48	3
	Tropical Premontane wet forest	205	21	380	286	-200	14	-186	3
		204	29	333	312	-192	40	-152	3
		206	28	313	246	-193	-26	-219	3
		207	22	227	191	-199	-80	-279	3
		208	28	474	415	-192	143	-49	3
		209	30	260	177	-191	-94	-285	3

*n= sample size of reference mature forests. ** Reference forests are in Pacific zone which has distinct annual dry season, while banana plantations are in Caribbean zone without a strong dry season. ***Reference forest are nearby but classified as Tropical dry forest life zone.

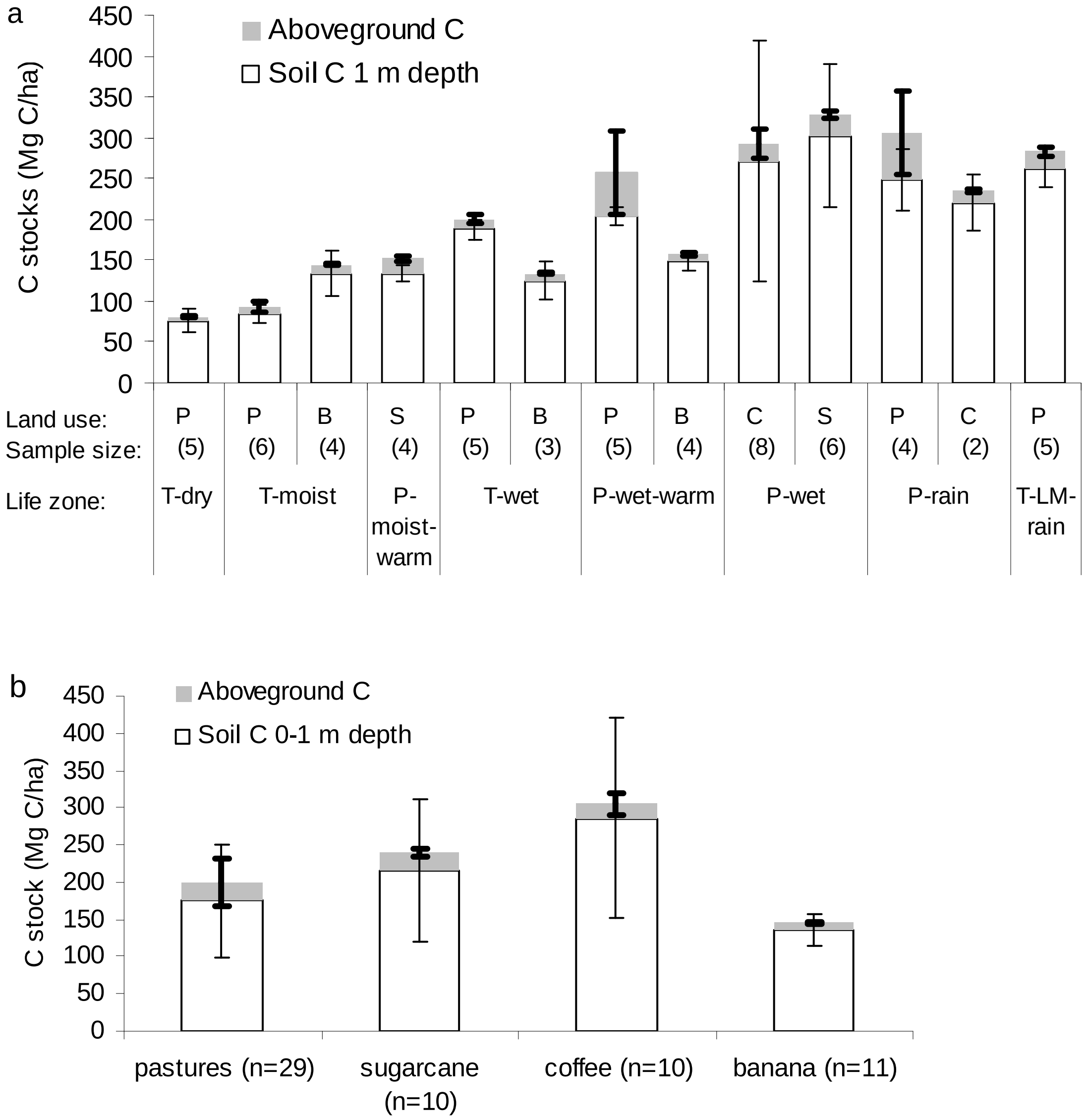

Figure 4.1. Mean (± SD) 0-1 m corrected soil, and aboveground C stocks (a) by land use and life zone, and (b) by land use across a climatic gradient in Costa Rica. Bold error bars are associated with mean aboveground C stocks, and thin error bars with mean soil C stocks. Land use: P = pastures, S = sugarcane, C = coffee, B = banana plantations. Life zone: T-dry = Tropical dry forest; T-moist = Tropical moist forest; P-moist-warm = Tropical Premontane moist forest-warm; T- wet = Tropical wet forest; P-wet-warm = Tropical Premontane wet forest-warm; P-wet = Tropical Premontane wet forest; P-rain = Tropical Premontane rain forest; T-LM-rain = Tropical Lower Montane rain forest.

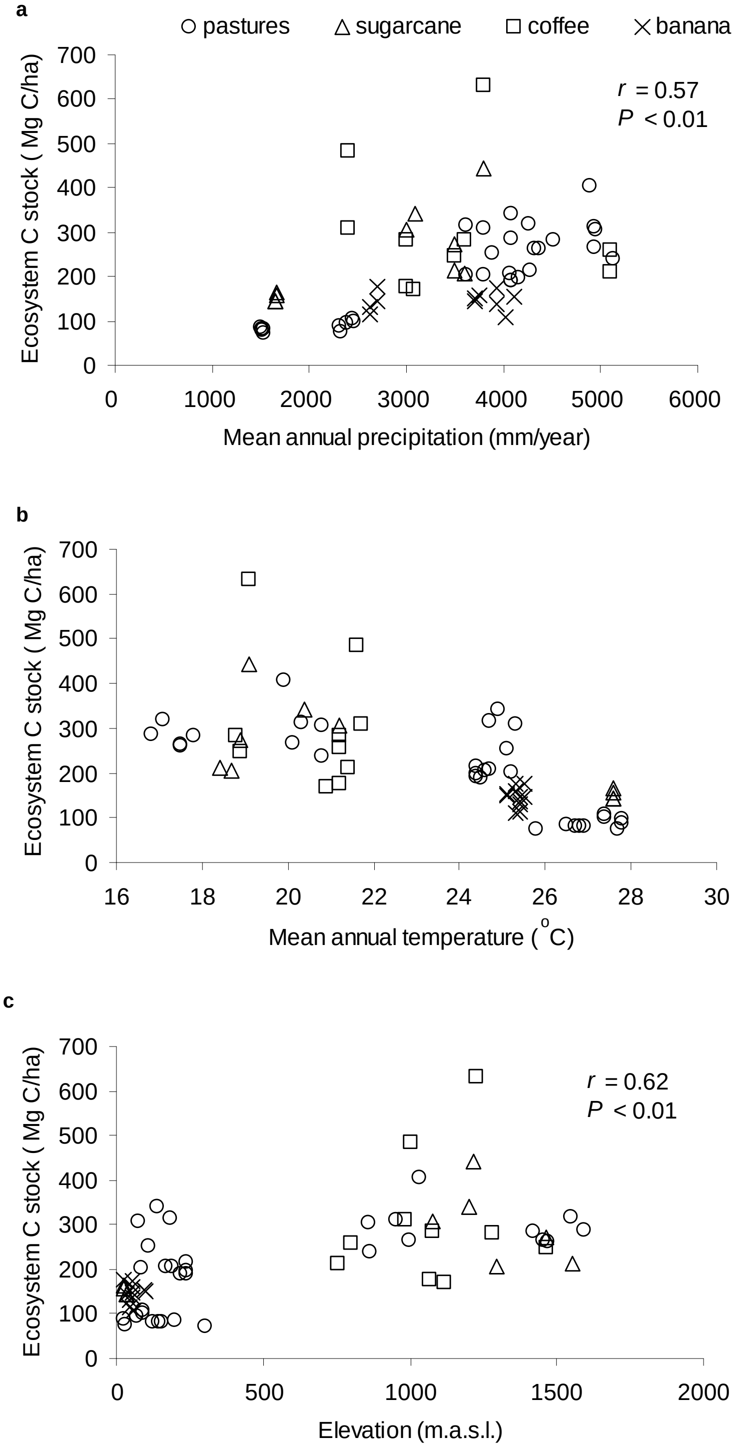

Figure 4.2. Relationship between ecosystem C stocks in agricultural sites (n = 62) and (a)mean annual temperature, (b) precipitation, and (c) elevation (meter above sea level) across a climatic gradient in Costa Rica.

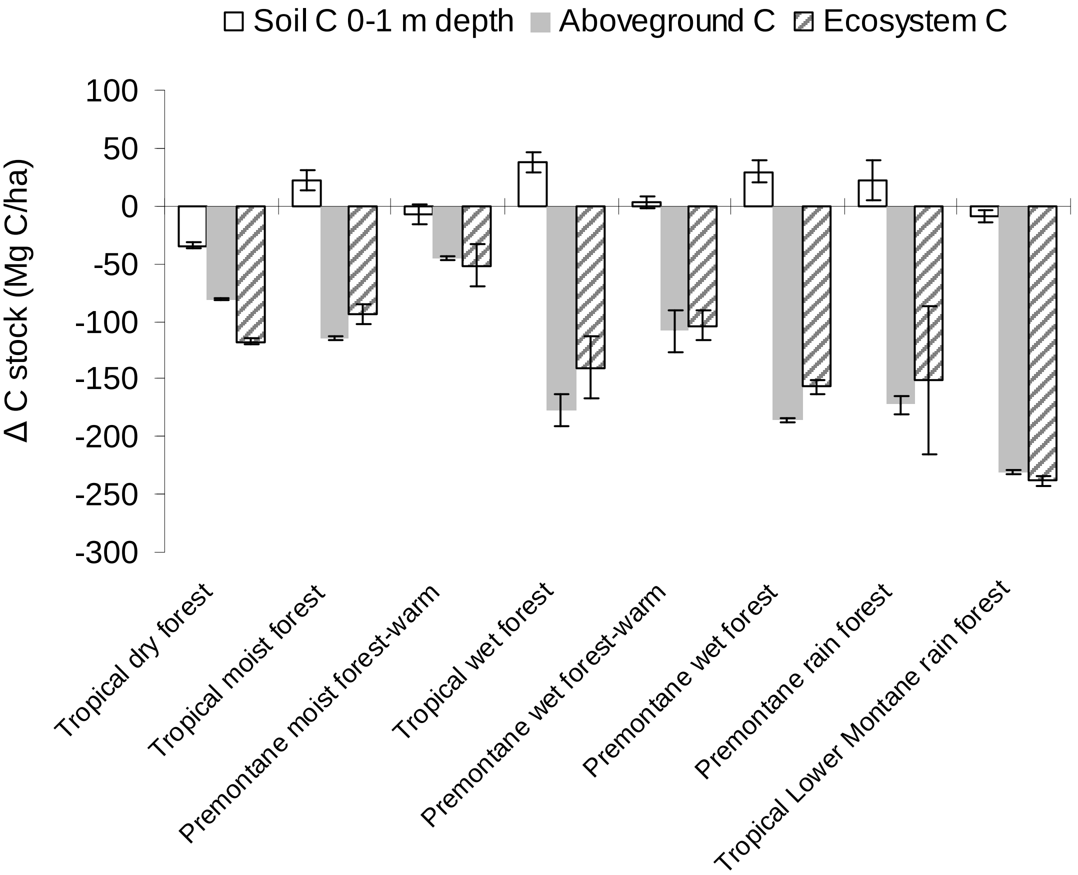

Figure 4.3. Mean (± SE) change (Δ) in 0-1 m soil, aboveground, and ecosystem C stocks in agricultural lands by life zone in Costa Rica.

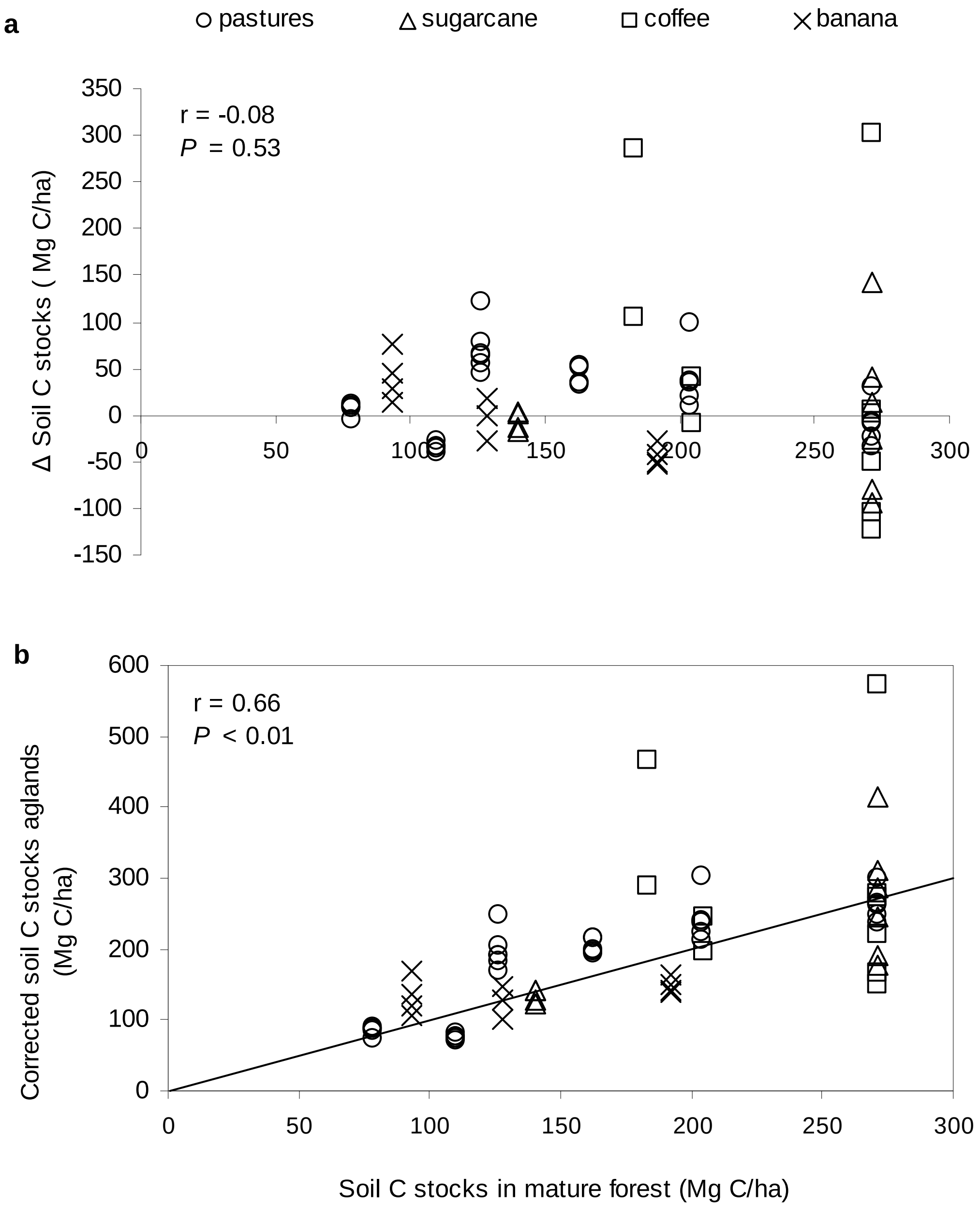

Figure 4.4: Relationship between soil C stocks in reference mature forest and (a) soil C stock changes (Δ) and (b) corrected soil C stocks in agricultural lands. Diagonal line is a 1:1 line.

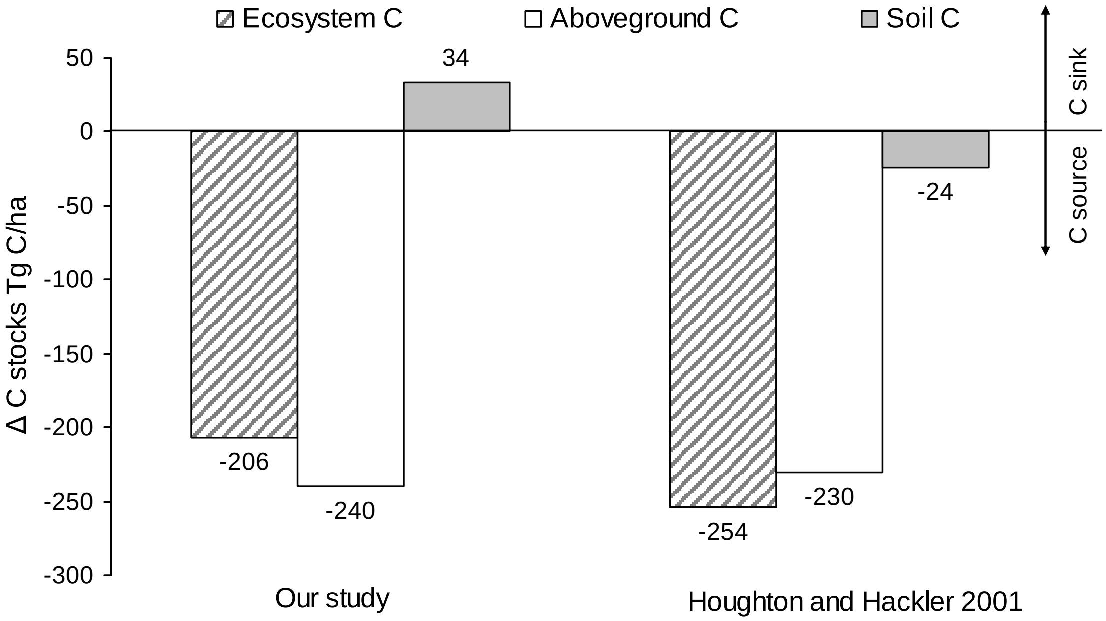

Figure 4.5. Ecosystem, aboveground and soil C stock change (Δ) due to forest-to-agricultural conversion for the land area covered by seven life zones in Costa Rica included in this study.

CHAPTER 5

GENERAL CONCLUSIONS

Chapter 5 General conclusions

5.1 Research questions and answers

In this dissertation I sought to answer several research questions to improve our understanding of the impacts of tropical land use change on terrestrial carbon (C) and nitrogen (N) stocks. I used Costa Rica as a case study, but many of the life zones and land uses investigated in this dissertation can be found throughout the (sub)tropics. In this chapter I summarized the most important conclusions that are discussed in detail in Chapters 2-4.

(1) How do aboveground and soil C and N stocks and their net changes due to forest-to-agricultural conversion differ among life zone and agricultural land use type in Costa Rica? I found that that soil and ecosystem C and N stocks varied more by life zone than by land use (Chapter 4). Net soil C and N stock changes due to forest-to-agricultural conversion were highly variable and increased or decreased depending on the site (Chapter 2 and 4). High spatial soil variability, potential inadequate reference mature forests, and the use of different sampling tools to estimate soil bulk density in mature forests and pastures contributed to uncertainties in net soil C and N stock changes due to forest-to-pasture conversion. Net soil C and N stock changes due to forest-to-pasture conversion differed by life zone. They decreased in the Tropical dry forest and Lower Montane rain forest life zones, and in the Tropical Premontane rain forest life zone when including estimates adjusted for potential sampling tool bias, and increased in the other life zones (Chapter 2). Furthermore, the presence of large remnant trees caused relatively high aboveground and ecosystem C stocks in 20% of our pastures, which is generally not accounted for in C flux models (Chapter 3).

(2) How do aboveground and soil C and N stocks and their changes due to forest-to-pasture conversion differ by pasture age? I found that pasture age was not as an important predictor of soil and aboveground C and N stocks as life zone (Chapter 2 and 3). In addition, the effect of land use change on soil and aboveground C and N stocks was far more important than the effect of land use duration (Chapter 2 and 3). Generally, 0-1 m soil C and N stocks decreased with pasture age (Chapter 2). Adding age to the variables life zone and temperature in our models to predict soil C stocks in pastures, improved model fit, but life zone and individual climate variables explained more of the variation in soil C and N stocks than age alone (Chapter 2). I did not find decreasing aboveground C and N stocks with pasture age in the majority of our chronosequences (Chapter 3). Although pasture age probably played some role in the amount of vegetation in pastures, the high level of variation in legacy components such as large remnant trees and downed wood among pastures within life zones prevented me from detecting an age effect in most life zones (Chapter 3).

(3) Can the use of life zones reduce potential biases and uncertainty of regional and global C flux estimates for forest-to-agricultural conversions? My Costa Rican agricultural ecosystem C stock estimates were 2-fold greater than Intergovernmental Panel on Climate Change (IPCC)-endorsed estimates (Denman et al. 2007, Houghton and Hackler 2001, Houghton 2003). In addition, my results indicated that IPCC's C flux estimates due to forest-to-agricultural conversions were overestimated by 8-19%. I suggest that incorporating climatic variability is more important than incorporating agricultural land use type variability in estimates of ecosystem C and N stocks and their changes due to conversion in tropical landscapes at regional scales. Assuming the 19% overestimate for C fluxes for all tropical forest-to-agricultural conversions based on our life zone analysis would indicate that the annual global C flux due to land use change has been overestimated by 0.4 Pg C/year (Chapter 4).

5.2 Implications

Models to predict how tropical ecosystems might respond to land use conversion, climate change, CO_2 fertilization, or N deposition should incorporate different scenarios depending on the life zone. This dissertation and companion studies (Cifuentes Jara 2008, Kauffman et al. unpublished data) suggested that the Life Zone system (Holdridge 1947 and 1967) is a useful classification system and mapping tool to estimate regional (in our case Costa Rica) and global ecosystem C and N stocks and fluxes. Incorporation of ecosystem C stock variability related to life zone into regional and global models is more important than including variability related to pasture age (Chapter 2 and 3) or land use type (Chapter 4).

I documented highly variable soil C stock estimates (especially in croplands), and potential biases and uncertainties in estimates of soil C and N stock changes due to conversion. In addition, I documented how these potential biases and uncertainties may influence estimates at larger scales, and therefore, I suggest that future research efforts be directed towards reduction of uncertainties in soil C stocks and their changes due to land use conversion.

My results also suggested that ecosystem N stocks may increase after pasture-to-forest conversion (Chapter 2 and 3). This could lead to short-term increased C storage and to long-term increases in N fluxes (Aber et al. 1998) especially under the anticipated increased N deposition rates (Matson 1999). Data on N cycling and the role of phosphorous in these pastures are needed to understand the mechanisms behind the ecosystem C and N stocks and changes documented in my study.

Protecting remaining mature forest in the Costa Rican Tropical Premontane and Lower Montane rain forest life zones is essential for reducing future C emissions from this country and may conserve more C per hectare than could be sequestered in reforestation of Costa Rica’s drier areas. In addition, I suggest that protection of large remnant trees in pastures in the Tropical Premontane rain forest and Premontane wet forest-warm life zones could conserve the same amount of C on a per-hectare basis as protecting tropical dry forest. The extent of large remnant trees across all pastures is not well enough known, but could have a significant effect on global C stocks. Nevertheless, besides C and N storage, large remnant trees in pastures provide benefits to many organisms and humans and therefore protection of these trees has great ecological and social value (Harvey and Haber 1999). The extent of pasture trees across large areas should be evaluated to determine the importance of large trees in (tropical) pastures for pan-tropical or global C stocks and flux estimates.

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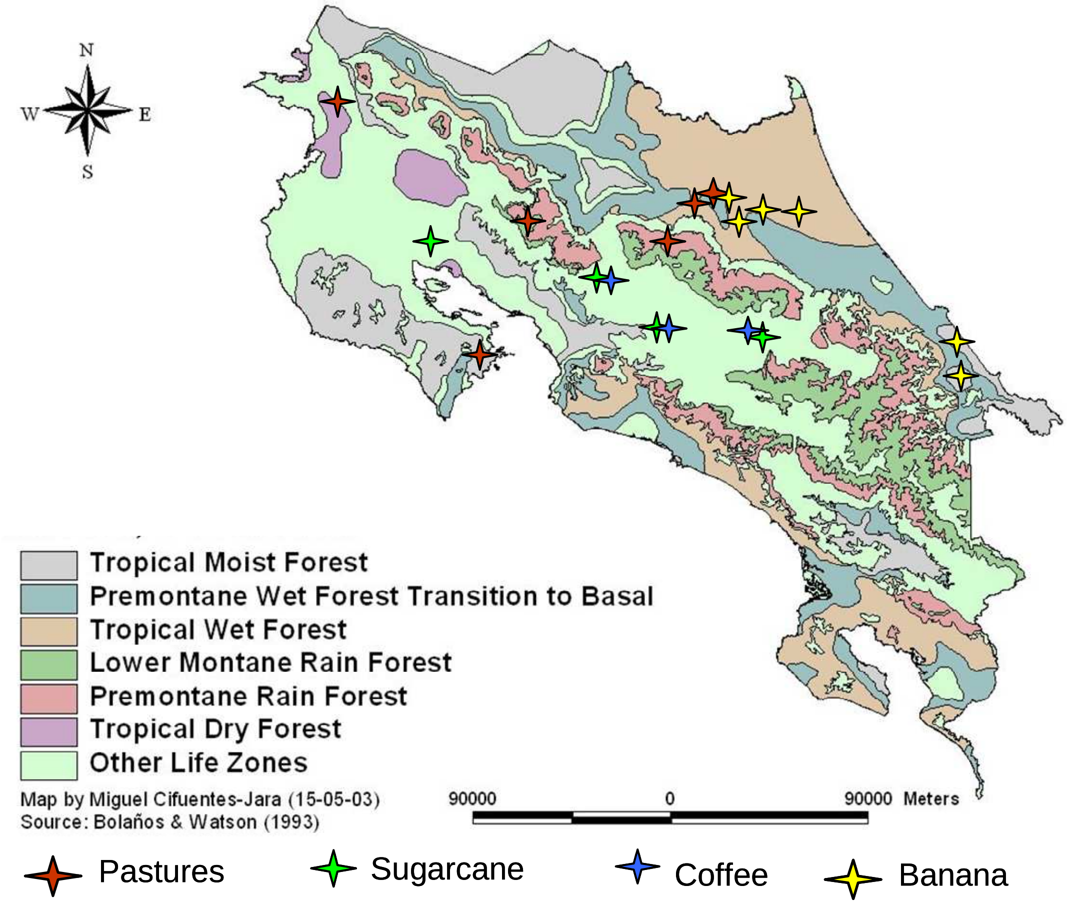
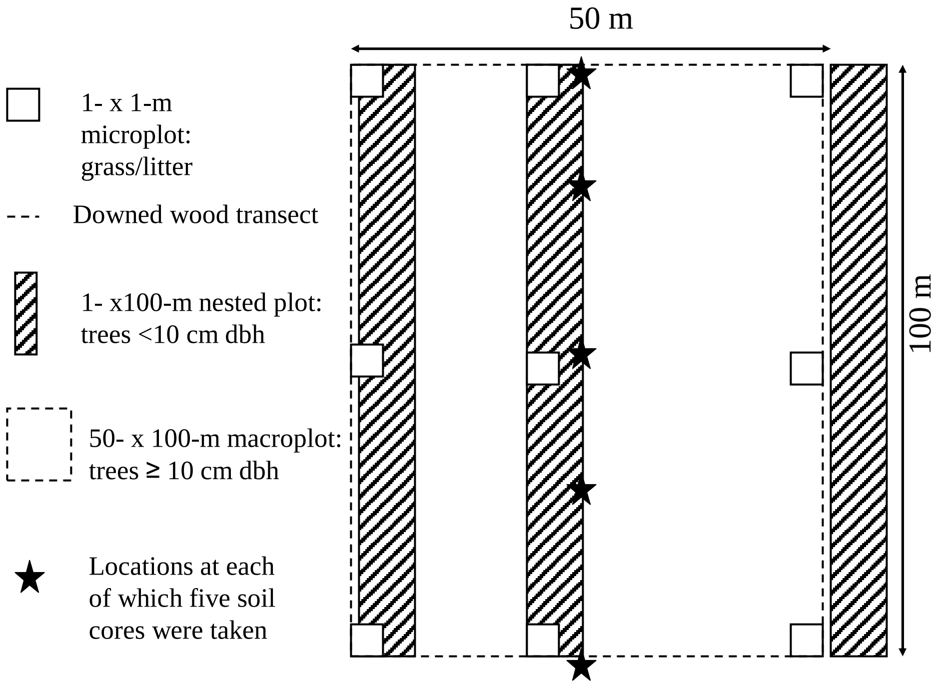
APPENDICES

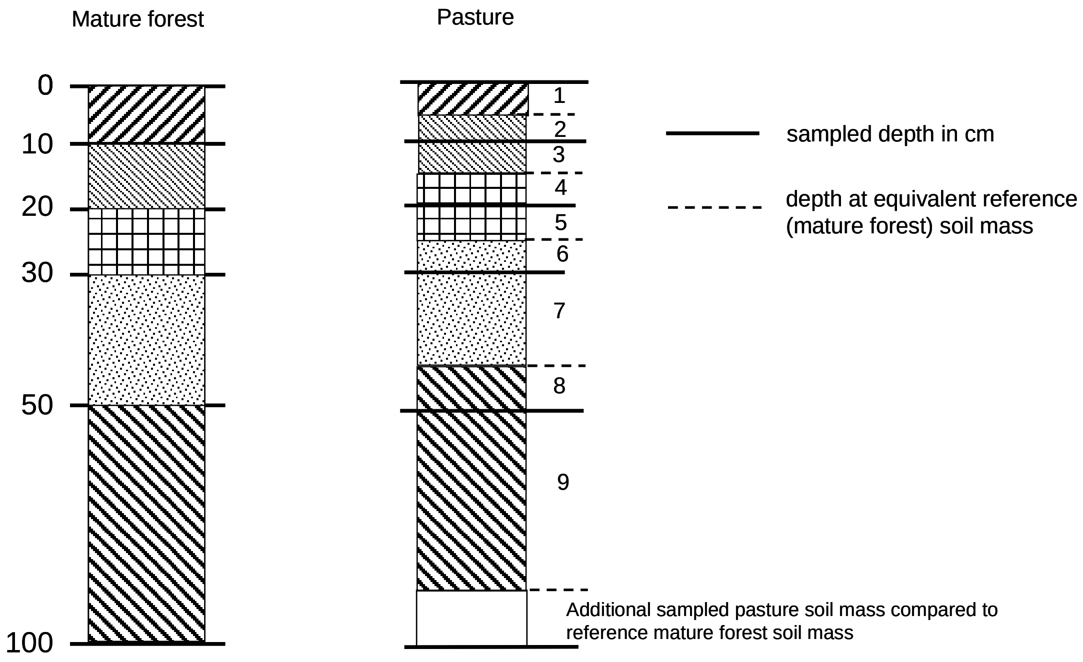
Appendix 1. Life zone map of Costa Rica showing the dominant life zones and the general area where pasture chronosequences, sugarcane, coffee and banana plantations were sampled.



Appendix 2. Nested plot sampling design used to collect aboveground biomass data and soil samples in pastures in Costa Rica.



Appendix 3. Example of the correction method for soil bulk density differences between mature forest and pastures. Soil C and N stocks in pastures were corrected using equations in Appendix 4. All soil layers in pastures for which soil C and N stocks should be calculated separately are distinguished with numbers (e.g. 1-9).



Appendix 4. Equations used to calculate soil C and N stocks in pastures corrected for soil bulk density differences between mature forest and pastures. Methods are similar to Veldkamp (1994) , Ellert and Bettany (1995), and Power and Veldkamp (2005).

Definitions:

BD = soil bulk density (g/cm^3)

%C = soil C concentration (%) (can be replaced with %N to calculate soil N stocks)

L = length of soil layer (cm)

MF = Soil mass of reference (mature forest) soil (g/m^2)

MP = Soil mass pasture soil (g/m^2)

MN = Additional soil mass needed for a specific soil layer to add up to the equivalent mass of the reference (mature forest) soil in that layer (g/m^2)

RM = Remaining pasture soil mass that could be used for the next depth layer of equivalent mass of the reference (mature forest) soil (g/m^2)

Layer $x_{f\ equiv.}$ soil C stock = Soil C stocks in pasture soil layer that is equivalent to a specific forest soil layer (g/m^2) (Multiply by 0.01 to convert to Mg C/ha)

The following equations were the same for all calculations:

$$MF_{layer\ x} = \text{forest } BD_{layer\ x} \times L_{layer\ x} \quad [1]$$

e.g. $MF_{0\text{-}10\ cm} = \text{forest } BD_{0\text{-}10cm} \times L_{0\text{-}10cm}$

$$MP_{layer\ x} = \text{pasture } BD_{layer\ x} \times L_{layer\ x} \quad [2]$$

e.g. $MP_{0\text{-}10\ cm} = \text{pasture } BD_{0\text{-}10cm} \times L_{0\text{-}10cm}$

$$MN_{layer\ x} = MF_{layer\ x} - RM_{layer\ x\text{-}1} \quad [3]$$

e.g. $MN_{0\text{-}10\ cm} = MF_{0\text{-}10\ cm}$

$MN_{10\text{-}20\ cm} = MF_{10\text{-}20\ cm} - RM_{0\text{-}10\ cm}$

$MN_{20\text{-}30\ cm} = MF_{20\text{-}230\ cm} - RM_{10\text{-}20\ cm}$

etc.

Appendix 4 (continued)

The following equations differed depending on the situation:

If $MP_{0\text{-}10\ cm} > MF_{0\text{-}10\ cm}$ then (no alternative shown):

$0\text{-}10\ cm_{f\ equiv.}$ soil C stock = $\%C_{0\text{-}10cm} \times MN_{0\text{-}10cm}$ [4]

If $RM_{0\text{-}10\ cm} < MF_{20\text{-}30\ cm}$ then (no alternative shown):

$10\text{-}20\ cm_{f\ equiv.}$ soil C stock = $(RM_{0\text{-}10cm} \times \%C_{0\text{-}10cm} + MN_{10\text{-}20cm} \times \%C_{10\text{-}20cm})$ [5]

$RM_{0\text{-}10\ cm} = MP_{0\text{-}10\ cm} - MF_{0\text{-}10\ cm}$ [6]

If $RM_{10\text{-}20\ cm} < MF_{20\text{-}30\ cm}$ then:

$20\text{-}30\ cm_{f\ equiv.}$ soil C stock = $(RM_{10\text{-}20cm} \times \%C_{10\text{-}20cm} + MN_{20\text{-}30cm} \times \%C_{20\text{-}30cm})$ [7a]

$RM_{10\text{-}20\ cm} = MP_{10\text{-}20\ cm} - MF_{10\text{-}20\ cm} - RM_{0\text{-}10\ cm}$ [8]

If $RM_{10\text{-}20\ cm} > MF_{20\text{-}30\ cm}$ then:

$20\text{-}30\ cm_{f\ equiv.}$ soil C stock = $MF_{20\text{-}30\ cm} \times \%C_{10\text{-}20\ cm}$ [7b]

If $RM_{20\text{-}30\ cm} + MP_{30\text{-}50\ cm} > MF_{30\text{-}50\ cm}$ then:

$30\text{-}50\ cm_{f\ equiv.}$ soil C stock = $(RM_{20\text{-}30cm} \times \%C_{20\text{-}30cm} + MN_{30\text{-}50cm} \times \%C_{30\text{-}50cm})$ [9a]

$RM_{20\text{-}30\ cm} = MP_{20\text{-}30\ cm} - MF_{20\text{-}30\ cm} - RM_{10\text{-}20cm}$ [10a]

$RM_{30\text{-}50cm} = MP_{30\text{-}50\ cm} - MF_{30\text{-}50\ cm} - RM_{20\text{-}30\ cm}$ [11a]

If $RM_{20\text{-}30\ cm} + MP_{30\text{-}50\ cm} < MF_{30\text{-}50\ cm}$ then:

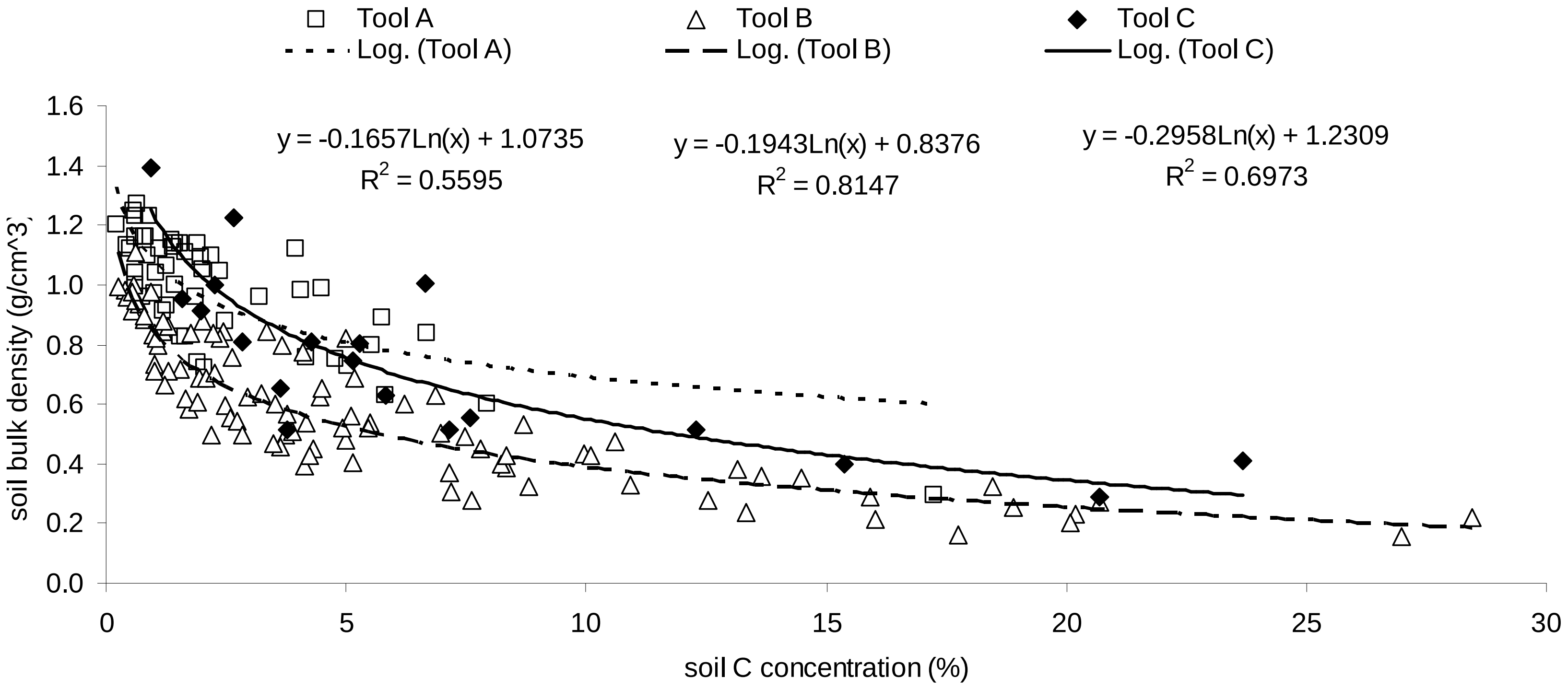
$30\text{-}50\ cm_{f\ equiv.}$ soil C stock = $- MN_{20\text{-}30cm} \times \%C_{20\text{-}30cm} + MP_{20\text{-}30\ cm} \times \%C_{10\text{-}20cm} - RM_{20\text{-}30cm} \times \%C_{30\text{-}50\ cm}$ [9b]

$RM_{20\text{-}30\ cm} = MP_{20\text{-}30\ cm} - MF_{30\text{-}50\ cm} - MN_{20\text{-}30\ cm}$ [10b]

$RM_{30\text{-}50cm} = MF_{30\text{-}50\ cm} + RM_{20\text{-}30\ cm}$ [11b]

If $RM_{30\text{-}50\ cm} + MP_{50\text{-}100\ cm} > MF_{30\text{-}50\ cm}$ then (no alternative shown):

$50\text{-}100\ cm_{f\ equiv.}$ soil C stock = $RM_{30\text{-}50\ cm} \times \%C_{30\text{-}50cm} + MN_{50\text{-}100\ cm} \times \%C_{50\text{-}100\ cm}$ [12]



Appendix 5. Relationships between soil C concentrations and soil bulk densities in Costa Rican mature forests sampled with tools A (n = 10), B (n = 20) and C (n = 4). Dimensions of tool B and C were described in section 2.2.5 and tool A in section 4.2.3.

Appendix 6. Mean (± SD) of soil variables for mature reference forests by soil layer and life zone for six life zones in Costa Rica.

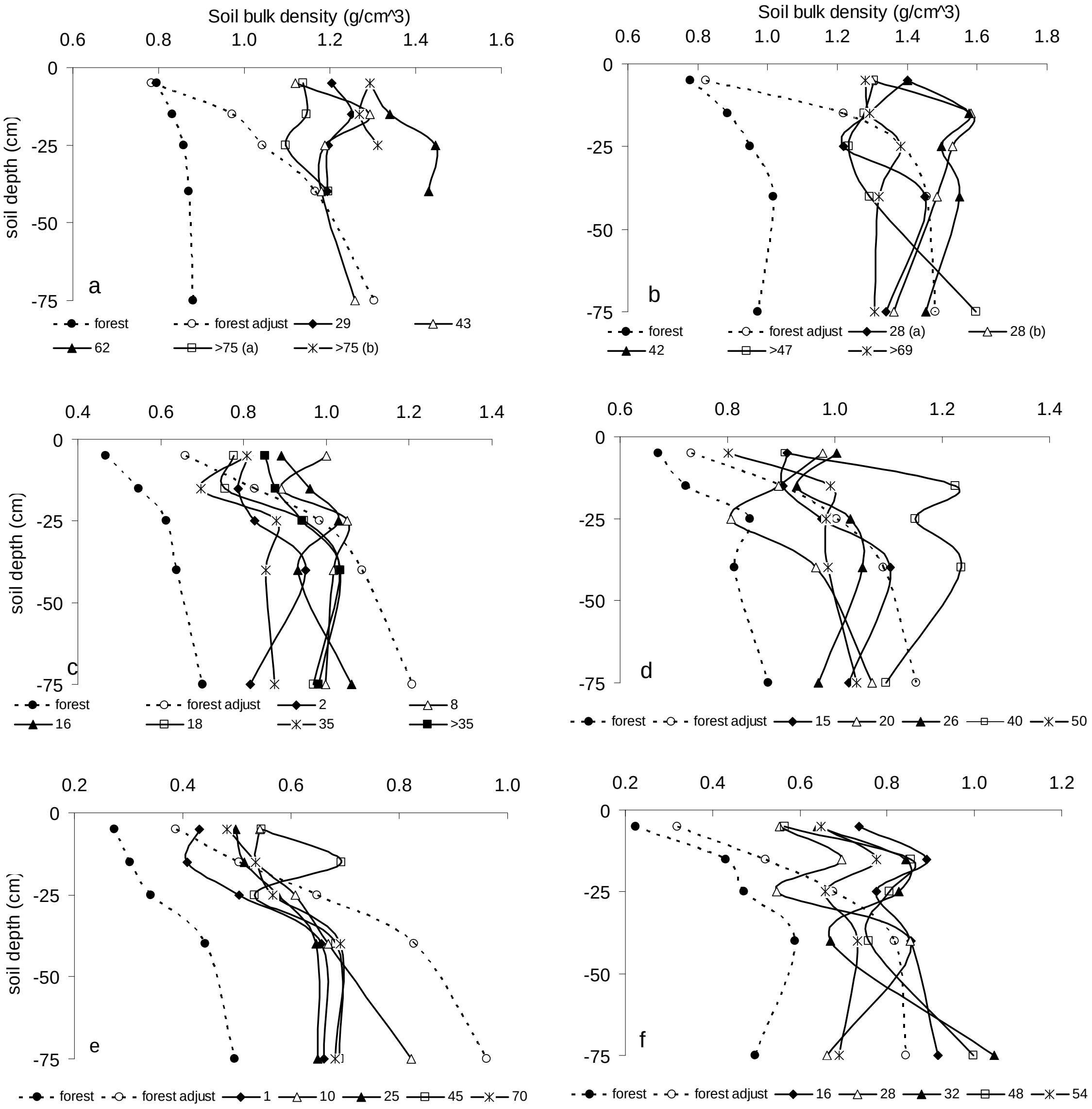
Life zone	Soil depth cm	Sample size #	Soil bulk density original g/cm^3	Soil bulk density adjusted g/cm^3	%Soil C %	%Soil N %	Soil C stock original Mg C/ha	Soil C stock adjusted Mg C/ha	Soil N stock original Mg N/ha	Soil N stock adjusted Mg N/ha
Tropical dry forest	0-10	2	0.80 ± 0.03	0.78 ± 0.04	4.5 ± 0.63	0.356 ± 0.057	36.2 ± 6.40	35.5 ± 3.05	2.83 ± 0.57	2.78 ± 0.30
	10-20	2	0.83 ± 0.01	0.97 ± 0.01	2.4 ± 0.05	0.205 ± 0.008	20.1 ± 0.77	23.4 ± 0.34	1.71 ± 0.10	1.99 ± 0.07
	20-30	2	0.86 ± 0.03	1.04 ± 0.03	1.9 ± 0.19	0.155 ± 0.013	16.3 ± 2.14	19.8 ± 1.38	1.33 ± 0.15	1.61 ± 0.09
	30-50	2	0.87 ± 0.01	1.17 ± 0.02	1.2 ± 0.06	0.100 ± 0.001	21.7 ± 0.83	29.1 ± 1.12	1.74 ± 0.00	2.33 ± 0.00
	50-100	1	0.88 ±	1.30 ±	0.8 ±	0.072 ±	31.3 ±	51.2 ±	2.87 ±	2.34 ± 3.31
Tropical moist forest	0-10	3	0.78 ± 0.08	0.82 ± 0.07	4.1 ± 0.96	0.317 ± 0.073	31.0 ± 3.91	32.9 ± 4.88	2.43 ± 0.30	2.57 ± 0.36
	10-20	3	0.89 ± 0.08	1.22 ± 0.04	1.1 ± 0.13	0.117 ± 0.009	9.3 ± 0.83	12.8 ± 1.23	1.04 ± 0.07	1.43 ± 0.07
	20-30	3	0.95 ± 0.05	1.38 ± 0.03	0.6 ± 0.07	0.076 ± 0.004	5.7 ± 0.70	8.3 ± 0.71	0.72 ± 0.03	1.05 ± 0.03
	30-50	3	1.02 ± 0.08	1.45 ± 0.07	0.5 ± 0.12	0.061 ± 0.005	9.9 ± 3.29	13.8 ± 2.72	1.25 ± 0.21	1.78 ± 0.06
	50-100	3	0.97 ± 0.02	1.48 ± 0.14	0.5 ± 0.19	0.053 ± 0.015	22.3 ± 8.71	33.3 ± 11.25	2.59 ± 0.70	3.88 ± 0.82
Tropical wet forest	0-10	3	0.47 ± 0.09	0.66 ± 0.08	7.1 ± 1.73	0.573 ± 0.153	32.0 ± 3.16	45.7 ± 6.54	2.58 ± 0.32	3.70 ± 0.62
	10-20	3	0.55 ± 0.07	0.83 ± 0.08	4.0 ± 1.04	0.354 ± 0.089	21.5 ± 2.85	32.7 ± 5.54	1.89 ± 0.25	2.87 ± 0.48
	20-30	3	0.61 ± 0.07	0.98 ± 0.04	2.3 ± 0.33	0.204 ± 0.032	14.1 ± 0.62	22.8 ± 2.32	1.24 ± 0.08	2.00 ± 0.23
	30-50	3	0.64 ± 0.07	1.09 ± 0.02	1.6 ± 0.08	0.143 ± 0.015	20.8 ± 1.21	35.5 ± 1.33	1.81 ± 0.10	3.10 ± 0.29
	50-100	3	0.70 ± 0.03	1.21 ± 0.03	1.1 ± 0.12	0.099 ± 0.016	37.9 ± 2.32	65.3 ± 5.35	3.47 ± 0.40	5.99 ± 0.79
Tropical Premontane wet forest-warm	0-10	2	0.67 ± 0.19	0.73 ± 0.01	5.4 ± 0.15	0.431 ± 0.039	36.0 ± 9.16	39.5 ± 0.67	2.92 ± 1.07	3.16 ± 0.32
	10-20	2	0.72 ± 0.12	0.90 ± 0.03	3.0 ± 0.29	0.261 ± 0.016	21.8 ± 1.56	27.4 ± 1.74	1.90 ± 0.42	2.36 ± 0.21
	20-30	2	0.84 ± 0.22	1.00 ± 0.02	2.2 ± 0.13	0.153 ± 0.082	18.3 ± 5.92	21.7 ± 0.93	1.38 ± 1.03	1.53 ± 0.80
	30-50	2	0.81 ± 0.14	1.09 ± 0.09	1.6 ± 0.50	0.141 ± 0.064	27.4 ± 12.74	35.4 ± 7.85	2.37 ± 1.45	3.01 ± 1.15
	50-100	2	0.88 ± 0.11	1.15 ± 0.08	1.3 ± 0.35	0.115 ± 0.052	59.2 ± 23.02	75.9 ± 15.10	5.16 ± 2.91	6.49 ± 2.52
Tropical Premontane rain forest	0-10	2	0.27 ± 0.02	0.39 ± 0.04	17.4 ± 2.12	1.302 ± 0.214	47.3 ± 1.62	67.0 ± 1.92	3.53 ± 0.27	5.00 ± 0.36
	10-20	2	0.30 ± 0.04	0.50 ± 0.03	11.7 ± 1.14	0.896 ± 0.127	35.3 ± 1.18	58.8 ± 2.37	2.69 ± 0.03	4.49 ± 0.38
	20-30	2	0.34 ± 0.04	0.65 ± 0.00	7.2 ± 0.03	0.549 ± 0.022	24.4 ± 3.10	46.5 ± 0.10	1.86 ± 0.17	3.56 ± 0.14
	30-50	2	0.44 ± 0.02	0.83 ± 0.03	3.9 ± 0.43	0.312 ± 0.035	34.5 ± 2.18	64.8 ± 4.56	2.74 ± 0.18	5.14 ± 0.37
	50-100	2	0.50 ± 0.00	0.96 ± 0.06	2.5 ± 0.47	0.205 ± 0.040	62.2 ± 11.48	120.0 ± 15.60	5.08 ± 0.97	9.80 ± 1.33
Tropical lower montane rain forest	0-10	3	0.22 ± 0.06	0.32 ± 0.07	22.3 ± 5.53	1.670 ± 0.425	50.3 ± 18.52	68.4 ± 0.90	3.76 ± 1.38	5.12 ± 0.05
	10-20	3	0.43 ± 0.07	0.52 ± 0.07	11.2 ± 2.63	0.857 ± 0.177	48.6 ± 15.17	57.2 ± 6.33	3.69 ± 0.99	4.38 ± 0.35
	20-30	3	0.47 ± 0.06	0.68 ± 0.06	6.6 ± 1.26	0.514 ± 0.115	31.5 ± 9.29	44.1 ± 4.98	2.46 ± 0.79	3.43 ± 0.51
	30-50	3	0.59 ± 0.21	0.82 ± 0.02	4.1 ± 0.26	0.321 ± 0.038	48.0 ± 18.78	66.2 ± 2.75	3.80 ± 1.54	5.24 ± 0.51
	50-100	3	0.50 ± 0.03	0.84 ± 0.02	3.7 ± 0.19	0.285 ± 0.005	92.7 ± 9.38	156.5 ± 5.31	7.11 ± 0.43	12.03 ± 0.30

Adjusted estimates were calculated using regression equation for tool C from Appendix 5 to standardized soil bulk density estimates sampled with different tools (section 2.2.5).
Original data from Kauffman et al. (unpublished).

Appendix 7. Mean (± SE) soil bulk density (g/cm^3) by pasture and soil layer in six pasture chronosequences in Costa Rica and mean soil bulk density for each soil layer by life zone

Life zone	Pasture age (yrs)	Soil depth (cm) 0-10	10-20	20-30	30-50	50-100
Tropical	29	1.20 ± 0.06	1.25 ± 0.05	1.20 ± 0.07	1.19 ± 0.06	n.s.
dry forest	43	1.12 ± 0.08	1.29 ± 0.03	1.19 ± 0.08	1.18 ± 0.02	1.26 ± 0.23 (2)
	62	1.29 ± 0.09	1.34 ± 0.05	1.45 ± 0.03	1.43 ± 0.09	n.s.
	>75 (a)	1.14 ± 0.10	1.15 ± 0.09	1.10 ± 0.10	1.20 ± 0.14	n.s.
	>75 (b)	1.29 ± 0.10	1.27 ± 0.09	1.31 ± 0.10	n.s.	n.s.
	average pasture ± SE	1.21 ± 0.04	1.26 ± 0.03 a	1.25 ± 0.06 a	1.25 ± 0.06 a	1.26 ab
Tropical	28 (a)	1.40 ± 0.15	1.29 ± 0.14	1.22 ± 0.05	1.45 ± 0.09	1.34 ± 0.09
moist forest	28 (b)	1.30 ± 0.06	1.58 ± 0.05	1.53 ± 0.06	1.49 ± 0.07	1.36 ± 0.14
	42	1.40 ± 0.08	1.58 ± 0.04	1.50 ± 0.09	1.55 ± 0.10	1.45 ± 0.09
	>47	1.30 ± 0.07	1.28 ± 0.05	1.23 ± 0.13	1.29 ± 0.10	1.60 ± 0.16
	>69	1.28 ± 0.09	1.29 ± 0.09	1.38 ± 0.10	1.32 ± 0.08	1.31 ± 0.04
	average pasture ± SE	1.34 ± 0.03	1.40 ± 0.07 a	1.37 ± 0.06 a	1.42 ± 0.05 a	1.41 ± 0.05 a
Tropical	2	0.81 ± 0.03	0.79 ± 0.02	0.83 ± 0.08	0.95 ± 0.03	0.82 ± 0.06
wet forest	8	1.00 ± 0.07	0.89 ± 0.07	1.05 ± 0.03	1.02 ± 0.06	1.00 ± 0.05
	16	0.89 ± 0.07	0.96 ± 0.03	1.03 ± 0.04	0.93 ± 0.07	1.06 ± 0.04
	18	0.78 ± 0.07	0.76 ± 0.06	0.95 ± 0.07	1.03 ± 0.05	0.97 ± 0.07
	35	0.81 ± 0.06	0.70 ± 0.03	0.88 ± 0.06	0.85 ± 0.05	0.88 ± 0.07
	>35	0.85 ± 0.05	0.88 ± 0.09	0.94 ± 0.03	1.03 ± 0.04	0.98 ± 0.03
	average pasture* ± SE	0.87 ± 0.04 a	0.83 ± 0.04 b	0.95 ± 0.03 b	0.97 ± 0.03 b	0.95 ± 0.04 bc
Tropical	15	0.91 ± 0.04	0.90 ± 0.04	0.98 ± 0.04	1.10 ± 0.03	1.03 ± 0.03
Premontane	20	0.98 ± 0.04	0.90 ± 0.10	0.81 ± 0.06	0.97 ± 0.06	1.07 ± 0.07
wet forest-	26	1.00 ± 0.05	0.93 ± 0.06	1.03 ± 0.02	1.05 ± 0.01	0.97 ± 0.04
warm	40	0.91 ± 0.09	1.22 ± 0.04	1.15 ± 0.03	1.24 ± 0.06	1.10 ± 0.04
	50	0.80 ± 0.06	0.99 ± 0.03	0.98 ± 0.03	0.99 ± 0.02	1.04 ± 0.03
	average pasture ± SE	0.92 ± 0.04 a	0.99 ± 0.06 b	0.99 ± 0.06 b	1.07 ± 0.05 b	1.04 ± 0.02 bc
Tropical	1	0.43 ± 0.03	0.41 ± 0.02	0.50 ± 0.03	0.66 ± 0.03	0.66 ± 0.04
Premontane	10	0.54 ± 0.04	0.54 ± 0.03 (4)	0.61 ± 0.03 (4)	0.67 ± 0.07 (3)	0.82 ± 0.01 (2)
rain forest	25	0.50 ± 0.04	0.51 ± 0.02	0.58 ± 0.05	0.65 ± 0.02	0.65 ± 0.04
	45	0.55 ± 0.03	0.69 ± 0.16	0.53 ± 0.02	0.68 ± 0.04	0.69 ± 0.05
	70	0.48 ± 0.03	0.53 ± 0.04	0.57 ± 0.04	0.69 ± 0.06	0.68 ± 0.06
	average pasture* ± SE	0.52 ± 0.02 b	0.54 ± 0.05 c	0.56 ± 0.02 c	0.67 ± 0.01 c	0.70 ± 0.03 d
Tropical	16	0.74 ± 0.04	0.89 ± 0.04	0.78 ± 0.07	0.85 ± 0.11	0.92 ± 0.07
lower montane	28	0.55 ± 0.05	0.70 ± 0.04	0.55 ± 0.04	0.85 ± 0.11	0.66 ± 0.04
rain forest	32	0.64 ± 0.06	0.84 ± 0.07	0.83 ± 0.09	0.67 ± 0.04	1.05 ± 0.08
	48	0.56 ± 0.02	0.86 ± 0.06	0.80 ± 0.04	0.76 ± 0.08	1.00 ± 0.12
	54	0.65 ± 0.07	0.78 ± 0.04	0.66 ± 0.06	0.73 ± 0.10	0.69 ± 0.03
	average pasture ± SE	0.63 ± 0.03 b	0.81 ± 0.03 bc	0.72 ± 0.05 c	0.77 ± 0.04 c	0.86 ± 0.08 cd

* Young pastures (1 and 2 years old) were not included in calculations of mean and SE.
n.s. means no samples collected due to hard soils. Sample size (n) is 5 unless otherwise stated in brackets. Means for each life zone followed by the same letter are similar to one another, means for each life zone not followed by a letter indicates mean for this life zone is different from all other life zones ($p_{adjusted} < 0.1$).



Appendix 8. Soil bulk density by depth in pastures of various ages and mature forests (measured and adjusted) for six life zones (a-f). For mature forests measured soil bulk density estimates were adjusted for sampling bias (section 2.2.5). Symbols and corresponding numbers represent time since deforestation in years. a = Tropical dry forest; b = Tropical moist forest; c = Tropical wet forest; d = Tropical Premontane wet forest-warm; e = Tropical Premontane rain forest; f = Tropical Lower Montane rain forest life zone.

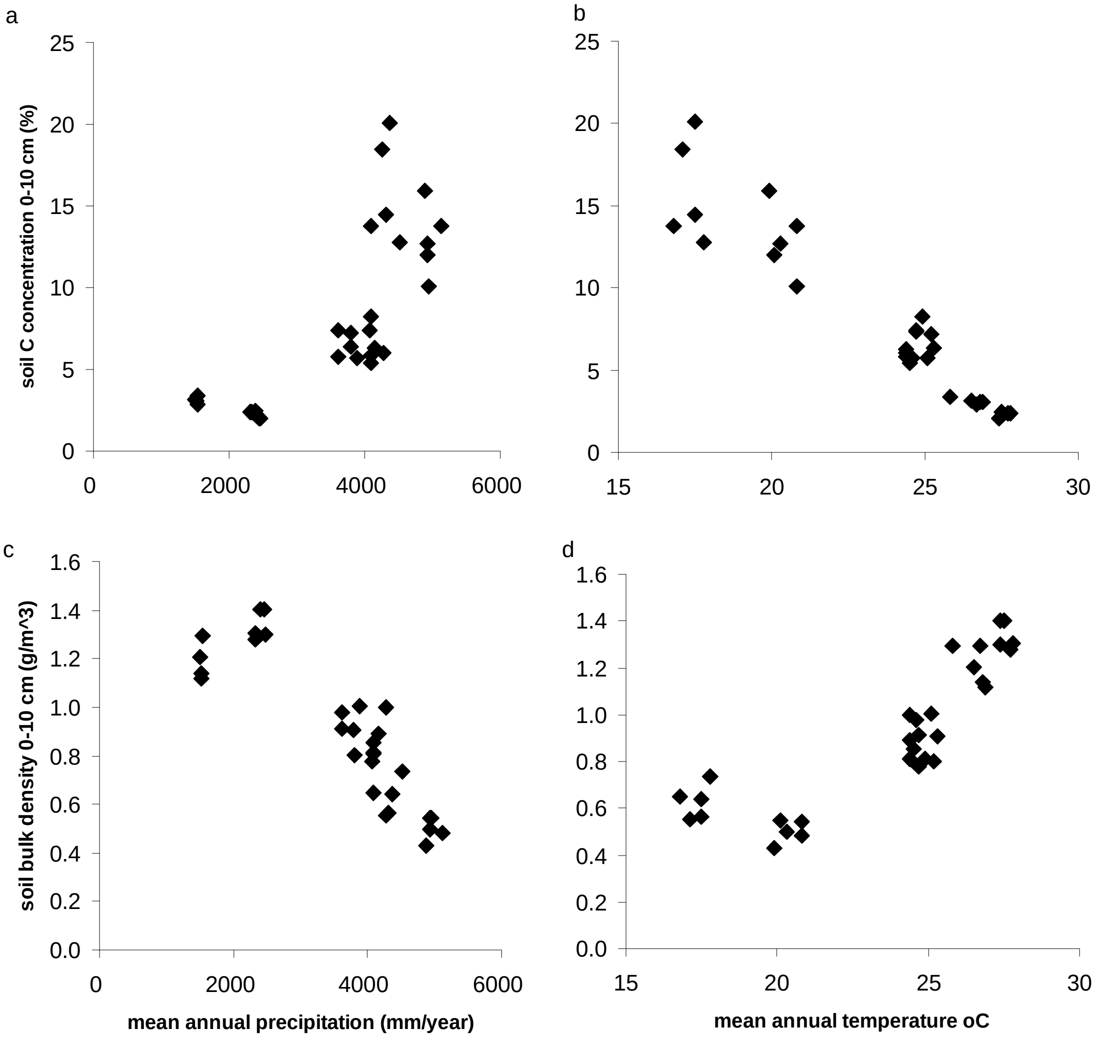
Appendix 9. Pearson coefficients of correlation between soil variables, and pasture age, elevation, and climate variables in 31 pastures along a climatic gradient in Costa Rica.

Response variables	Age	Elevation	Temperature	Precipitation
soil bulk density 0-10 cm	0.31 *	-0.74 ***	0.86 ***	-0.89 ***
soil bulk density 10-20 cm	0.38 **	-0.59 ***	0.73 ***	-0.86 ***
soil bulk density 20-30 cm	0.33 *	-0.72 ***	0.83 ***	-0.84 ***
soil bulk density 30-50 cm	0.25	-0.74 ***	0.85 ***	-0.84 ***
soil bulk density 50-100 cm	0.23	-0.63 ***	0.75 ***	-0.87 ***
%soil C 0-10 cm	-0.24	0.91 ***	-0.95 ***	0.76 ***
%soil C 10-20 cm	-0.40 **	0.71 ***	-0.80 ***	0.84 ***
%soil C 20-30 cm	-0.38 **	0.58 ***	-0.68 ***	0.78 ***
%soil C 30-50 cm	-0.27	0.83 ***	-0.91 ***	0.89 ***
%soil C 50-100 cm	-0.37 *	0.71 ***	-0.78 ***	0.76 ***
%soil N 0-10 cm	-0.17	0.91 ***	-0.94 ***	0.73 ***
%soil N 10-20 cm	-0.32 *	0.70 ***	-0.78 ***	0.83 ***
%soil N 20-30 cm	-0.34 *	0.56 ***	-0.65 ***	0.77 ***
%soil N 30-50 cm	-0.22	0.83 ***	-0.90 ***	0.88 ***
%soil N 50-100 cm	-0.29	0.74 ***	-0.80 ***	0.73 ***
soil C stock 0-10 cm (Mg C/ha)	-0.30 *	0.33 *	-0.48 ***	0.58 ***
soil C stock 10-20 cm (Mg C/ha)	-0.26	0.84 ***	-0.88 ***	0.62 ***
soil C stock 20-30 cm (Mg C/ha)	-0.56 ***	0.45 ***	-0.62 ***	0.78 ***
soil C stock 30-50 cm (Mg C/ha)	-0.35 *	0.73 ***	-0.83 ***	0.86 ***
soil C stock 50-100 cm (Mg C/ha)	-0.40 **	0.63 ***	-0.76 ***	0.89 ***
soil C stock 0-1 m (Mg C/ha)	-0.50 ***	0.70 ***	-0.84 ***	0.91 ***
soil N stock 0-1 m (Mg C/ha)	-0.44 **	0.72 ***	-0.84 ***	0.90 ***
Δ soil C stocks 0-30 cm (Mg C/ha)	-0.55 ***	-0.01	-0.17	0.48 ***
Δ soil C stocks 0-1 m (Mg C/ha)	-0.65 ***	-0.16	-0.02	0.58 ***
Δ soil N stock 0-1 m (Mg C/ha)	-0.59 ***	0.07	-0.23	0.72 ***
relative Δ soil C stocks 0-30 cm (%)	-0.60 ***	0.02	-0.21	0.64 ***
relative Δ soil C stocks 0-1 m (%)	-0.67 ***	-0.20	0.02	0.55 ***
relative Δ soil N stock 0-1 m (%)	-0.62 ***	-0.06	-0.11	0.67 ***

***$P_{\text{critical}} < 0.01$

** $P_{\text{critical}} < 0.05$

* $P_{\text{critical}} < 0.1$



Appendix 10. Relationships of (a and b) soil C concentrations and (c and d) soil bulk density with mean annual precipitation and temperature in 31 Costa Rican pastures.

Appendix 11. Mean (± SE) soil carbon concentration (%) by pasture and soil layer in six pasture chronosequences in Costa Rica and mean % soil C for each soil layer by life zone.

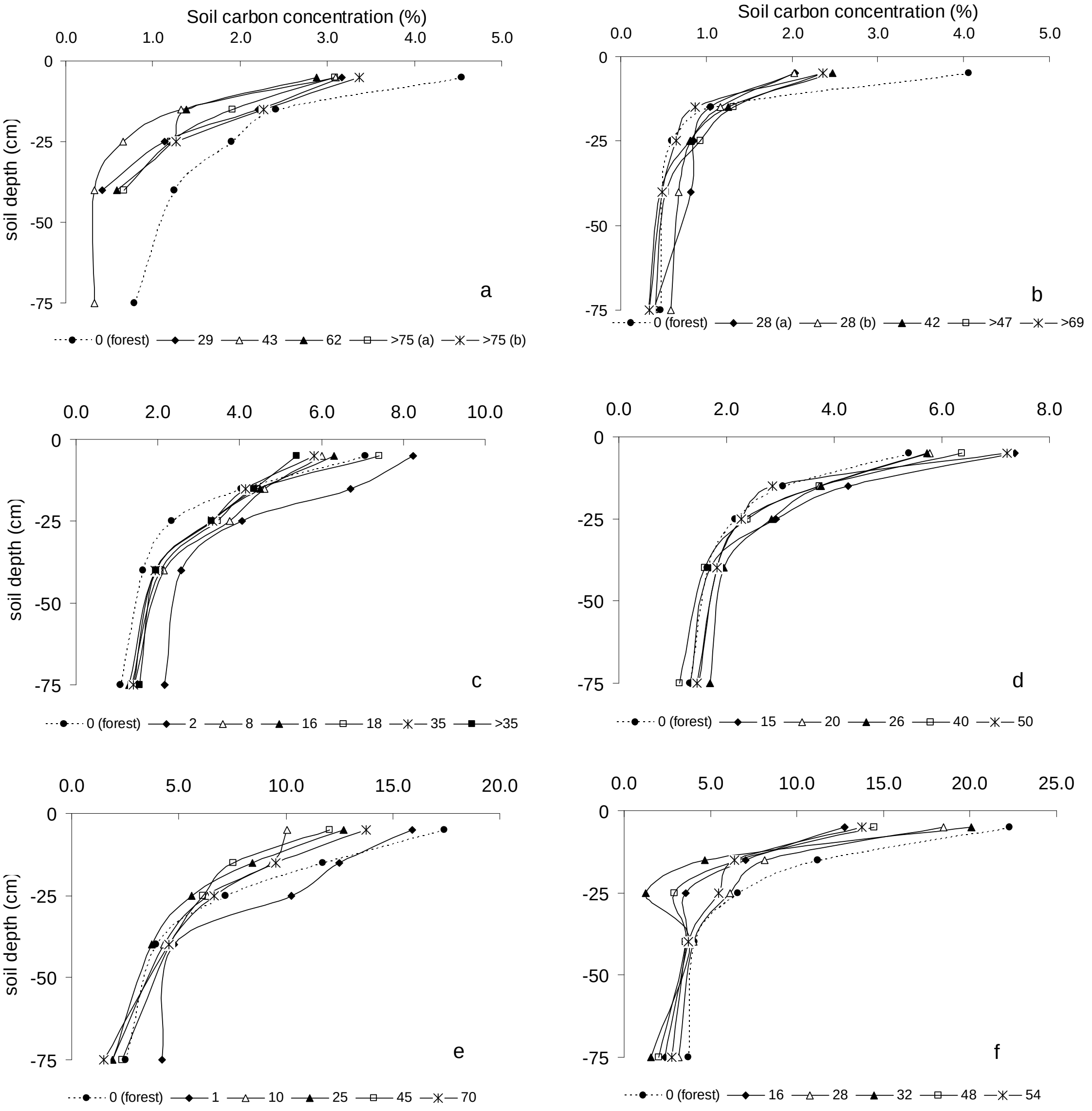
	Pasture	Soil depth (cm)				
Life zone	age (yrs)	0-10	10-20	20-30	30-50	50-100
Tropical	29	3.2 ± 0.3	2.2 ± 0.2	1.1 ± 0.1	0.4 ± 0.1	n.s.
dry forest	43	3.1 ± 0.1	1.3 ± 0.2	0.7 ± 0.1	0.3 ± 0.0	0.3 ± 0.0 (2)
	62	2.9 ± 0.3	1.4 ± 0.2	1.2 ± 0.2	0.6 ± 0.1	n.s.
	>75 (a)	3.1 ± 0.2	1.9 ± 0.2	1.2 ± 0.1	0.7 ± 0.1	n.s.
	>75 (b)	3.4 ± 0.4	2.3 ± 0.5	1.3 ± 0.3	n.s.	n.s.
average pasture ± SE		3.1 ± 0.1	1.8 ± 0.2	1.1 ± 0.1 a	0.5 ± 0.1 a	0.3 a
Tropical	28 (a)	2.0 ± 0.2	1.0 ± 0.2	0.9 ± 0.1	0.8 ± 0.1	0.4 ± 0.0
moist forest	28 (b)	2.0 ± 0.3	1.2 ± 0.2	0.8 ± 0.1	0.7 ± 0.1	0.6 ± 0.1
	42	2.5 ± 0.2	1.3 ± 0.2	0.8 ± 0.1	0.5 ± 0.1	0.3 ± 0.1
	>47	2.4 ± 0.2	1.3 ± 0.3	0.9 ± 0.3	0.5 ± 0.1	0.4 ± 0.1
	>69	2.4 ± 0.6	0.9 ± 0.1	0.6 ± 0.1	0.5 ± 0.1	0.3 ± 0.1
average pasture ± SE		2.2 ± 0.1	1.1 ± 0.1	0.8 ± 0.0 a	0.6 ± 0.1 a	0.4 ± 0.0 a
Tropical	2	8.2 ± 0.7	6.7 ± 0.3	4.0 ± 0.6	2.6 ± 0.2	2.2 ± 0.1
wet forest	8	6.0 ± 0.5	4.6 ± 0.3	3.8 ± 0.5	2.1 ± 0.2	1.4 ± 0.2
	16	6.3 ± 0.4	4.5 ± 0.4	3.3 ± 0.5	1.9 ± 0.1	1.3 ± 0.1
	18	7.4 ± 0.4	4.4 ± 0.5	3.5 ± 0.1	2.1 ± 0.1	1.3 ± 0.1
	35	5.8 ± 0.6	4.1 ± 0.5	3.3 ± 0.6	1.9 ± 0.3	1.4 ± 0.1
	>35	5.4 ± 0.3	4.4 ± 0.3	3.3 ± 0.4	2.0 ± 0.1	1.6 ± 0.1
average pasture* ± SE		6.2 ± 0.3 a	4.4 ± 0.1 a	3.4 ± 0.1 b	2.0 ± 0.0 b	1.4 ± 0.0 b
Tropical	15	7.4 ± 0.6	4.3 ± 0.4	2.9 ± 0.2	1.7 ± 0.0	1.3 ± 0.1
Premontane	20	5.8 ± 0.3	3.7 ± 0.1	2.3 ± 0.1	1.8 ± 0.1	1.5 ± 0.1
wet forest-	26	5.7 ± 0.3	3.8 ± 0.5	2.8 ± 0.4	2.0 ± 0.1	1.7 ± 0.0
warm	40	6.4 ± 0.1	3.7 ± 0.1	2.4 ± 0.2	1.6 ± 0.1	1.1 ± 0.1
	50	7.2 ± 0.4	2.9 ± 0.0	2.3 ± 0.1	1.8 ± 0.1	1.4 ± 0.1
average pasture ± SE		6.5 ± 0.3 a	3.7 ± 0.2 a	2.6 ± 0.1 b	1.8 ± 0.1 b	1.4 ± 0.1 b
Tropical	1	15.9 ± 2.5	12.5 ± 1.6	10.3 ± 1.2	4.8 ± 0.6	4.2 ± 0.7
Premontane	10	10.1 ± 0.5	9.3 ± 1.3	6.3 ± 0.6	4.3 ± 0.5	1.9 ± 0.3
rain forest	25	12.7 ± 1.4	8.4 ± 0.8	5.6 ± 0.6	3.8 ± 0.6	1.9 ± 0.2
	45	12.0 ± 0.4	7.6 ± 0.4	6.1 ± 0.2	4.6 ± 0.9	2.4 ± 0.3
	70	13.7 ± 0.6	9.5 ± 0.7	6.7 ± 0.9	4.5 ± 0.7	1.5 ± 0.4
average pasture* ± SE		12.1 ± 0.8	8.7 ± 0.5 b	6.2 ± 0.2	4.3 ± 0.2 c	1.9 ± 0.2 bc
Tropical	16	12.7 ± 1.2	7.0 ± 1.5	3.6 ± 0.7	3.6 ± 0.2	2.3 ± 0.4
lower montane	28	18.5 ± 2.2	8.1 ± 0.7	6.1 ± 0.6	4.0 ± 0.7	3.2 ± 0.3
rain forest	32	20.1 ± 3.6	4.7 ± 1.0	1.3 ± 0.2	3.8 ± 0.3	1.6 ± 0.3
	48	14.5 ± 0.8	6.6 ± 0.7	2.9 ± 0.9	3.5 ± 0.5	2.0 ± 0.2
	54	13.8 ± 1.4	6.4 ± 0.7	5.5 ± 0.5	3.7 ± 0.2	2.8 ± 0.1
average pasture ± SE		15.9 ± 1.4	6.6 ± 0.6 b	3.9 ± 0.9 b	3.7 ± 0.1 c	2.4 ± 0.3 c

* Young pastures (1 and 2 years old) were not included in calculations of mean and SE.
n.s. means no samples collected due to hard soils. Sample size (n) is 5 unless otherwise stated in brackets. Means for each life zone followed by the same letter are similar to one another, means for each life zone not followed by a letter indicates mean for this life zone is different from all other life zones ($p_{adjusted} < 0.1$).

Appendix 12. Mean (± SE) soil nitrogen concentration (%) by pasture and soil layer in six pasture chronosequences in Costa Rica.

Life zone	Pasture age (yrs)	Soil depth (cm) 0-10	10-20	20-30	30-50	50-100
Tropical dry forest	29	0.248 ± 0.024	0.182 ± 0.010	0.102 ± 0.009	0.040 ± 0.004	n.s.
	43	0.255 ± 0.010	0.113 ± 0.011	0.067 ± 0.007	0.037 ± 0.003	0.042 ± 0.000
	62	0.244 ± 0.024	0.125 ± 0.015	0.110 ± 0.019	0.059 ± 0.008	n.s.
	>75 (a)	0.259 ± 0.015	0.171 ± 0.012	0.112 ± 0.009	0.069 ± 0.007	n.s. (2)
	>75 (b)	0.244 ± 0.027	0.184 ± 0.032	0.100 ± 0.017	n.s.	n.s.
Tropical moist forest	28 (a)	0.190 ± 0.017	0.126 ± 0.021	0.106 ± 0.015	0.088 ± 0.015	0.046 ± 0.005
	28 (b)	0.177 ± 0.018	0.128 ± 0.017	0.096 ± 0.009	0.078 ± 0.010	0.063 ± 0.014
	42	0.235 ± 0.015	0.133 ± 0.015	0.096 ± 0.011	0.058 ± 0.006	0.038 ± 0.006
	>47	0.211 ± 0.016	0.132 ± 0.023	0.089 ± 0.013	0.062 ± 0.007	0.051 ± 0.008
	>69	0.232 ± 0.042	0.105 ± 0.011	0.080 ± 0.004	0.059 ± 0.008	0.046 ± 0.007
Tropical wet forest	2	0.548 ± 0.036	0.453 ± 0.020	0.313 ± 0.049	0.189 ± 0.010	0.120 ± 0.006
	8	0.440 ± 0.043	0.356 ± 0.022	0.307 ± 0.033	0.175 ± 0.017	0.102 ± 0.012
	16	0.513 ± 0.038	0.364 ± 0.032	0.283 ± 0.035	0.164 ± 0.006	0.109 ± 0.005
	18	0.539 ± 0.028	0.338 ± 0.032	0.278 ± 0.009	0.165 ± 0.010	0.103 ± 0.010
	35	0.482 ± 0.042	0.355 ± 0.036	0.294 ± 0.043	0.166 ± 0.017	0.124 ± 0.007
	>35	0.411 ± 0.019	0.356 ± 0.024	0.274 ± 0.028	0.160 ± 0.007	0.123 ± 0.005
Tropical Premontane wet forest-warm	15	0.588 ± 0.044	0.377 ± 0.028	0.270 ± 0.018	0.154 ± 0.004	0.125 ± 0.006
	20	0.450 ± 0.030	0.320 ± 0.013	0.217 ± 0.008	0.175 ± 0.010	0.119 ± 0.004
	26	0.468 ± 0.031	0.302 ± 0.037	0.221 ± 0.027	0.144 ± 0.007	0.118 ± 0.005
	40	0.547 ± 0.017	0.348 ± 0.007	0.234 ± 0.018	0.151 ± 0.009	0.116 ± 0.005
	50	0.619 ± 0.042	0.254 ± 0.003	0.199 ± 0.007	0.168 ± 0.008	0.116 ± 0.006
Tropical Premontane rain forest	1	1.226 ± 0.142	0.984 ± 0.077	0.852 ± 0.082	0.398 ± 0.046	0.335 ± 0.052
	10	0.766 ± 0.054	0.701 ± 0.074	0.510 ± 0.048	0.344 ± 0.045	0.148 ± 0.022
	25	0.991 ± 0.096	0.699 ± 0.061	0.487 ± 0.049	0.316 ± 0.031	0.165 ± 0.018
	45	0.935 ± 0.020	0.605 ± 0.024	0.518 ± 0.010	0.378 ± 0.065	0.178 ± 0.025
	70	1.209 ± 0.045	0.904 ± 0.060	0.637 ± 0.081	0.418 ± 0.059	0.140 ± 0.030
Tropical lower montane rain forest	16	0.947 ± 0.093	0.527 ± 0.115	0.296 ± 0.056	0.310 ± 0.022	0.187 ± 0.030
	28	1.590 ± 0.197	0.669 ± 0.054	0.507 ± 0.056	0.332 ± 0.062	0.251 ± 0.024
	32	1.649 ± 0.264	0.374 ± 0.074	0.100 ± 0.014	0.308 ± 0.037	0.126 ± 0.020
	48	1.150 ± 0.061	0.545 ± 0.057	0.244 ± 0.071	0.301 ± 0.045	0.158 ± 0.016
	54	1.175 ± 0.156	0.509 ± 0.053	0.442 ± 0.043	0.308 ± 0.020	0.221 ± 0.011

* Young pastures (1 and 2 years old) were not included in calculations of mean and SE. Sample size (n) is 5 unless otherwise stated in brackets, n.s. means no samples collected due to hard soils.



Appendix 13. Soil carbon concentration by soil depth in pastures of various ages and mature forests for six life zones (a-f). Symbols and corresponding numbers represent time since deforestation in years. a = Tropical dry forest; b = Tropical moist forest; c = Tropical wet forest; d = Tropical Premontane wet-warm; e = Tropical Premontane rain forest; f = Tropical Lower Montane rain forest life zone.

Appendix 14. Mean (± SE) corrected soil C (Mg C/ha) by pasture and soil layer in six pasture chronosequences in Costa Rica and mean corrected soil C for each soil layer by life zone.

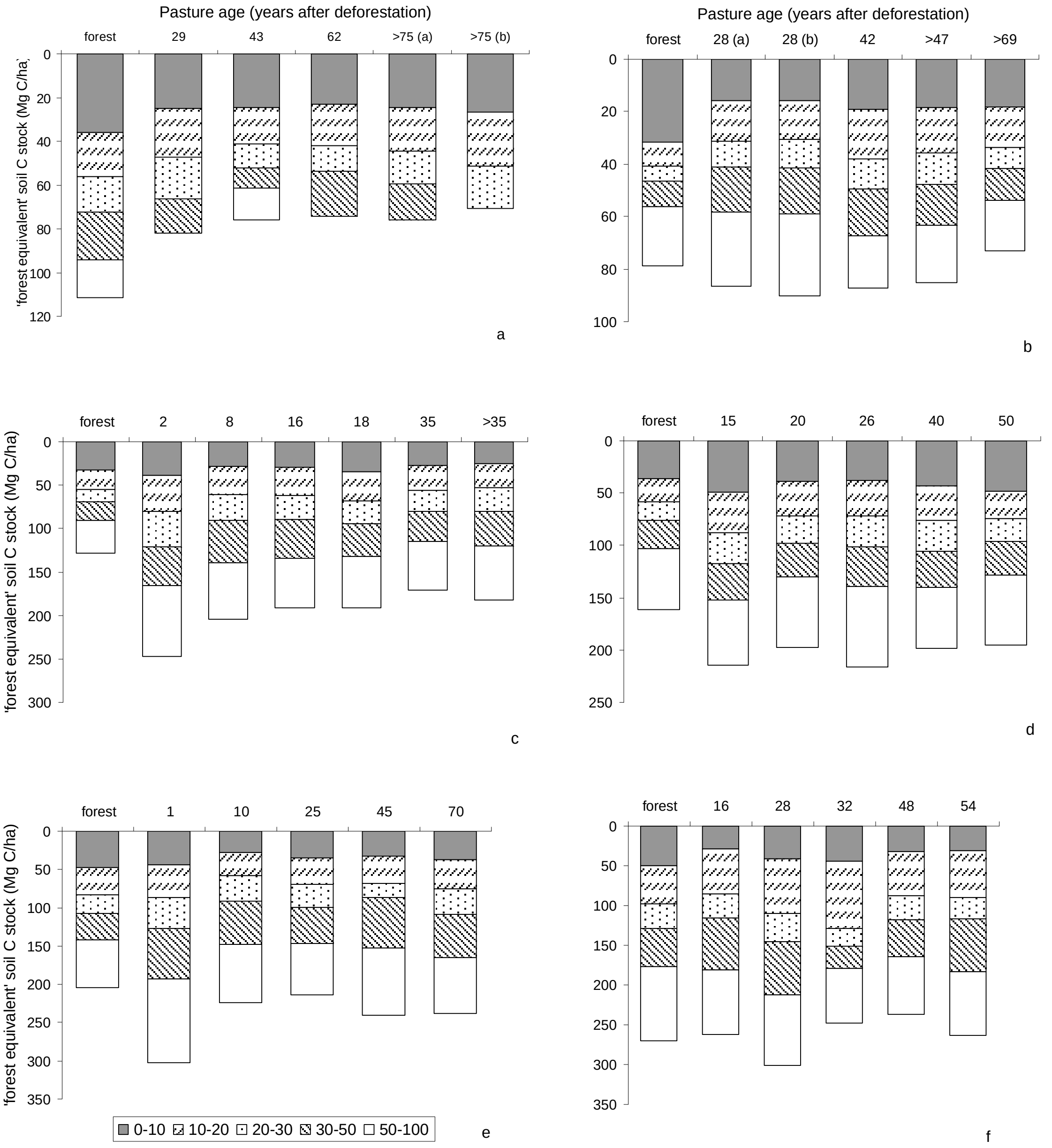
Life zone	Pasture age (yrs)	Soil depth layer equivalent to average reference mature forest (cm)				
		0-10	20	20-30	50	50-100
Tropical dry forest	29	25.2	22.3	18.7	15.7	n.s.
	43	24.6	16.7	10.8	9.3	14.5
	62	22.9	19.0	12.0	20.4	n.s.
	>75 (a)	24.6	19.9	15.0	16.4	n.s.
	>75 (b)	26.8	24.4	19.6	n.s.	n.s.
average pasture ± SE		24.8 ± 0.6	20.5 ± 1.3	15.2 ± 1.7	15.5 ± 2.1	14.5
Tropical moist forest	28 (a)	15.8	15.4	9.8	17.3	28.2
	28 (b)	15.8	14.8	10.9	17.4	31.2
	42	19.2	18.7	11.7	17.8	19.8
	>47	18.4	17.2	12.4	15.5	21.6
	>69	18.3	15.2	8.1	12.1	19.4
average pasture ± SE		17.5 ± 0.7	16.2 ± 0.7	10.6 ± 0.7	16.0 ± 1.1	24.1 ± 2.4
Tropical wet forest	2	38.4	42.0	40.4	44.7	81.8
	8	28.0	32.7	30.0	48.3	65.4
	16	29.3	32.2	28.3	44.1	57.1
	18	34.5	33.5	26.2	38.3	59.0
	35	27.1	28.4	24.4	35.2	55.3
	>35	25.2	27.9	27.0	39.9	61.9
average pasture* ± SE		28.8 ± 1.6	30.9 ± 1.2	27.2 ± 1.0	41.2 ± 2.3	59.7 ± 1.8
Tropical Premontane wet forest-warm	15	49.3	38.2	30.2	34.4	62.1
	20	38.7	33.2	26.4	31.9	67.6
	26	38.4	33.7	28.9	38.2	77.4
	40	42.7	33.2	30.0	34.1	58.0
	50	48.3	26.3	21.5	32.0	66.7
average pasture ± SE		43.5 ± 2.3	32.9 ± 1.9	27.4 ± 1.6	34.1 ± 1.1	66.4 ± 3.3
Tropical Premontane rain forest	1	43.4	43.2	40.8	65.6	109.7
	10	27.5	30.3	33.5	56.6	76.5
	25	34.7	35.1	29.6	47.3	67.4
	45	32.8	35.1	18.4	65.6	88.5
	70	37.5	37.7	33.0	56.6	73.0
average pasture* ± SE		33.1 ± 2.1	34.5 ± 1.5	28.6 ± 3.5	56.5 ± 3.7	76.4 ± 4.5
Tropical lower montane rain forest	16	28.5	56.6	30.8	65.2	80.9
	28	41.3	68.9	35.6	66.5	88.8
	32	44.9	84.3	21.8	27.5	69.0
	48	32.3	55.2	29.8	47.0	72.2
	54	30.8	58.7	26.7	66.7	80.4
average pasture ± SE		35.6 ± 3.2	64.7 ± 5.4	28.9 ± 2.3	54.6 ± 7.7	78.3 ± 3.5

* Young pastures (1 and 2 years old) were not included in calculations of mean and SE
n.s. means no samples collected due to hard soils.

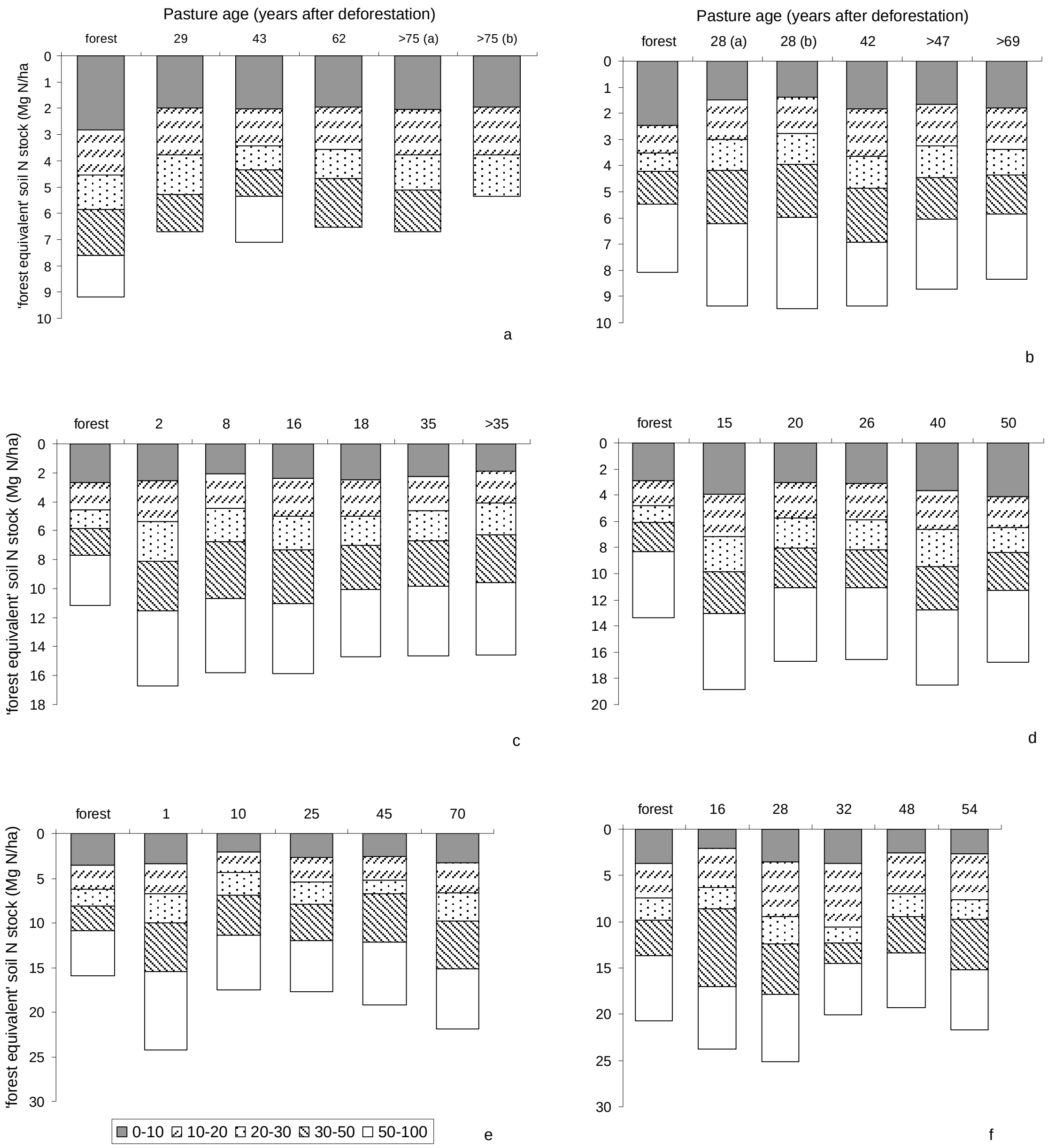
Appendix 15. Mean (± SE) corrected soil N (Mg N/ha) by pasture and soil layer in six pasture chronosequences in Costa Rica and mean corrected soil N for each soil layer by life zone.

Life zone	Pasture age (yrs)	Soil depth layer (cm) 0-10	10-20	20-30	30-50	50-100
Tropical dry forest	29	1.97	1.78	1.54	1.42	n.s.
	43	2.03	1.40	0.93	0.98	1.75
	62	1.94	1.63	1.09	1.85	n.s.
	>75 (a)	2.06	1.72	1.35	1.58	n.s.
	>75 (b)	1.94	1.83	1.58	n.s.	n.s.
average pasture ± SE		1.99 ± 0.02	1.67 ± 0.08	1.30 ± 0.13	1.46 ± 0.16	1.75
Tropical moist forest	28 (a)	1.48	1.51	1.19	2.04	3.14
	28 (b)	1.37	1.39	1.21	2.01	3.48
	42	1.83	1.81	1.24	2.05	2.43
	>47	1.64	1.58	1.24	1.58	2.66
	>69	1.80	1.57	0.99	1.48	2.50
average pasture ± SE		1.62 ± 0.09	1.57 ± 0.07	1.17 ± 0.05	1.83 ± 0.12	2.84 ± 0.20
Tropical wet forest	2	2.55	2.81	2.74	3.41	5.21
	8	2.05	2.39	2.33	3.90	5.15
	16	2.39	2.63	2.29	3.72	4.84
	18	2.51	2.47	2.01	3.07	4.62
	35	2.25	2.38	2.10	3.09	4.84
	>35	1.91	2.16	2.21	3.29	4.99
average pasture* ± SE		2.22 ± 0.11	2.41 ± 0.08	2.19 ± 0.06	3.41 ± 0.17	4.89 ± 0.09
Tropical Premontane wet forest-warm	15	3.94	3.23	2.73	3.14	5.79
	20	3.02	2.71	2.32	3.03	5.63
	26	3.14	2.73	2.30	2.90	5.48
	40	3.67	2.99	2.82	3.32	5.72
	50	4.15	2.31	1.90	2.90	5.52
average pasture ± SE		3.58 ± 0.22	2.79 ± 0.15	2.41 ± 0.17	3.06 ± 0.08	5.63 ± 0.06
Tropical Premontane rain forest	1	3.35	3.36	3.25	5.45	8.84
	10	2.09	2.30	2.52	4.49	6.07
	25	2.71	2.77	2.45	4.07	5.72
	45	2.55	2.73	1.47	5.40	7.10
	70	3.30	3.38	3.13	5.37	6.72
average pasture* ± SE		2.66 ± 0.25	2.80 ± 0.22	2.39 ± 0.34	4.83 ± 0.33	6.40 ± 0.31
Tropical lower montane rain forest	16	2.12	4.21	2.30	8.35	6.84
	28	3.56	5.91	2.93	5.50	7.22
	32	3.69	6.92	1.74	2.18	5.57
	48	2.57	4.41	2.46	3.91	5.99
	54	2.63	5.01	2.13	5.38	6.57
average pasture ± SE		2.91 ± 0.30	5.29 ± 0.50	2.31 ± 0.20	5.07 ± 1.02	6.44 ± 0.29

* Young pastures (1 and 2 years old) were not included in calculations of mean and SE.
n.s. means no samples collected due to hard soils.



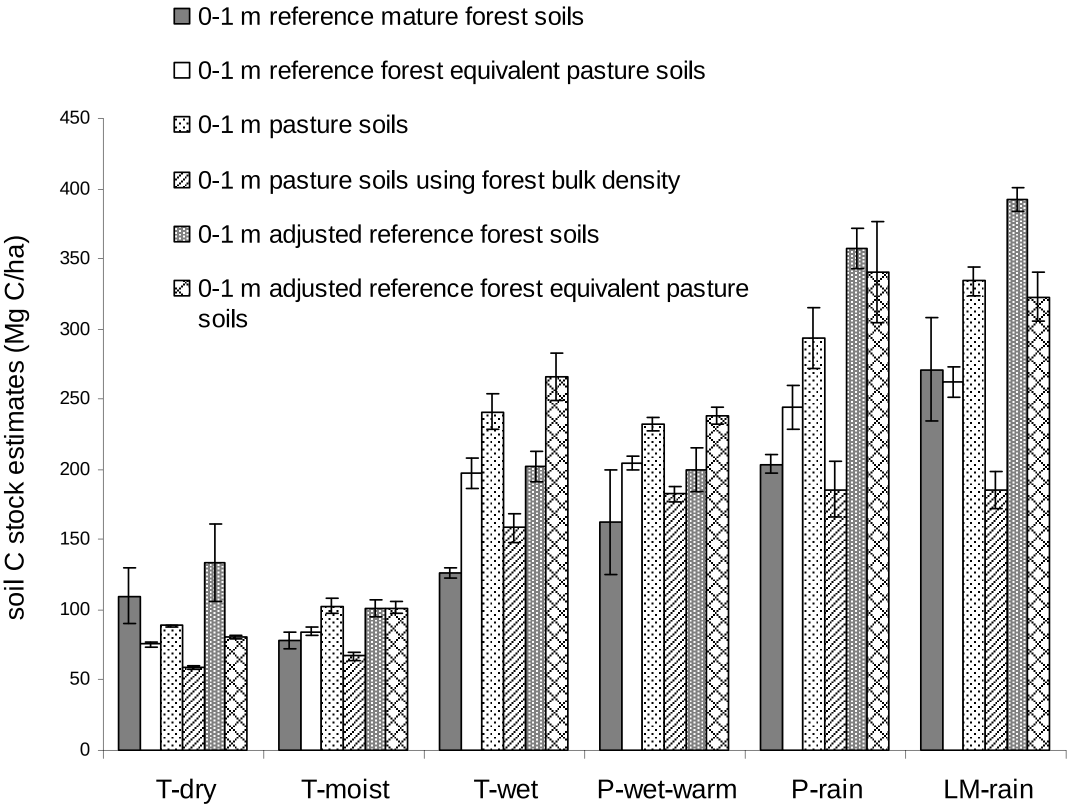
Appendix 16. Soil C stocks by forest equivalent soil depth layer (in cm) in pastures of various ages and average mature forests in six life zones (a-f). a = Tropical dry forest; b = Tropical moist forest; c = Tropical wet forest; d = Tropical Premontane wet forest-warm; e = Tropical Premontane rain forest; f = Tropical Lower Montane rain forest life zone.



Appendix 17. Soil N stocks by forest equivalent soil depth layer (in cm) in pastures of various ages and average mature forests in six life zones (a-f). a = Tropical dry forest; b = Tropical moist forest; c = Tropical wet forest; d = Tropical Premontane wet forest-warm; e = Tropical Premontane rain forest; f = Tropical Lower Montane rain forest life zone.

Appendix 18. A-priori set of linear models predicting 0-30 cm soil C stocks (natural log transformed) in pasture chronosequences across six life zones in Costa Rica ranked by Bayesian Information Criterion (BIC) for (a) all pastures, and (b) pastures ≥8 years. Delta BIC is the difference between the BIC scores of the model in question and the “best” (lowest BIC score) model.

Model terms	k (# of parameters)	delta BIC
life zone	7	0
age, life zone	8	1
*age, life zone age * life zone*	13	11.3
age, temperature	4	28.1
temperature	3	30.4
*age, temperature, age * temperature*	5	30.9
precipitation	3	31.8
age, precipitation	4	35.1
*age, precipitation, age *precipitation*	5	37.7
age	3	54.5
(null model, intercept only)	2	56.5

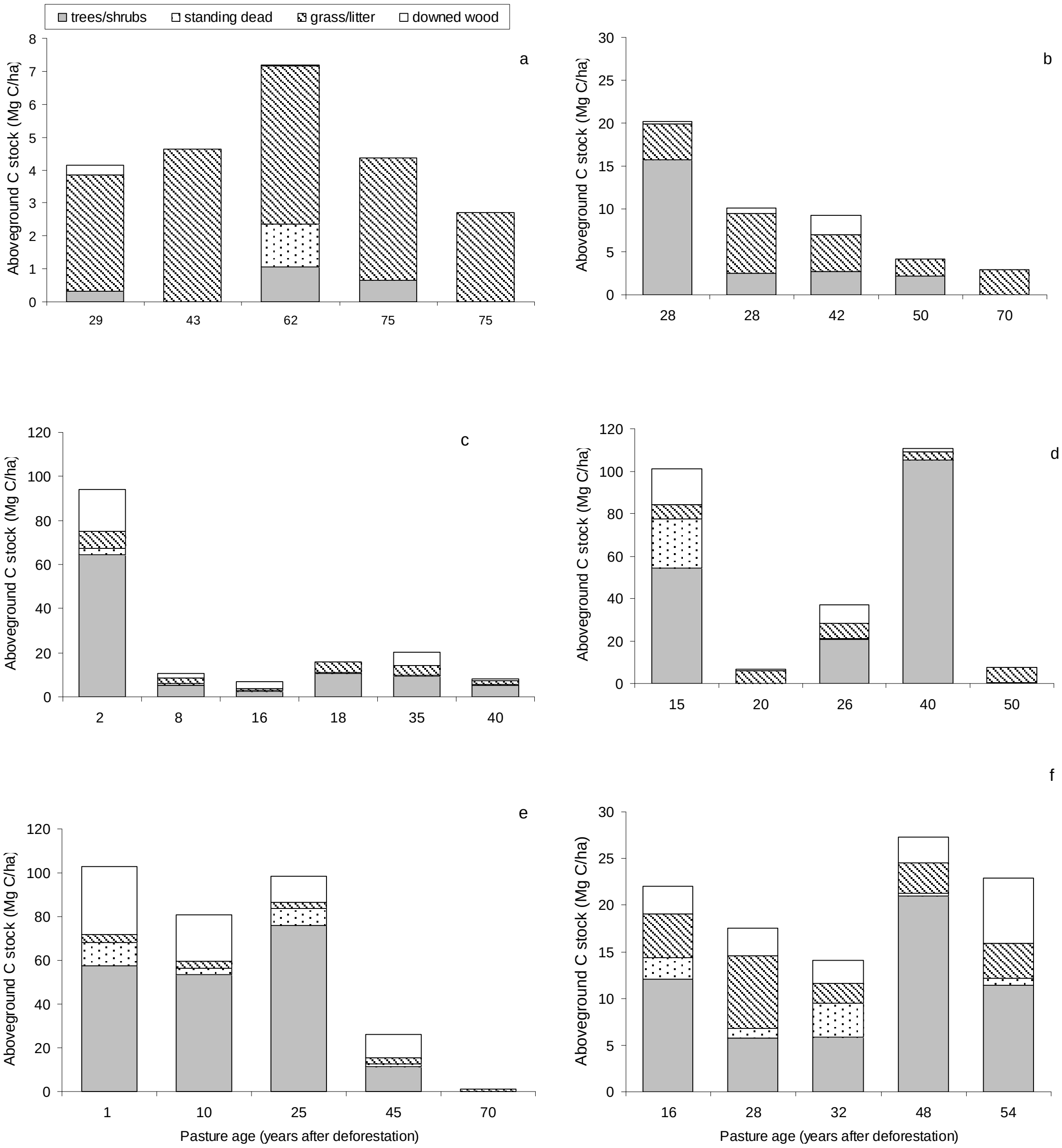


Appendix 19. Mean original and adjusted ± 1 SE 0-1 m soil carbon stock estimates in mature reference forests (n=2 or 3 per life zone) and pastures using 4 methods of estimation (n=5 or 6 per life zone) in six life zones. T-dry = Tropical dry forest; T-moist = Tropical moist forest; T- wet = Tropical wet forest; P-wet-warm = Tropical Premontane wet forest-warm; P-rain = Tropical Premontane rain forest; T-lm-rain = Tropical Lower Montane rain forest.

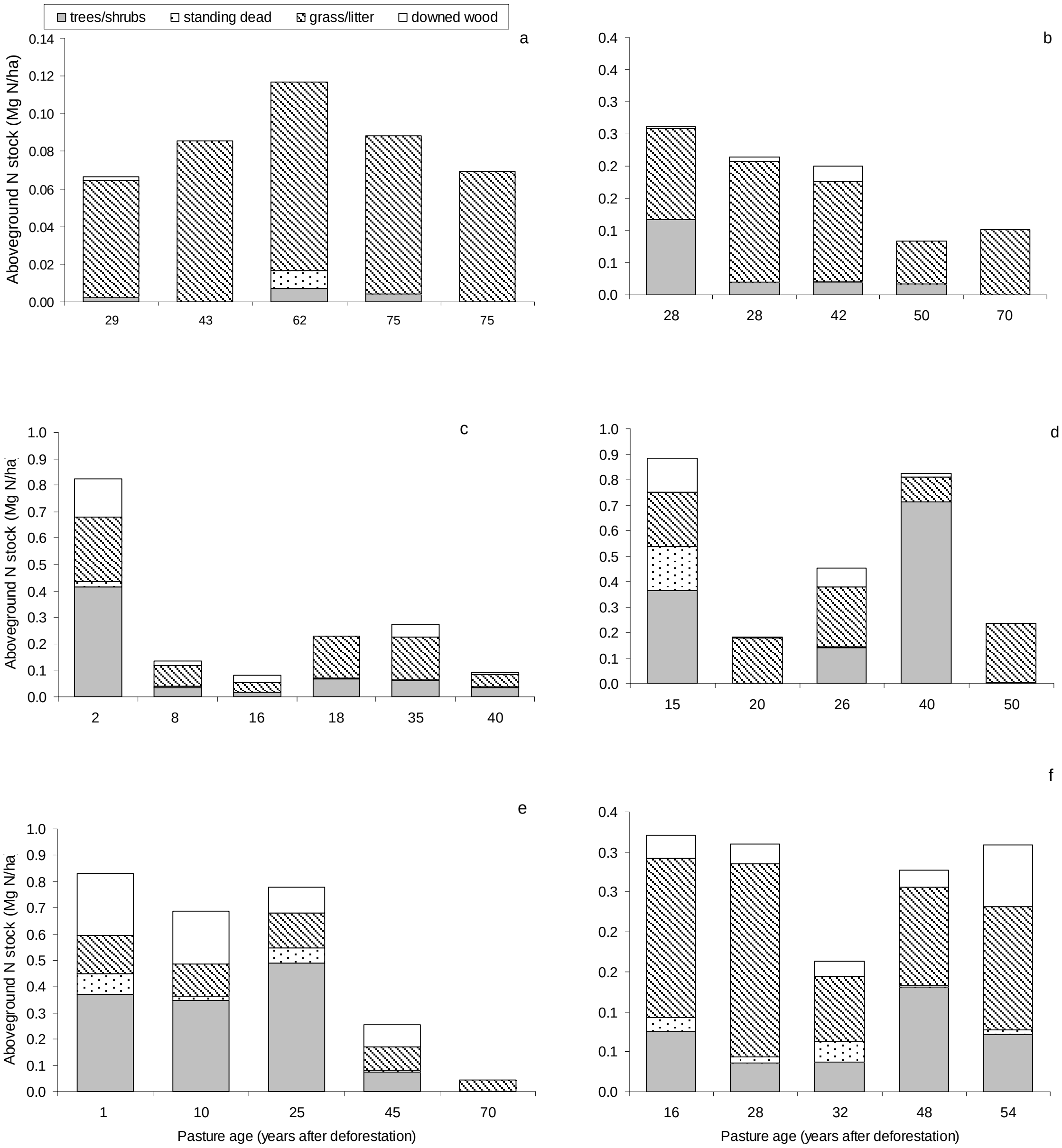
Appendix 20. Aboveground biomass (Mg organic matter/ha) by ecosystem component in pastures arranged in chronosequences for six life zones in Costa Rica.

Life zone	Age (yrs)	Trees/ shrubs	Standing dead	Grass/litter		Downed wood		Total aboveground
				mean	SE	mean	SE	
Tropical dry forest	29	0.7	0.0	8.4	± 1.2	0.6	± 0.5	9.7
	43	0.0	0.0	11.5	± 1.5	0.0	± 0.0	11.5
	62	2.3	2.6	10.7	± 1.2	0.1	± 0.1	15.6
	>75 (a)	1.4	0.0	9.0	± 0.9	0.0	± 0.0	10.5
	>75 (b)	0.0	0.0	6.3	± 1.3	0.0	± 0.0	6.3
Tropical moist forest	28 (a)	33.5	0.0	10.4	± 1.4	0.6	± 0.3	44.6
	28 (b)	5.4	0.0	17.2	± 3.4	1.2	± 0.7	23.8
	42	5.7	0.1	10.9	± 1.4	4.5	± 2.6	21.3
	>47	4.6	0.0	4.8	± 2.2	0.0	± 0.0	9.4
	>69	0.0	0.0	7.0	± 1.5	0.0	± 0.0	7.0
Tropical wet forest	2	133.9	5.3	17.6	± 2.7	38.1	± 11.1	194.9
	8	11.3	1.4	5.8	± 1.1	3.4	± 1.5	21.9
	16	5.0	0.7	2.5	± 0.2	6.2	± 3.3	14.4
	18	21.9	0.5	12.1	± 1.4	0.4	± 0.2	34.8
	35	19.4	1.1	10.0	± 1.7	12.4	± 6.3	42.8
	> 35	11.3	0.2	4.2	± 0.6	1.3	± 1.3	17.0
Tropical Premontane wet forest-warm	15	114.2	46.4	16.2	± 1.7	33.4	± 19.9	210.2
	20	0.0	0.0	14.7	± 1.9	1.3	± 0.9	16.0
	26	43.4	1.2	16.4	± 1.5	17.5	± 5.3	78.4
	40	222.4	0.0	8.4	± 0.7	3.6	± 2.2	234.4
	50	1.0	0.0	17.5	± 3.3	0.0	± 0.0	18.5
Tropical Premontane rain forest	1	123.7	21.4	8.1	± 0.7	61.6	± 17.9	214.8
	10	115.3	5.1	7.6	± 1.3	43.0	± 9.9	170.9
	25	163.4	15.2	6.3	± 0.7	23.1	± 9.3	208.1
	45	24.5	2.3	6.9	± 0.8	20.8	± 12.1	54.5
	70	0.0	0.0	2.8	± 0.4	0.5	± 0.3	3.3
Tropical Lower Montane rain forest	16	25.0	4.7	13.5	± 1.3	5.9	± 3.8	49.1
	28	11.9	2.1	17.0	± 1.8	6.0	± 2.8	37.0
	32	12.2	7.2	5.3	± 0.5	5.0	± 3.1	29.7
	48	43.7	0.4	8.2	± 1.2	5.6	± 3.8	57.9
	54	23.7	1.6	9.2	± 1.0	14.2	± 12.2	48.7

Labels (a) and (b) were used to distinguish between two pastures with the same age within one life zone.



Appendix 21. Aboveground C stock estimates (Mg C/ha) by ecosystem component in pastures arranged in chronosequences for six life zones in Costa Rica. a = Tropical dry forest; b = Tropical moist forest; c = Tropical wet forest; d = Tropical Premontane wet forest-warm; e = Tropical Premontane rain forest; f = Tropical Lower Montane rain forest life zone.

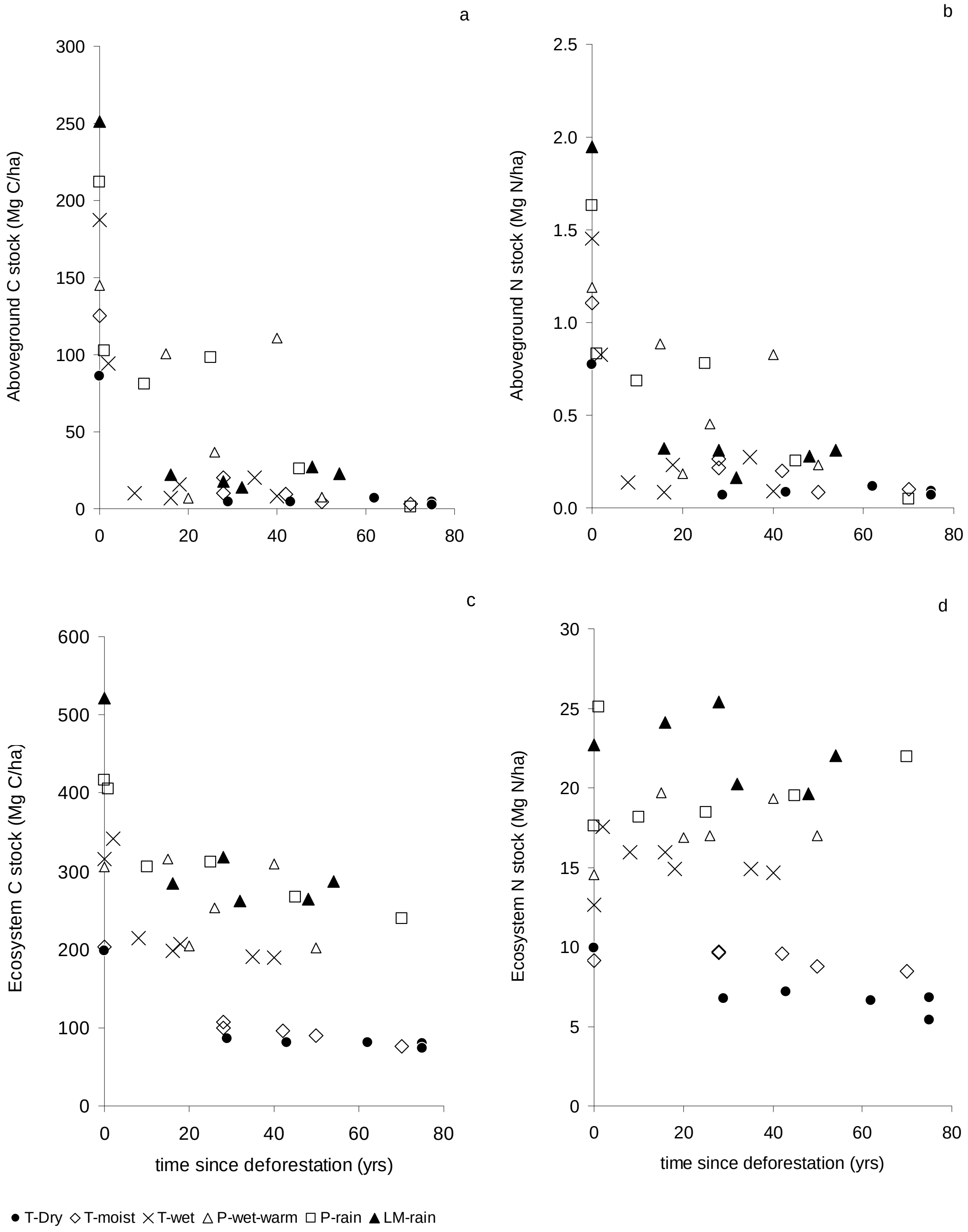


Appendix 22. Aboveground nitrogen stock estimates (Mg N/ha) by ecosystem component in pastures arranged in chronosequences for six life zones in Costa Rica. a = Tropical dry forest; b = Tropical moist forest; c = Tropical wet forest; d = Tropical Premontane wet forest-warm; e = Tropical Premontane rain forest; f = Tropical Lower Montane rain forest life zone.

Appendix 23. Tree and shrub aboveground biomass (in Mg organic matter/ha and % of total) partitioned in pasture components in six pasture chronosequences in Costa Rica and mean ± SE pasture biomass stocks by life zone.

Life zone	Age	Vines		Trees 0-10		Trees 10-30		Trees > 30		Palms	
		biomass	% of total	biomass	% of total	biomass	% of total	biomass	% of total	biomass	% of total
	(yrs)	(Mg/ha)	trees/shrub	(Mg/ha)	trees/shrub	(Mg/ha)	trees/shrub	(Mg/ha)	trees/shrub	(Mg/ha)	trees/shrub
Tropical dry forest	29	0.0	0	0.0	0	0.7	100	0.0	0	0.0	0
	43	0.0	-	0.0	-	0.0	-	0.0	-	0.0	-
	62	0.0	0	0.0	0	2.3	100	0.0	0	0.0	0
	>75 (a)	0.0	0	0.0	0	1.4	100	0.0	0	0.0	0
	>75 (b)	0.0	-	0.0	-	0.0	-	0.0	-	0.0	-
	mean pasture ± SE	0.0 ± 0.0	0 ± 0	0.0 ± 0.0	0 ± 0	0.9 ±0.4	100 ± 0	0.0 ± 0.0	0 ± 0	0.0 ± 0.0	0 ± 0
Tropical moist forest	28	0.0	0	0.1	0	0.8	3	32.6	97	0.0	0
	28	0.2	3	1.2	22	1.0	19	3.0	55	0.1	1
	42	0.1	2	0.0	0	2.5	43	3.0	53	0.2	3
	>47	0.0	0	0.0	0	4.6	100	0.0	0	0.0	0
	>69	0.0	0	0.0	100	0.0	0	0.0	0	0.0	0
	mean pasture ± SE	0.1 ± 0.0	1 ± 1	0.3 ± 0.2	25 ± 19	1.8 ± 0.8	33 ± 18	7.7 ± 6.2	41 ±19	0.0 ± 0.0	1 ± 1
Tropical wet forest	2	0.0	0	0.0	0	11.3	8	121.2	90	1.5	1
	8	0.1	1	1.1	10	8.8	78	1.4	12	0.0	0
	16	0.0	0	1.0	19	4.0	81	0.0	0	0.0	0
	18	0.0	0	0.6	3	3.5	16	17.7	81	0.0	0
	35	0.0	0	0.0	0	7.5	39	11.8	61	0.0	0
	> 35	0.0	0	0.0	0	11.3	100	0.0	0	0.0	0
	mean pasture ± SE	*0.0 ± 0.0	*0 ± 0	*0.5 ± 0.2	*6 ± 4	*7.0 ± 1.5	*63 ± 15	*6.2 ± 3.6	*31 ±17	*0.0 ± 0.0	*0 ± 0
Tropical Premontane wet forest transition to basal	15	3.9	3	0.0	0	5.7	5	104.8	92	0.0	0
	20	0.0	-	0.0	-	0.0	-	0.0	-	0.0	-
	26	0.0	0	0.0	0	1.0	2	42.3	98	0.0	0
	40	0.0	0	0.0	0	0.0	0	222.4	100	0.0	0
	50	0.0	0	0.0	0	0.9	85	0.0	0	0.2	15
	mean pasture ± SE	0.8 ± 0.8	1 ± 1	0.0 ± 0.0	0 ± 0	1.5 ± 1.1	23 ± 21	73.9 ± 41.8	58 ± 24	0.0 ± 0.0	3 ± 3
Tropical Premontane rain forest	1	0.0	0	0.0	0	3.1	2	120.6	98	0.0	0
	10	0.0	0	0.0	0	0.3	0	114.8	100	0.2	0
	25	1.8	1	0.0	0	162.2	99	0.0	0	0.1	0
	45	0.0	0	0.0	0	6.8	28	17.7	72	0.0	0
	70	0.0	0	0.0	100	0.0	0	0.0	0	0.0	0
	mean pasture ± SE	*0.5 ± 0.5	*0 ± 0	*0.0 ± 0.0	*25 ± 25	2.3 ± 40.0	*32 ±23	33.1 ± 27.5	*43 ± 25	*0.1 ± 0.1	*0 ± 0
Tropical Lower Montane rain forest	16	0.0	0	0.8	3	21.6	86	2.6	10	0.0	0
	28	0.0	0	0.0	0	1.0	8	10.9	92	0.0	0
	32	0.0	0	0.5	4	2.0	17	9.7	80	0.0	0
	48	0.0	0	0.0	0	2.5	6	41.2	94	0.0	0
	54	0.0	0	0.0	0	0.5	2	23.3	98	0.0	0
	mean pasture ± SE	0.0 ± 0.0	0 ± 0	0.3 ± 0.2	1 ± 1	5.5 ± 4.0	24 ± 16	17.5 ± 6.8	75 ± 16	0.0 ± 0.0	0 ± 0

*Young pastures (1 and 2 years old) were not included in calculations of mean and SE.

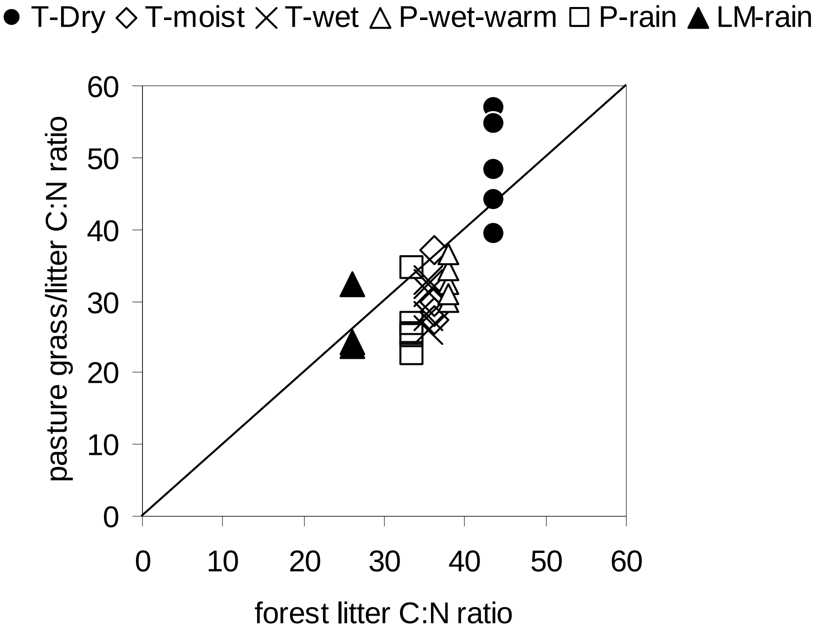


Appendix 24. Aboveground (a and b) and ecosystem C and N stock estimates (c and d) (Mg/ha) by pasture age in six life zones in Costa Rica. T-dry = Tropical dry forest; T-moist = Tropical moist forest; T- wet = Tropical wet forest; P-wet-warm = Tropical Premontane wet forest transition-warm; P-rain = Tropical Premontane rain forest; LM-rain = Tropical Lower Montane rain forest.

Appendix 25. Pearson coefficients of correlation for various response variables an age, elevation, temperature, and precipitation in 31 pastures in six chronosequences along a broad climatic gradient in Costa Rica.

Response variables	Age	Elevation	Temperature	Precipitation
%C grass/litter	-0.17	0.04	-0.09	0.17
%N grass/litter	-0.30	0.51 ***	-0.58 ***	0.74 ***
C:N ratio grass/litter	0.26	0.43 **	0.51 ***	-0.73 ***
Aboveground biomass stocks (Mg/ha)	-0.51 ***	0.13	-0.26	0.44 **
Aboveground C stocks (Mg C/ha)	-0.51 ***	0.13	-0.23	0.44 **
Aboveground N stocks (Mg N/ha)	-0.55 ***	0.15	-0.25	0.46 **
Ecosystem C stocks (Mg C/ha)	-0.57 ***	0.59 ***	-0.73 ***	0.87 ***
Ecosystem N stocks (Mg N/ha)	-0.45 **	0.71 ***	-0.83 ***	0.90 ***
Δ Aboveground C stock (Mg C/ha)	0.04	-0.72 ***	0.73 ***	-0.58 ***
Δ Aboveground N stock (Mg N/ha)	-0.04	-0.70 ***	0.69 ***	-0.52 ***
Relative Δ aboveground C stock (%)	-0.45 **	-0.03	-0.07	0.31 *
Relative Δ aboveground N stock (%)	-0.47 ***	-0.06	-0.03	0.28
Δ Ecosystem C stock (Mg C/ha)	-0.36 **	-0.68 ***	0.58 ***	-0.13
Δ Ecosystem N stock (Mg N/ha)	-0.52 ***	-0.02	-0.14	0.65 ***
Relative Δ ecosystem C stock (%)	-0.65 ***	0.00	-0.18	0.58 ***
Relative Δ ecosystem N stock (%)	-0.63 ***	0.00	-0.17	0.71 ***

* $P < 0.10$, ** $P < 0.05$, *** $P < 0.01$, *P*-values are for two sides tests that the correlation coefficient is not equal to zero.

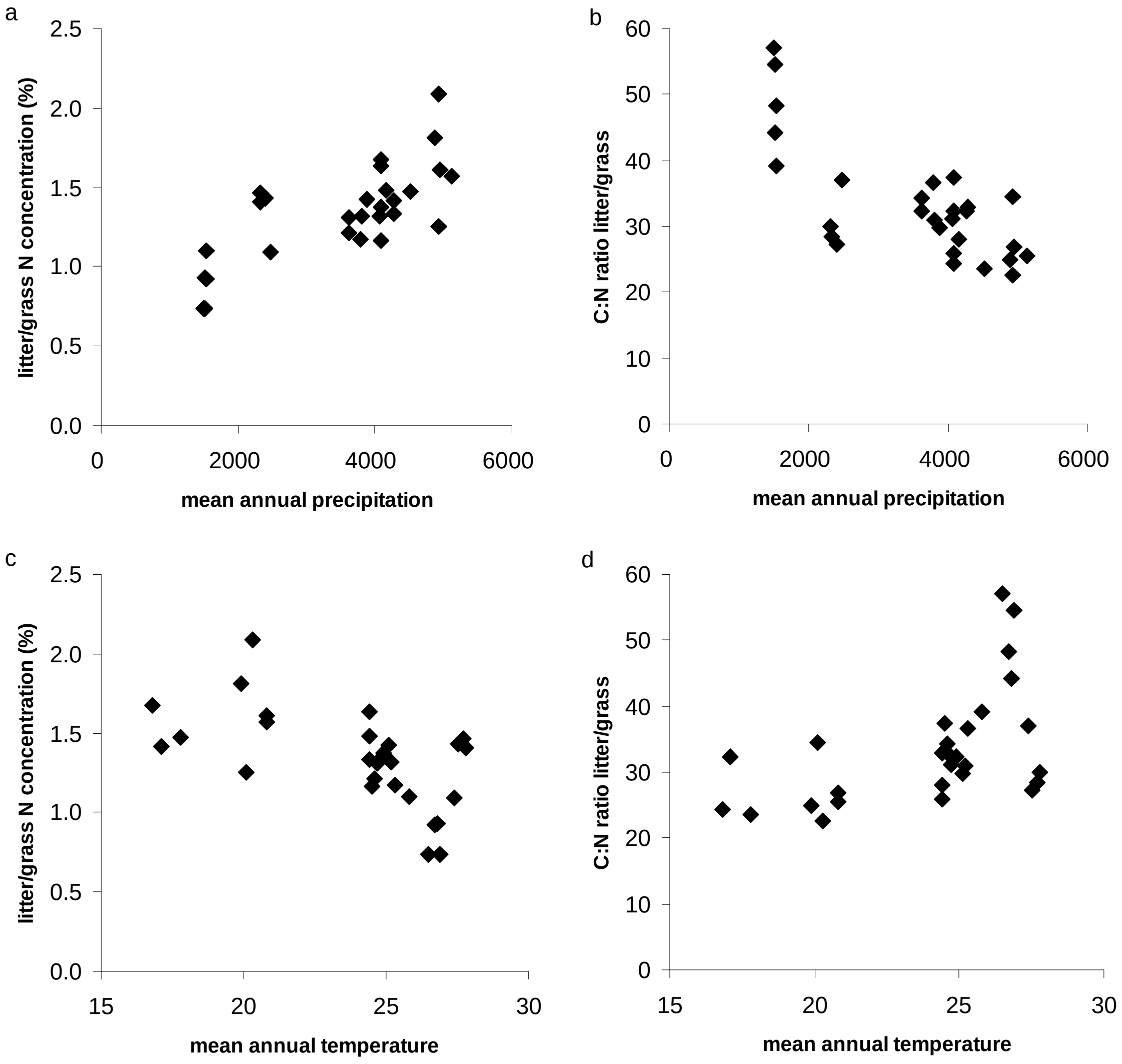


Appendix 26. Correlations of C:N ratio's in litter/grass samples of 31 Costa Rican pastures and C:N ratio's of mature reference forest litter. T-dry = Tropical dry forest; T-moist = Tropical moist forest; T- wet = Tropical wet forest; P-wet-warm = Tropical Premontane wet forest-warm; P-rain = Tropical Premontane rain forest; LM-rain = Tropical Lower Montane rain forest.

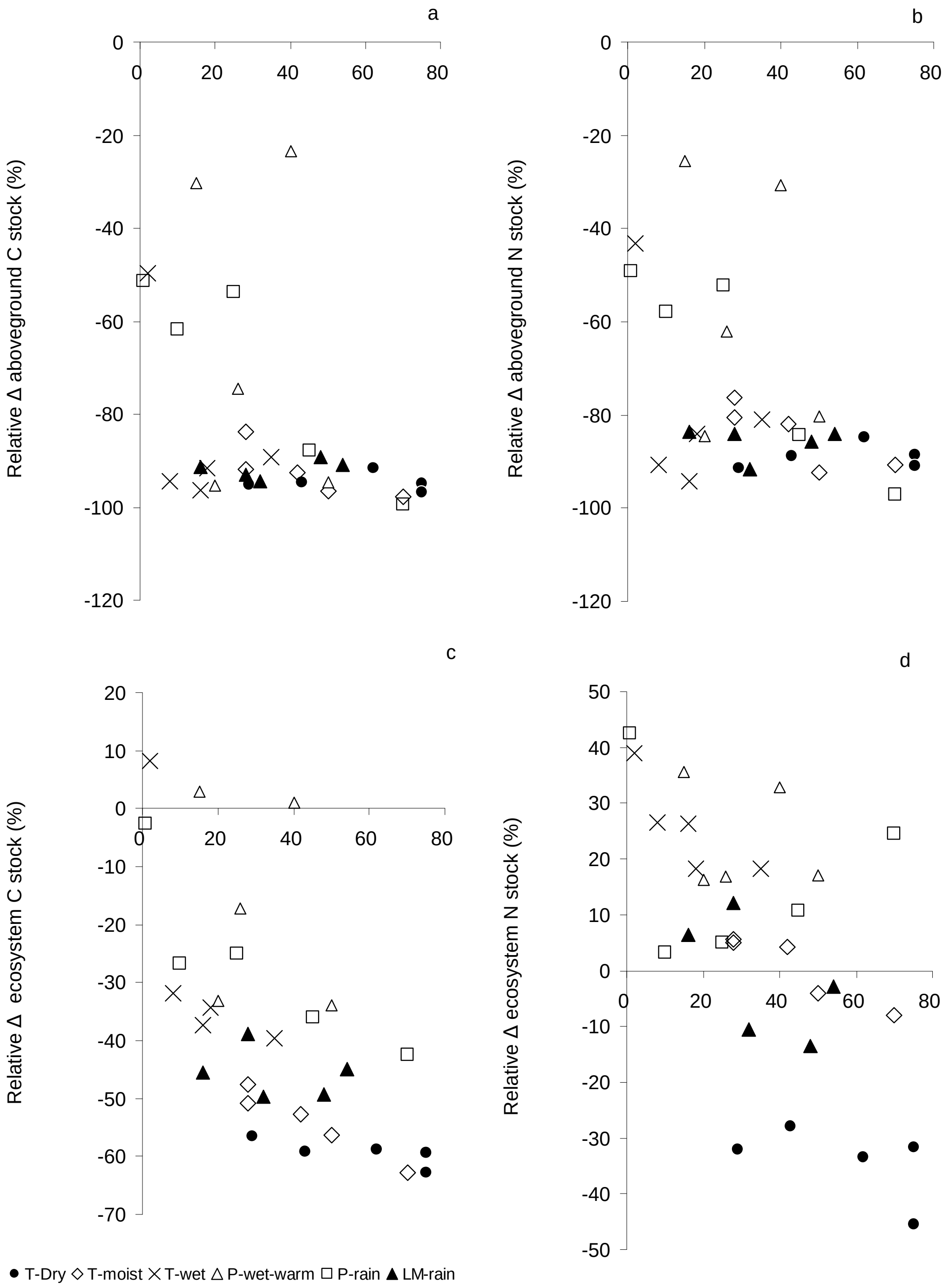
Appendix 27. Concentrations (%) of C and N, and CN-ratios in pasture litter/grass in six chronosequences in Costa Rica.

Life zone	Pasture age (yrs)	C	N	C:N ratio
Tropical dry forest	29	42.07 ± 0.397	0.74 ± 0.003	57.1
	43	40.30 ± 0.368	0.74 ± 0.008	54.6
	62	44.79 ± 0.160	0.93 ± 0.004	48.4
	>75 (a)	40.98 ± 0.090	0.93 ± 0.013	44.2
	>75 (b)	43.08 ± 0.009	1.10 ± 0.073	39.2
	mean pasture	42.24 ± 0.793 a	0.89 ± 0.068	48.7
Tropical moist forest	28 (a)	n.s.	n.s.	n.s.
	28 (b)	40.40 ± 0.193	1.09 ± 0.017	37.1
	42	38.97 ± 0.233	1.43 ± 0.020	27.2
	>47	42.20 ± 0.365	1.41 ± 0.024	30.0
	>69	41.55 ± 0.199	1.46 ± 0.053	28.5
	mean pasture	40.78 ± 0.708 a	1.35 ± 0.077 a	30.7 a
Tropical wet forest	2	44.42 ± 0.295	1.38 ± 0.054	32.3
	8	43.96 ± 0.150	1.33 ± 0.021	33.0
	16	41.58 ± 0.347	1.48 ± 0.012	28.0
	18	41.06 ± 0.305	1.32 ± 0.032	31.2
	35	42.30 ± 0.376	1.64 ± 0.025	25.9
	>35	43.50 ± 0.362	1.17 ± 0.002	37.3
	mean pasture	42.48 ± 0.551 a	1.39 ± 0.080 a	31.1 a
Premontane wet forest transition to basal	15	42.28 ± 0.364	1.31 ± 0.035	32.3
	20	41.63 ± 0.261	1.21 ± 0.018	34.3
	26	42.53 ± 0.482	1.43 ± 0.015	29.8
	40	42.87 ± 0.030	1.17 ± 0.014	36.6
	50	40.76 ± 0.242	1.32 ± 0.015	30.9
	mean pasture	42.01 ± 0.372 a	1.29 ± 0.044 a	32.8 a
Premontane rain forest	1	45.27 ± 0.620	1.81 ± 0.019	25.0
	10	43.21 ± 0.430	1.61 ± 0.039	26.9
	25	47.43 ± 0.612	2.09 ± 0.055	22.7
	45	43.27 ± 0.462	1.25 ± 0.003	34.5
	70	39.98 ± 0.383	1.57 ± 0.042	25.4
	mean pasture	43.83 ± 1.237 a	1.67 ± 0.138 a	26.9 a
Tropical lower montane rain forest	16	34.72 ± 0.451	1.47 ± 0.067	23.6
	28	45.78 ± 0.583	1.42 ± 0.054	32.2
	32	n.s.	n.s.	n.s.
	48	n.s.	n.s.	n.s.
	54	40.80 ± 0.338	1.68 ± 0.073	24.3
	mean pasture	40.44 ± 3.198 a	1.52 ± 0.061 a	26.7 a

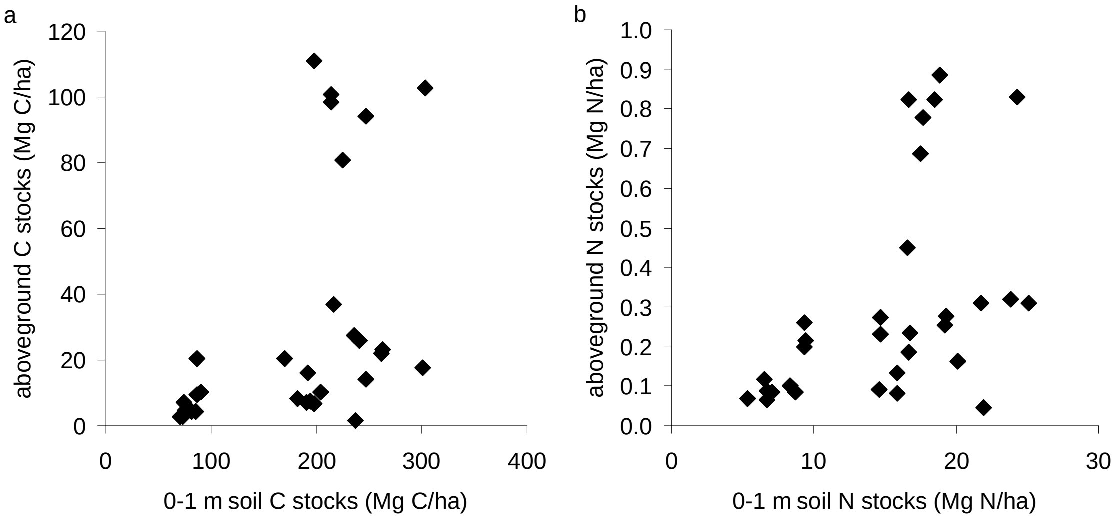
n.s. = no sample available. Labels (a) and (b) were used to distinguish between two pastures with the same age within one life zone. Means for each life zone followed by the same letter are similar to one another, means for each life zone not followed by a letter indicates median for this life zone is different from all other life zones ($P_{\text{adjusted}} < 0.1$).



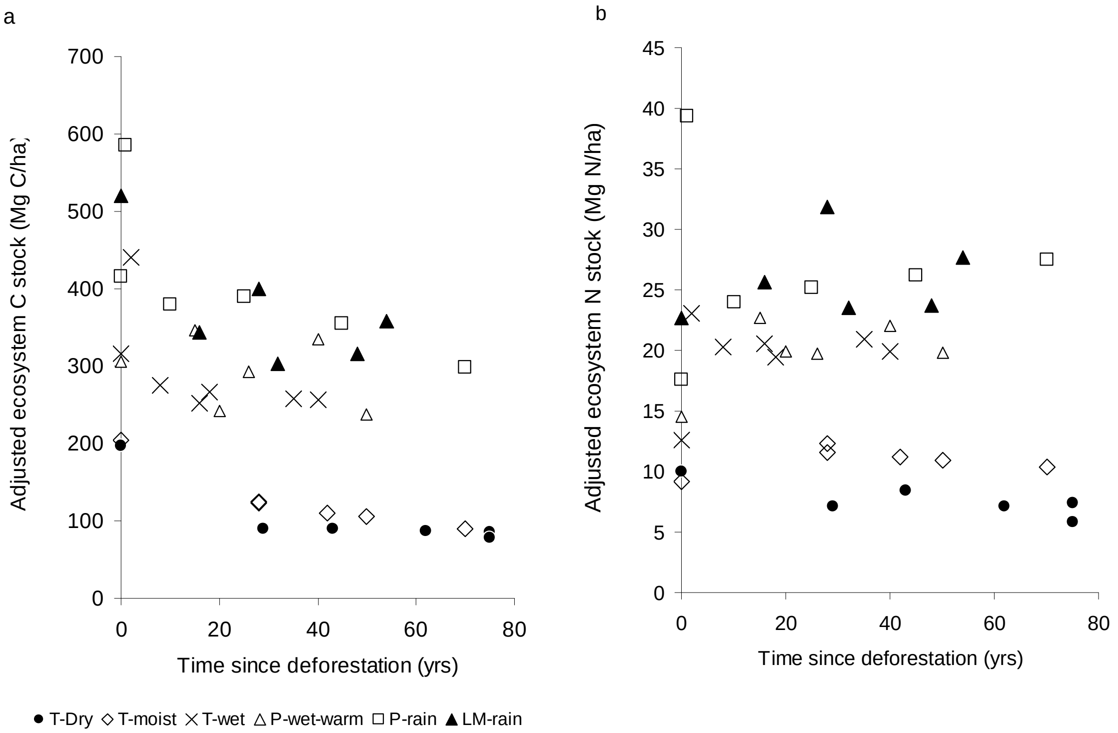
Appendix 28. Relationships between mean (a and c) N concentration and (b and d) C:N ratio in litter/grass samples of 31 Costa Rican pastures with mean annual precipitation (mm/year) and temperature (^{o}C).



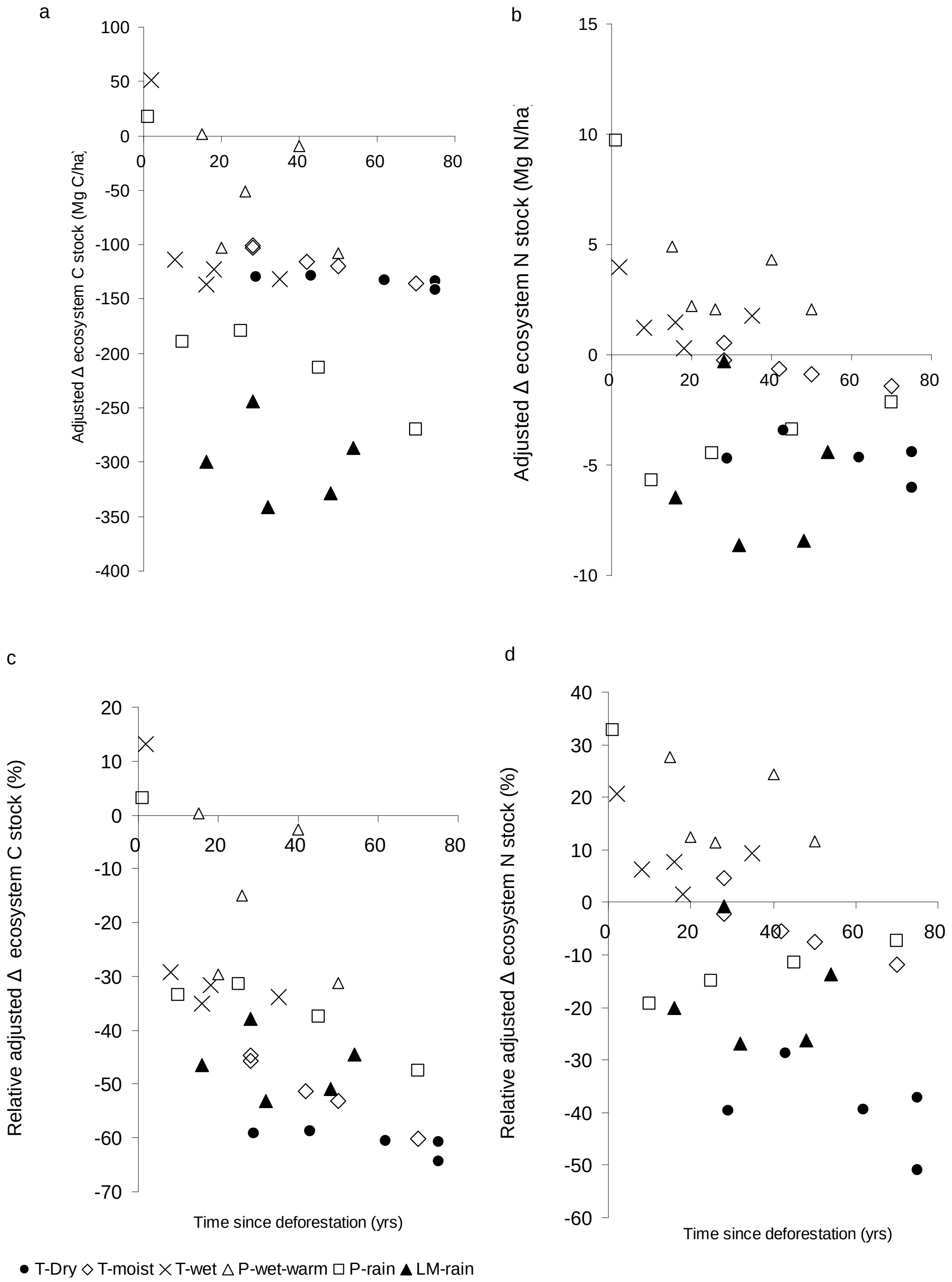
Appendix 29. Relative Δ (a-b) aboveground and (c-d) ecosystem C and N stock (%) in six life zones in Costa Rica. Positive percentages indicate C gains and negative percentages indicate C losses due to conversion. T-dry = Tropical dry forest; T-moist = Tropical moist forest; T- wet = Tropical wet forest; P-wet-warm = Tropical Premontane wet forest-warm; P-rain = Tropical Premontane rain forest; LM-rain = Tropical Lower Montane rain forest.



Appendix 30. Relationship between aboveground (a) C and (b) N stocks with 0-1 m soil C and N stocks in 31 Costa Rican pastures of various ages along a climatic gradient.



Appendix 31. Ecosystem (a) C and (b) N stock estimates adjusted for potential sampling tool bias by pasture age in six life zones in Costa Rica. T-dry = Tropical dry forest; T-moist = Tropical moist forest; T- wet = Tropical wet forest; P-wet-warm = Tropical Premontane wet forest transition-warm; P-rain = Tropical Premontane rain forest; LM-rain = Tropical Lower Montane rain forest.



Appendix 32. Absolute adjusted Δ (a-b) ecosystem and (c-d) relative adjusted Δ ecosystem C and N stock estimates in six life zones in Costa Rica. Positive numbers and percentages indicate C gains and negative percentages indicate C losses due to forest-to-pasture conversion. T-dry = Tropical dry forest; T-moist = Tropical moist forest; T- wet = Tropical wet forest; P-wet-warm = Tropical Premontane wet forest-warm; P-rain = Tropical Premontane rain forest; LM-rain = Tropical Lower Montane rain forest.

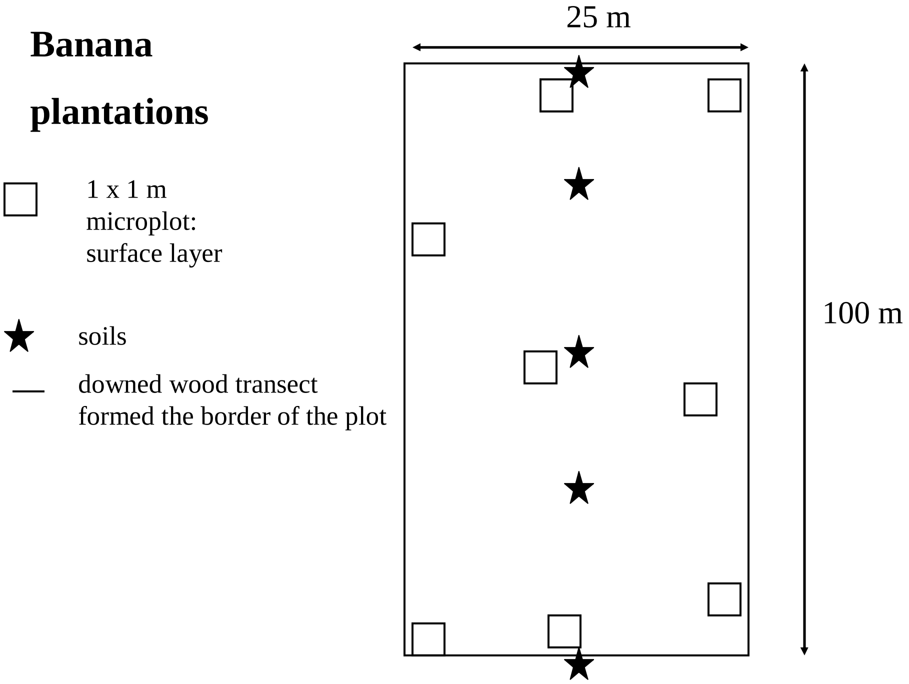
Appendix 33. Life zone, location, elevation, and climate data of croplands sampled in Costa Rica.

Landuse	Life zone	Site #	Elevation (m)	Precipitation* (mm/year)	Temperature* (°C)	Latitude- N	Longitude-W	Management
Banana	Tropical moist forest	224	43	2622	25.4	9.7225	-82.9995	No apperent differences in management, no trees, well established
		225	44	2622	25.4	9.7340	-82.9988	
		226	36	2700	25.5	9.8750	-82.9974	
		227	27	2700	25.5	9.8741	-82.9960	
	Tropical Premontane wet forest-warm	222	97	3700	25.1	10.3441	-83.7447	
		230	53	3700	25.4	10.1917	-83.4678	
		229	57	3750	25.3	10.2023	-83.4825	
		221	57	3925	25.3	10.4757	-84.0069	
	Tropical wet forest	220	55	3925	25.4	10.4753	-84.0120	
		228	59	4025	25.3	10.4634	-83.9564	
		223	94	4107	25.1	10.3354	-83.8718	
Coffee	Tropical Premontane wet forest	218	984	2400	21.7	9.9105	-84.2829	Mixed trees > 5 yrs
		219	1000	2400	21.6	9.9108	-84.2802	No trees
		216	1282	3600	18.8	9.9047	-83.7520	No trees
		217	1226	3800	19.1	9.9206	-83.7311	Trees > 4 yrs (*Eucalyptus*)
		211	1067	3000	21.2	10.0840	-84.2941	Trees > 10 yrs (*Inga*)
		212	1075	3000	21.2	10.0862	-84.2954	No trees
		210	1119	3080	20.9	10.1000	-84.2883	Coffee & trees (*Inga*) = 2 yrs, organic
		213	1465	3500	18.9	10.1453	-84.3283	Trees > 10 yrs (*Erythrina*)
	Tropical Premontane rain forest	214	755	5103	21.4	10.2939	-84.1837	Coffee & mixed trees < 3 yrs, organic
		215	801	5103	21.2	10.3057	-84.1885	No trees, coffee > 10 yrs, 2 yrs abandoned
Sugarcane	Tropical Premontane moist forest-warm	201	36	1652	27.6	10.4117	-85.1784	Machine harvest, cane-rice rotation
		202	36	1652	27.6	10.4117	-85.1784	Fire & manual harvest, cane-rice rotation
		200	24	1660	27.6	10.3864	-85.2038	Machine harvest, cane-rice rotation
		203	24	1660	27.6	10.3864	-85.2038	Fire & manual harvest, cane-rice rotation
	Tropical Premontane wet forest	205	1075	3000	21.2	10.0862	-84.2954	Manual harvest
		204	1202	3097	20.4	10.1086	-84.2862	Manual harvest
		206	1465	3500	18.9	10.1453	-84.3283	Fire & manual harvest
		207	1554	3500	18.4	10.1509	-84.3291	Fire & manual harvest
		208	1216	3800	19.1	9.9216	-83.7336	Manual harvest
		209	1296	3600	18.7	9.9104	-83.7423	Fire & manual harvest

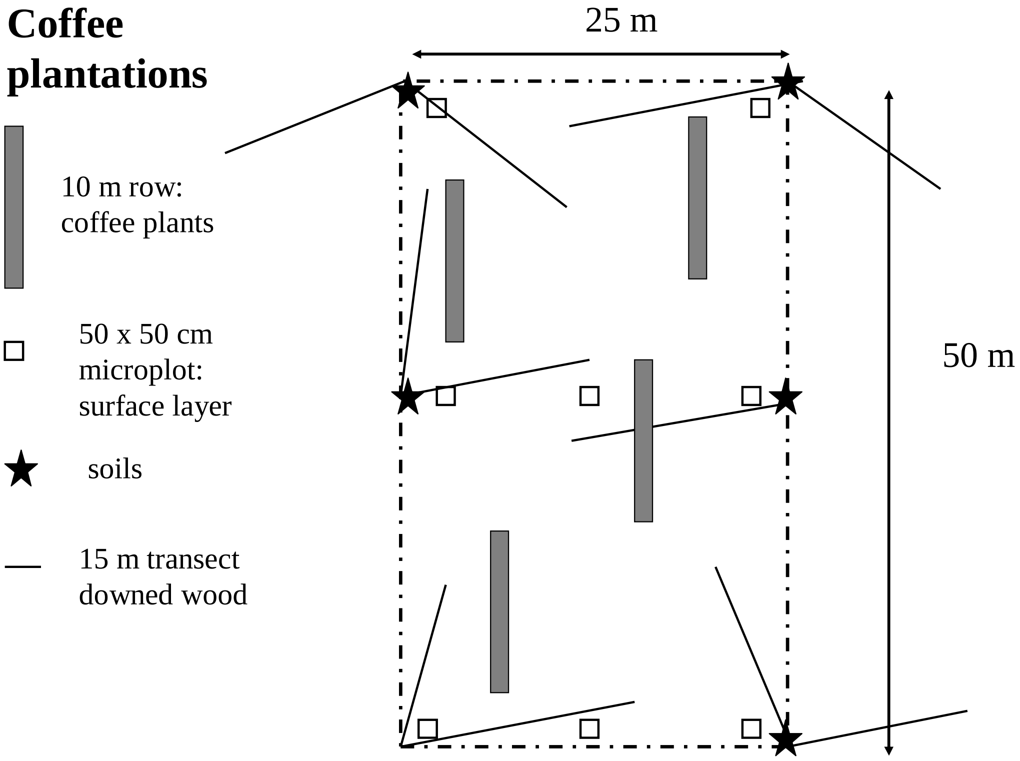
* Climatic data are annual means.

Appendix 34. Sampling design banana, coffee and sugarcane plantations

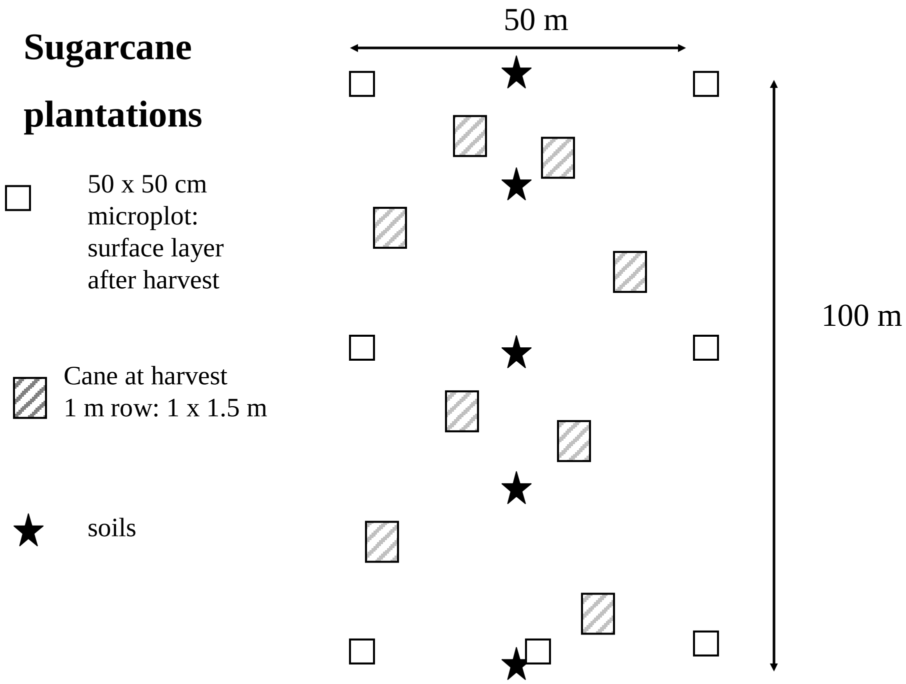
Banana plantations

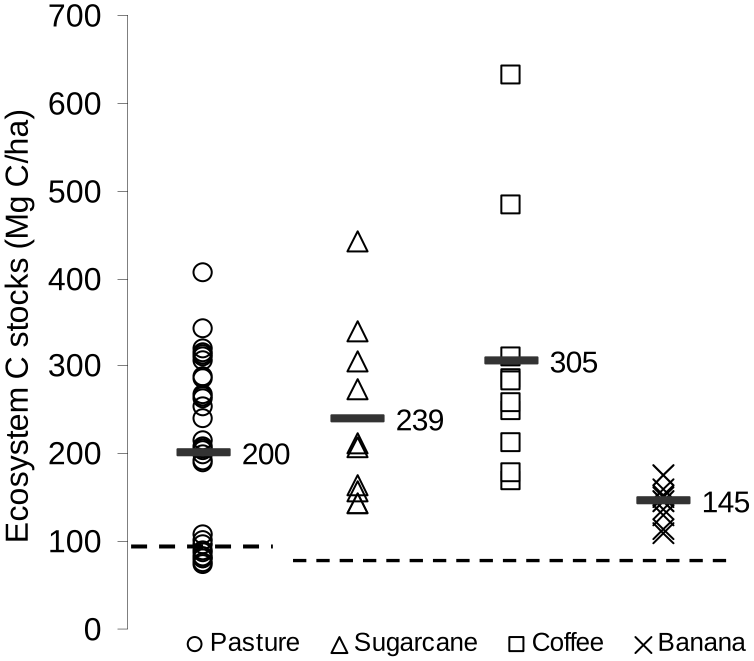


Coffee plantations



Appendix 34 (continued). Sampling design banana, coffee and sugarcane plantations





Appendix 35. Ecosystem C stocks for pastures years (n= 29), sugarcane (n = 10), coffee (n = 10), and banana plantations (n = 11). The horizontal bar indicates mean ecosystem C stock by land use and dashed lines are estimates assumed for ecosystem C stocks (97 and 79 Mg C/ha) 20 years after mature forest-to-agricultural conversion by Houghton and Hackler (2001).

Appendix 36. Aboveground and soil C stock estimates adjusted for potential sampling tool bias in croplands and differences (Δ) between cropland and mature forest stocks by life zone in Costa Rica.

				Adjusted		Adjusted		
Land use	Life zone	Site #	Aboveground C	soil C	Δ Aboveground C	Δ Soil C	Δ Ecosystem C	n*
Banana	Tropical moist forest	224	8	128	-115 **	19 **	-96	5
		225	9	149	-114 **	39 **	-75	5
		226	7	181	-115 **	71 **	-44	5
		227	7	209	-116 **	99 **	-17	5
	Tropical Premontane wet forest-warm	222	8	143	-130	-57	-186	3
		230	7	140	-131	-60	-190	3
		229	9	153	-129	-47	-176	3
		221	11	174	-127	-26	-152	3
	Tropical wet forest	220	10	181	-178	-23	-201	3
		228	8	136	-179	-67	-247	3
		223	8	187	-180	-17	-197	3
Coffee	Tropical Premontane wet forest	218	22	290	-122	119	-3	1
		219	17	471	-128	300	173	1
		216	10	373	-211	2	-208	3
		217	58	795	-163	424	261	3
		211	28	185	-193	-186	-378	3
		212	7	358	-214	-13	-226	3
		210	4	198	-217	-172	-389	3
		213	26	304	-195	-66	-261	3
	Tropical Premontane rain forest	214	16	287	-196	-71	-268	2
		215	13	409	-198	51	-148	2
Sugarcane	Tropical Premontane moist forest-warm	201	22	130	-42 ***	-8 ***	-50	3
		202	17	125	-47 ***	-12 ***	-60	3
		200	22	153	-42 ***	15 ***	-27	3
		203	16	145	-48 ***	7 ***	-41	3
	Tropical Premontane wet forest	205	21	376	-200	5	-194	3
		204	29	393	-192	23	-169	3
		206	28	330	-193	-40	-233	3
		207	22	250	-199	-121	-320	3
		208	28	568	-192	197	5	3
		209	30	242	-191	-129	-320	3

*n= sample size of reference mature forests. ** Reference forests are in Pacific zone which has distinct annual dry season, while banana plantations are in Caribbean zone without a strong dry season. ***Reference forest are nearby but classified as Tropical dry forest life zone.

Appendix 37. Comparison of ecosystem C stock estimates in agricultural lands for the eight life zones included in this study versus those based on Houghton & Hackler (2001).

	Our study*			Houghton & Hackler**		
	Pasture	Crop	Total	Pasture	Crop	Total
Tropical dry forest	5,612,532		5,612,532	6,775,738		6,775,738
Tropical moist forest	38,121,631	6,402,721	44,524,352	39,455,499	3,570,429	43,025,928
Tropical wet forest	64,314,853	4,766,248	69,081,101	31,161,542	2,819,888	33,981,430
Premontane moist forest-warm	21,050,195	4,441,261	25,491,456	25,412,882	2,299,677	27,712,559
Premontane wet forest-warm	113,031,627	7,694,728	120,726,356	42,680,838	3,862,298	46,543,136
Premontane wet forest		92,339,573	92,339,573		23,385,010	23,385,010
Premontane rain forest	28,453,325	2,640,056	31,093,381	9,821,966	888,815	10,710,781
Lower Montane rain forest	7,650,500		7,650,500	2,623,457		2,623,457
Total included in this study	278,234,663	118,284,588	396,519,251	157,931,922	36,826,116	194,758,038

* Estimates based on our study were calculated using results in Table 4.2.

** Estimates based on Houghton and Hackler (2001) were calculated by assuming all agricultural lands in Costa Rica were classified as Tropical seasonal forest: ecosystem C stock in pastures were 97 Mg C/ha and croplands 79 Mg C/ha. Land area data taken from Appendix 32.

Appendix 38. Comparison of soil C stock estimates (Mg C/ha) in agricultural lands for the eight life zones included in this study versus those based on Houghton & Hackler (2001).

	Our study*			Houghton & Hackler**		
	Pasture	Crop	Total	Pasture	Crop	Total
Life zone	Mg C	Mg C	Mg C	Mg C	Mg C	Mg C
Tropical dry forest	5,289,868		5,289,868	6,077,208		6,077,208
Tropical moist forest	34,329,872	6,050,743	40,380,615	35,387,922	3,344,452	38,732,374
Tropical wet forest	60,331,315	4,463,177	64,794,492	27,949,012	2,641,414	30,590,426
Premontane moist forest-warm	19,840,025	3,881,546	23,721,571	22,792,997	2,154,127	24,947,125
Premontane wet forest-warm	89,890,256	7,260,128	97,150,384	38,280,752	3,617,849	41,898,600
Premontane wet forest		85,410,296	85,410,296		21,904,946	21,904,946
Premontane rain forest	23,208,192	2,476,180	25,684,372	8,809,392	832,561	9,641,953
Lower Montane rain forest	7,088,156		7,088,156	2,352,997		2,352,997
Total included in this study	239,977,685	109,542,070	349,519,755	141,650,280	34,495,349	176,145,630

* Estimates based on our study were calculated using results in Table 4.2.

** Estimates based on Houghton and Hackler (2001) were calculated by assuming all agricultural lands in Costa Rica were classified as Tropical seasonal forest: soil C stock in pastures were 87 Mg C/ha and croplands 74 Mg C/ha. Land area data taken from Appendix 32.

Appendix 39. Comparison of ecosystem Δ C stocks (Mg C/ha) in agricultural lands for the eight life zones included in this study versus those based on Houghton & Hackler (2001).

	Our study*			Houghton & Hackler**		
	Pasture	Cropland	Total	Pasture	Cropland	Total
Tropical dry forest	-8,205,216		-8,205,216	-9,849,268		-9,849,268
Tropical moist forest	-44,826,081		-44,826,081	-57,352,838		-57,352,838
Tropical wet forest	-37,072,597	-6,498,225	-43,570,823	-45,296,675	-5,675,470	-50,972,144
Premontane wet forest-warm	-21,683,767	-8,433,408	-30,117,174	-62,041,218	-7,773,486	-69,814,704
Premontane wet forest		-57,506,015	-57,506,015		-47,066,033	-47,066,033
Premontane rain forest	-13,710,250	-2,042,783	-15,753,033	-14,277,291	-1,788,880	-16,066,171
Lower Montane rain forest	-6,436,162		-6,436,162	-3,813,479		-3,813,479
Total included in this study	-131,934,072	-74,480,431	-206,414,504	-192,630,769	-62,303,869	-254,934,638

* Estimates based on our study were calculated using results in Table 4.2.

** Estimates based on Houghton and Hackler (2001) were calculated by assuming all agricultural lands in Costa Rica were classified as Tropical seasonal forest: ecosystem C stock losses in pastures were -141 Mg C/ha and croplands -159 Mg C/ha. Land area data taken from Appendix 32.

Appendix 40. Comparison of soil Δ C stocks in agricultural lands for the eight life zones included in this study versus those based on Houghton & Hackler (2001).

	Our study*			Houghton & Hackler**		
Life zone	Pasture Mg C	Cropland Mg C	Total Mg C Mg C	Pasture Mg C	Cropland Mg C	Total Mg C Mg C
Tropical dry forest	-2,392,591		-2,392,591	-768,383		-768,383
Tropical moist forest	2,514,843		2,514,843	-4,474,335		-4,474,335
Tropical wet forest	19,789,185	-110,410	19,678,776	-3,533,783	-856,675	-4,390,458
Premontane wet forest-warm	18,276,157	-2,125,848	16,150,310	-4,840,095	-1,173,356	-6,013,451
Premontane wet forest		-4,144,179	-4,144,179		-7,104,307	-7,104,307
Premontane rain forest	2,571,938	177,319	2,749,256	-1,113,831	-270,020	-1,383,851
Lower Montane rain forest	-243,705		-243,705	-297,505		-297,505
Total included in this study	40,515,827	-6,203,118	34,312,709	-15,027,932	-9,404,358	-24,432,290

* Estimates based on our study were calculated using results in Table 4.2.

** Estimates based on Houghton and Hackler (2001) were calculated by assuming all agricultural lands in Costa Rica were classified as Tropical seasonal forest: soil C stock in pastures were -11 Mg C/ha and croplands -24 Mg C/ha based. Land area taken from Appendix 32.

Appendix 41. Estimates of agricultural land area, adjusted ecosystem and soil C stock estimates and their changes (Δ) due to forest-to-agriculture conversion for the eight life zones sampled in our study.

	ha				Mg C/ha							
	Area				Pasture ≥ 8 years				Cropland			
		Non-forested			C stock		Δ C stock		C stock		Δ C stock	
Life zone	Costa Rica	in 2005	Pasture*	Cropland*	Ecosystem	Soil	Ecosystem	Soil	Ecosystem	Soil	Ecosystem	Soil
Tropical dry forest	116,140	69,853	69,853	0	86	82	-133	-52				
Tropical moist forest ***	714,962	451,953	406,758	45,195	111	102	-115	1	174	166	***	***
Tropical wet forest	832,934	356,948	321,253	35,695	262	249	-128	47	176	168	-215	-36
Premontane moist forest-warm**	471,897	291,098	261,988	29,110	86	82	**	**	157	138	**	**
Premontane wet forest-warm	706,880	488,898	440,009	48,890	291	238	-54	38	162	153	-176	-47
Premontane wet forest ****	429,002	296,013	0	296,013					390	367	-225	-32
Premontane rain forest	437,216	112,508	101,257	11,251	356	304	-213	-53	363	348	-208	-10
Lower Montane rain forest	334,869	27,046	27,046	0	344	323	-300	-69				
Total included for C stocks	4,043,900	2,094,318	1,628,164	466,153								
Total included for Δ C stocks	3,572,003	1,803,219	1,366,176	391,848								

* We assumed 90% of agricultural land is in pasture ≥ 8 years and 10% in croplands within each life zone, unless we report no C stock and Δ C stock data for pastures or croplands. ** We assumed that soil C stocks in pastures in the Tropical Premontane moist forest-warm life zone is similar to pastures in the Tropical dry forest life zone, which is a conservative estimate. *** We excluded Δ soil C stocks in croplands in the Tropical moist forest life zone due to a lack of reference mature forest data. **** We excluded two coffee plantations with exceptional high Δ soil C stocks when calculating mean Δ ecosystem and soil C for the Tropical Premontane wet forest life zone