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*On the cover: Cover image prepared by Sarah Graves, University of Florida; see article by Ewel et al. in this issue. Lidar data draped over visible imagery show tropical tree plantations of short-longevity (black), intermediate longevity (blue-green), and uncut (yellow-red). Map Data: 2014 Digital Globe, 2007 Google. Lidar Data: U.S. Army Corps of Engineers Topographic Engineering Center.*



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# Soil Changes in Model Tropical Ecosystems: Effects of Stand Longevity Outweigh Plant Diversity and Tree Species Identity in a Fertile Volcanic Soil

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## ABSTRACT

Plant or community longevity can strongly influence soil fertility, yet it is seldom among the functional traits considered in studies of biodiversity and ecosystem functioning. For 11 years we tracked the influences of plant longevity, life-form richness, and tree species identity on 12 soil chemical properties in model ecosystems on an allophanic Andisol in the humid lowlands of Costa Rica. The design employed three levels of plant longevity: 1 year and 4 years (trees cut without biomass removal and replanted to same species), and uncut; two levels of life-form diversity (tree alone, or tree plus palm plus giant perennial herb); and three eudicot, non-nitrogen (N)-fixing tree species. The site's Andisol proved remarkably resistant to treatment-induced loss of fertility. Although the magnitude of changes was low, most properties declined during the early phases of plant growth, then stabilized or increased. The greatest declines occurred in stands of shortest life

span, where organic matter inputs were low and leaching rates were high. In contrast, massive depositions of organic matter every 4 years sustained or augmented surface-soil cation concentrations, pH, organic carbon (SOC), and extractable phosphorus (P). An increase in diversity from one life form to three led to more SOC and calcium (Ca), whereas potassium (K) decreased due to a species effect: high K uptake by the giant herb. The most notable tree-species effects concerned P: It increased under the species that had the highest litterfall and may facilitate apatite weathering; it decreased under the species of highest tissue-N concentrations. Through its effects on soil exposure and organic matter returns, plant longevity exerted greater influence on more soil properties than either diversity or species identity.

**Key words:** Andisol; acidity; biodiversity; cations; organic matter; extractable phosphorus.

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## INTRODUCTION

Soil is particularly vulnerable to degradation in the humid tropics, where rainfall typically exceeds evapotranspiration two-to-three fold or more. Plants mitigate nutrient losses through uptake and recy-



cling, but the degree to which different functional traits affect nutrient loss and retention is not well understood. We compared the relative influence of three plant-community characteristics—plant (and stand) longevity, life-form diversity, and tree species identity—on soil fertility. Siting the study on a fertile soil in a warm, wet climate reduced abiotic constraints to plant growth and enabled us to test the influences of plant-community traits on ecological processes in a relatively short-time period. The study involved several measures of ecosystem functioning, and one of those—maintenance or loss of soil fertility—is reported here.

## Longevity

Plant longevity affects soil fertility in both natural and managed ecosystems, yet it is seldom considered in ecological studies. As perennial plants age and grow, they exploit ever larger volumes of soil, and they take up and store increasing quantities of nutrients. Upon plant death, uptake and storage cease, and the processes begin anew with recolonization. In some natural systems plant life is truncated by episodic phenomena (for example, floods, fires, wind storms, insect outbreaks), whereas in other systems longevity reflects life history traits (for example, annual or perennial grasslands, desert annuals and perennials, monocarpy). Without simultaneous manipulation of life span and species composition, it is difficult to decouple the effects of longevity from other influences on ecosystem functioning. Thus, the lack of attention to longevity in ecological studies is not surprising.

Unlike ecologists, agronomists and agroforesters have devoted substantial attention to longevity, particularly the annual–perennial dichotomy (for example, Hartemink 2003; Glover and others 2010). The broad finding is that long-lived plants sustain soil organic matter better than annual crops. For example, long-term data (>80 years) from continuously cultivated plots demonstrate that annual crops inevitably cause declines of soil organic carbon (SOC) compared with nearby natural systems (Soil Quality Institute 2001). Perennial systems, in contrast, sustain the soil subecosystem, including organic matter, extensive root systems, tillth, and the microbial community that recycles nutrients (for example, Cox and others 2006; Culman and others 2010; DuPont and others 2010). In addition, perennials can improve the synchrony between plant demand and nutrient availability (Crews 2005). Nonetheless, life span is a species trait (as well as a plant-community trait), making it as difficult to decouple longevity effects

from species-identity effects in agronomic studies as in ecological studies. There are opportunities to distinguish longevity and species-identity effects using cultivars—for example, sugarcane grown from 1–10-year-old ratoons; strawberries or cotton grown as annuals or perennials—but we are aware of no such studies that have assessed soil fertility.

In a previous experiment in the humid tropics, we found that soil under short-lived monocultures (3–12 months) underwent substantial nutrient depletion, whereas tree monocultures as young as 3 years were almost as effective at nutrient retention as equal-aged hyperdiverse communities (Ewel and others 1991). Although we attributed that finding to the tree's sustained growth and the rapid development of a deep network of fine roots, we had only weak grounds for claiming a longevity effect rather than a species-identity effect. That study motivated the research reported here, which was designed to decouple plant and stand longevity from two community attributes that have received substantial attention in the ecological literature: biodiversity and species identity.

## Biodiversity

Species diversity is known to influence many aspects of ecosystem functioning, yet few plant diversity studies have included direct measurements of soil, and almost all of them are from temperate grasslands (see review by Cardinale and others 2011). When soil processes are considered, they usually involve measurement of inorganic N in leachate or N-mineralization. Tilman and others (1996), for example, reported a nitrate decline in the rooting zone (presumably due to plant uptake) and below the rooting zone (indicating lower leaching losses) with increasing species richness. Others, however, have been unable to separate diversity effects on leaching losses (Hooper and Vitousek 1998; Scherer-Lorenzen and others 2003) or N storage in plant tissues (Symstad and others 1998; Spehn and others 2005) from effects due to number of functional groups, species identity, or biomass accrual. The same is true of N mineralization studies: Zak and others (2003), for example, found that N mineralization did increase in response to diversity, but that increases in other soil-microbe responses (microbial biomass, respiration, fungal abundance) were caused by the increase in biomass that accompanied increasing diversity, not by diversity per se. At our site there was no significant difference in N mineralization rates or nitrate leaching between stands of one or three functional groups (Ewel 2006; Ewel and Bigelow 2011).

Most research that assesses effects of tree diversity on soil properties consists of landscape sampling, in which unknown initial conditions, lack of replication, and no opportunity for randomization preclude definitive conclusions despite sometimes tantalizing findings. The study of Saha and others (2009), who sampled home gardens in India (Kerala) and reported a trend of increasing SOC with increasing species diversity, is typical of the genre. Nevertheless, what landscape-sampling studies lack in statistical rigor is sometimes compensated for by breadth of coverage (see reviews by Nadrowski and others 2010; Scherer-Lorenzen 2014). Perhaps the most comprehensive soil studies of this type were conducted in Germany in mature forests of one, three, or five deciduous tree species, with European beech (*Fagus sylvatica* L.) as a common element (see Guckland and others 2009, 2010; Talkner and others 2009). Among their findings, increasing diversity was correlated with lower soil acidity and higher rates of gross N mineralization; concentrations of exchangeable calcium (Ca) and magnesium (Mg) (but not potassium, K) were an order of magnitude higher in diverse stands than under monospecific beech as a result of nutrient uptake from depth and subsequent re-deposition; and the rate of turnover of organic P was faster in mixed-species stands due to more easily decomposable litter and the presence of a soil-mixing fauna.

Thus, from studies of both N (and occasionally P) in well-replicated temperate grasslands, to measures of a broad array of soil variables in less-controlled landscape sampling of forests, there is evidence for effects of biodiversity on soil properties. Nevertheless, our ability to predict those effects more broadly is impeded by ignorance of mechanisms and by the degree to which other effects can outweigh those due to species diversity.

### Tree Species Identity

The effects of particular tree species on soil properties are well documented (reviewed by Binkley 1995; Binkley and Fisher 2013), but most studies have compared two strongly contrasting pairs of functional groups: angiosperms with gymnosperms (for example, Washburn and Arthur 2003; Reich and others 2005), or N fixing with non-fixers (for example, Resh and others 2002; Forrester and others 2006; Siddique and others 2008). As a result, the soil responses most-often studied have been acidification/base accumulation and N mineralization (for example, Finzi and others 1998a, b; Mueller and others 2012). In wet tropical forests

gymnosperms are rare, and most tree species are not symbiotic with N-fixing microorganisms.

Nevertheless, tropical tree species, even those that do not fall into strongly contrasting groups, do differ in traits that have the potential to influence soil properties. Litter quality, particularly lignin:N is important, as it controls the rate of decomposition and nutrient release back to the soil (see review by Binkley 1995). Likewise, nutrient use efficiency is a function not only of nutrient uptake, which draws on soil pools, but also nutrient residence time in leaves prior to abscission. Although plant habit (evergreen or deciduous) is often used as a surrogate for leaf turnover, the utility of this distinction breaks down in the tropics, where some evergreen tree species have short-lived leaves (Kikuzawa 1991). Just as the tissue quality of leaves and their life spans can influence soil properties, the same is true of fine roots (Gordon and Jackson 2000).

### Time

Like stand longevity, time is an under-studied aspect of the influence of plant communities on soil. We can surmise, from chronosequence studies (for example, Werner 1984), that there are important temporal dynamics in soil properties, but they are not revealed by otherwise informative research that documents differences in soil at the beginning and end of long-term studies (for example, Russell and others 2007; Mueller and others 2012).

Particularly in the humid tropics, rapid changes in community composition and accompanying plant traits can influence soil chemical properties: Phenology (Seiwa 1999; Ewel and Hiremath 2005) and plant stature drive the timing and rate of detritus return to the soil surface; allocation patterns influence the location of nutrient stores and their eventual return to the soil (Gleeson and Tilman 1994); and age-dependent morphology of leaves (Reich and others 2004) and roots (Kochsiek and others 2013), together with tissue chemistry, determine rates of tissue decomposition and nutrient cycling. Repeated measures on the same site are needed to understand the direction and duration of influence of such factors on soil properties.

### Objectives

The main objectives of the research reported here were to assess the role of plant longevity on soil fertility in comparison with the roles of plant diversity and plant identity, to track temporal shifts in soil fertility, and to relate plant-induced changes to the special characteristics of fertile volcanic soils.

For 11 years we studied changes in chemical properties of a tropical Andisol on which three fast-growing tree species were grown (a) in high-density monocultures subjected to cutting (without biomass removal) and replanting cycles of 1 or 4 years, or left uncut (that is, unconstrained longevity), and (b) uncut stands whose composition was enriched by the addition of two large-stature, perennial monocots.

The study plots had offered clues to the kinds of changes we might expect in the soil. For example, we knew that leaching losses decreased as a function of stand longevity in the following order: 1 year > 4 years > unconstrained (Bigelow and others 2004). There was also evidence that leaching losses were somewhat lower in stands containing three life forms than monocultures (Ewel and Bigelow 2011). But changes in soil chemistry are also governed by losses resulting from plant uptake and by gains resulting from the return of plant detritus to the soil surface. To help interpret observed changes in soil variables, we include summary information on cumulative organic matter returns to the soil. There was no a priori basis for predicting whether longevity, diversity, or tree species identity would have larger effects. Nevertheless, based on a previous experiment comparing monocultures and hyperdiverse communities (Ewel and others 1991) we did predict that soil fertility would decline under stands of short longevity and increase as a function of both longevity and diversity.

## MATERIALS AND METHODS

### Study Site

The study was conducted at the Organization for Tropical Studies' La Selva Biological Station, located in Sarapiquí Province in the humid Atlantic lowlands of Costa Rica (10°26'N, 83°59'W, 41 masl). The climate at La Selva is warm and wet, with mean temperatures of around 25°C and long-term mean annual rainfall of about 4,000 mm but with considerable inter-annual variation; during this study annual total rainfall ranged from 2,900 to 5,300 mm. About 72% of rainfall drains downward through the soil (Bigelow and others 2004). No month has a long-term average rainfall below 100 mm, but there is an annual drier season from January to April.

The 8-ha research site occupied an alluvial terrace at the junction of the rivers Sarapiquí and Puerto Viejo. The soil has developed in multiple layers of andesitic/basaltic alluvium derived from

volcanic parent materials; it is a deep Andisol ( $\gg 4$  m), classified as Eutric Hapludand (Weitz and others 1997), and is high in base cations. Like other allophane-rich soils, it is well drained (sandy loam from 0 to 30 cm) and characterized by a high capacity to stabilize organic matter and retain P and water (Sollins and others 1994; Ewel and Mazzarino 2008). Prior to the start of the research, the soil was sampled intensively using a high density of corings ( $n = 45$ ) and two large (2 m  $\times$  2 m  $\times$  2 m) pits to assess needs for blocking in the design and to fully characterize the profile physically and chemically. This initial sampling confirmed that the study site soil was extremely homogeneous.

Prior to the establishment of the study plots, the site was occupied by an abandoned cacao plantation dominated by woody species characteristic of second-growth forests in the area (for example, genera such as *Cordia*, *Goethalsia*, *Trema*, *Ochroma*, *Cecropia*, *Miconia*). Site preparation consisted of felling and broadcast burning of that vegetation, after which trees were immediately planted.

### Experimental Design

The experimental design was a split-plot, randomized block ( $n = 3$  blocks) in which tree species was the main treatment and stand longevity and diversity (tree plus two monocots) were subtreatments (Figure 1). Each block consisted of three main plots, each planted to one of three tree species. Every main plot comprised four subplots separated by root-barrier cloth to a depth of 1.0 m. The longevity of plants on three of those subplots was manipulated by subjecting each subplot to a particular cutting (without biomass removal) and replanting (same tree species) cycle: a 0.04 ha subplot on which the trees were cut and replanted annually; a 0.12 ha subplot on which trees were cut and replanted every 4 years; and a 0.16 ha subplot on which the trees were not cut (unconstrained longevity). A fourth subplot (0.16 ha) was also uncut but consisted of two more life forms—a palm and a giant, perennial herb—planted additively to the tree species that constituted the matrix of the entire main plot. Thus, the three monocultures of each species provided stand longevity gradients (1 year, 4 years, or unconstrained), and the two systems of unconstrained longevity provided a species-richness gradient (one life form or three).

Tree seedlings (9–12 months old; 20–30 cm tall) were planted in a diamond pattern, with 2.0 m between individuals, resulting in a density of 2,887 trees ha<sup>-1</sup>. The purpose of this high density was to hasten plant interactions and ensure full

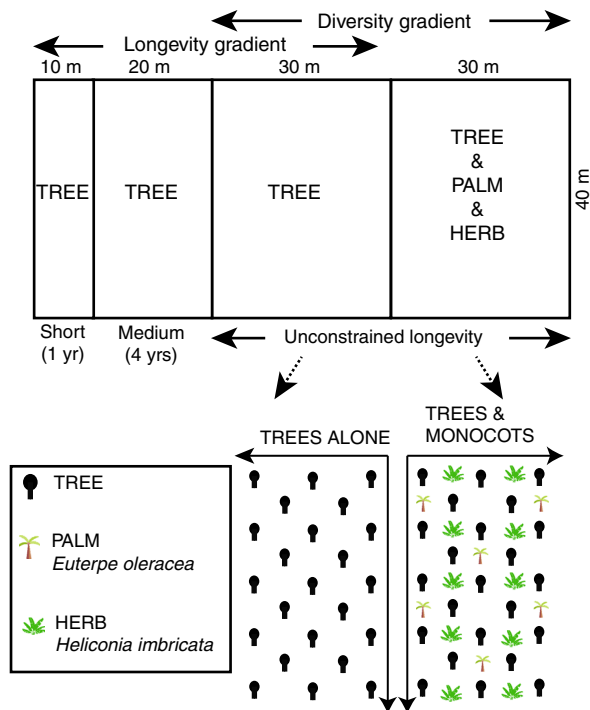


Figure 1. Schematic of plot layout. The design comprised three such blocks for each of three tree species.

utilization of the site's resources. In the three-life-form plots, the palm was planted additively at one-fourth the density of the trees, and the herb at one-half the density of the trees. Crown and root closure occurred within 2 years. To avoid stand stagnation, the plantations of unconstrained longevity were periodically thinned lightly from below. After 11 years, natural mortality and thinning had reduced stocking to 20–33% of the initial planting density, but basal area was high, with averages of 19–26 m<sup>2</sup> ha<sup>-1</sup> among tree species. The plantations of 4-year longevity were lightly thinned once, between ages 2 and 3 years, if they had full crown closure. Biomass cut in thinning was not removed from the site.

## Species

The three tree species (each referred to by genus after first mention) were native and known to be capable of rapid growth on the study-site soil; none of them is symbiotic with N-fixing microorganisms. *Hieronyma alchorneoides* Allemão (Phyllanthaceae) is a massive, long-lived tree of the local rain forest. It is evergreen and in monospecific plantations forms a dense canopy, allowing little light to reach the forest floor. Roots of 11-year-old trees penetrated to depths greater than 3 m. *Cedrela odorata* L. (Meliaceae) is a large tree, dry-season deciduous

after about age 5 years. Its canopy is intermediate in density between those of the other two tree species. The thick roots of *Cedrela* store substantial amounts of starch. *Cordia alliodora* (Ruiz & Pav.) Oken (Boraginaceae) is a tree of secondary forests and has a shorter life span (<100 years) than the other two species. At La Selva it is evergreen in youth but leafless for approximately 1 month during the rainy season once it attains the age of reproduction, about 5–7 years. *Cordia*'s tiered branching pattern creates an open crown that allows substantial light penetration into the understory. *Cordia* roots are finer than those of the other two species, and laterals extend horizontally far beyond the drip line.

None of the tree species produced dense networks of fine roots in the fertile soil of the study site (average root length density 2–4 cm cm<sup>-3</sup>; Ewel and Bigelow 2011), but there were differences, in addition to leaf phenology, among the species that might have been expected to affect soil properties. For example, lignin:N values ranged from about 10–30 for leaves and 16–26 for roots (Russell and others 2004); leaf life spans varied threefold or more among species; and cumulative N and P nutrient-use efficiencies were significantly higher in *Hieronyma* than in *Cedrela* and *Cordia* (Hiremath 2000).

The other two life forms, both monocots, differed considerably in stature but shared the common trait of having large leaf blades subtended vertically, or arching. One monocot was a palm, *Euterpe oleracea* Mart. (Arecaceae), native to Amazonian floodplains and as such the only alien species used in the study. *Euterpe* individuals produce clumps of about 20 shoots and attain heights of approximately 25 m. *Euterpe* develops leaf area as high as 10 m<sup>2</sup> m<sup>-2</sup> of ground, which blocks most light from reaching the understory. The other monocot, *Heliconia imbricata* (Kuntze) Baker (Heliconiaceae), is a banana-like herb with large leaf blades: about 0.3 m wide and 2 m long. *Heliconia* produces multiple monocarpic shoots and, unlike the palm, has a basal meristem that constrains its height to about 6 m due to the mass of foliage subtended by each shoot.

## Stand Development

Various descriptions of the experimental ecosystems have been published (see Haggard and Ewel 1997; Hiremath and others 2002; Ewel and Mazzarino 2008; Ewel and Bigelow 2011 and papers cited therein) and are briefly summarized here. Plant growth was extremely fast; average tree



heights in the stands of 1-year longevity were 2.0 m for *Hieronyma* and about 1.3 m for *Cedrela* and *Cordia*. By the time they were 4 years old, stands of all species were 8–12 m tall and one could traverse them unimpeded by tree crowns. Average aboveground biomass accrual at 4 years was high: *Hieronyma*, 36 Mg ha<sup>-1</sup>; *Cedrela*, 29 Mg ha<sup>-1</sup>; and *Cordia*, 40 Mg ha<sup>-1</sup>. In the tree monocultures of unconstrained longevity at the end of the 11-year study, the three species averaged 27 m tall and 30 cm in diameter at 1.3 m (dbh); stand-level mean leaf area index at that age was *Hieronyma*, 5.2; *Cedrela*, 5.7; and *Cordia*, 3.7.

The diverse stands changed in species dominance over time, and the successional trajectories differed among tree species. In diverse stands containing *Hieronyma*, the tree dominated and *Heliconia* never prospered. *Euterpe* began to grow well when the *Hieronyma*-dominated stands were about 4 years old, and by the end of the study it formed a dense subcanopy layer beneath the taller *Hieronyma*. In the diverse plots containing either of the deciduous tree species, *Cedrela* or *Cordia*, however, the developmental sequence was different. For the first couple of years, the trees were clear dominants, overtopping both *Heliconia* and *Euterpe*. By about age 3 years, however, *Heliconia* was a vigorous component, forming an almost impenetrable layer 2–6 m tall and comprising about 60% of the stand-level leaf area. Soon, however, *Euterpe* began to grow rapidly, overtopping the *Heliconia* (many of which soon died) and leading to stands dominated by two species: tree and palm. *Euterpe* continued to grow vigorously and eventually began to outcompete the trees by a novel mechanism: compression from below of the space available for tree crown development (Ewel and Mazzarino 2008).

## Soil Measurements

Following the initial characterization, soil was sampled annually at four depths that approximated the natural horizons in the profile: 0–10, 10–25, 25–70, and 70–120 cm. In one of the three blocks the deepest sampling extended from 70 to 155 cm in an attempt to capture changes due to roots known to extend to that depth. Each sample consisted of a well-mixed composite of three cores per subplot for each depth. Surface-horizon cores were 10 cm in diameter; deeper cores were 5.7 cm in diameter. Samples were taken annually during the rainy season, in September–October.

Samples were air dried, ground to pass a 2-mm sieve and analyzed for several variables: pH, Ca, magnesium (Mg), potassium (K), sodium (Na),

exchangeable acidity (aluminum (Al) + hydrogen (H)), cation exchange capacity at pH 7, SOC, total N, and Olsen-extractable phosphorus (P). Soil pH in water (pH<sub>water</sub>) and in 1 M KCl (pH<sub>KCl</sub>) was measured using a soil-to-solution ratio of 1:2.5. Divalent cations (Ca and Mg) and exchangeable acidity (Al + H) were extracted with 1 M KCl, and Na was extracted with NH<sub>4</sub>OAc at pH 7.0. For K and P, the Olsen solution (NaHCO<sub>3</sub> at pH 8.5) modified by addition of 0.01 M disodium ethylenediaminetetraacetic acid (as a chelating agent) and 0.05% Superfloc<sup>R</sup> (as a filtrate aid) was employed (method of Díaz-Romeau and Hunter, described in Bertsch 1995). This method has long been used in Central America as a measure of extractable P on volcanic soils of near-neutral or slightly acid pH such as those at the study site. Throughout this paper the symbol P refers to Olsen-extracted phosphorus.

Determinations were made by atomic absorption spectrometry (Ca, Mg, Na, K), titration (Al + H), the ascorbic acid–molybdate method (P), or the 1 M NH<sub>4</sub>OAc method (CEC at pH 7). Effective cation exchange capacity (CEC<sub>e</sub>) was calculated as the sum of extractable cations plus exchangeable acidity. SOC was determined by wet digestion (Walkley-Black) and total N using an elemental analyzer.

## Organic Matter Returns

The amount of organic matter returned to the soil consisted of two components: litterfall and cut biomass. Litter was collected biweekly from three screen-bottomed litter traps, 0.5 by 1.73 m, in each plot. The contents of the three traps were pooled to yield a single sample for each replication, after which litter was separated by type (leaf, branch, reproductive parts) and species, then oven-dried to constant weight at 70°C and weighed.

Biomass returns to the soil surface from cuttings were estimated from annual measurements of heights and diameters of all trees. More than 1,000 individuals were harvested for allometric determinations during the course of the experiments, and the resulting allometric equations (Cole and Ewel 2006) were used to convert inventory data of cut trees to biomass.

## Statistical Analyses

Repeated measures analysis was conducted using the MIXED procedure (SAS 2008), with blocks as a random effect, tree species as a whole-plot fixed effect, and longevity and diversity as subplot fixed effects. When the dataset had entries for each year



of the study period, time intervals were coded as continuous, and an autoregressive covariance structure was implemented for the repeated measures; when there was a data gap of at least 1 year, a spatial power covariance structure was used with time as a location variable.

Selection of the best-fit linear model for each variable at each soil depth was a multi-step process. First, we examined the fit of the data to a model that contained all interaction terms among the main variables: treatment (longevity or diversity), tree species, and time. We then examined a model that included only main effects and any significant interactions ( $P = 0.05$ ). To determine which of the two models best fit the data, we compared them using a Likelihood Ratio Test (LRT), Akaike Information Criterion (AIC), and Bayesian Information Criterion (BIC), following Bolker (2008). Time was a significant component in all best-fit models. In cases where the best-fit model indicated a significant interaction of time with treatment (longevity, diversity, or tree species), the process of best model selection stopped at this point; when time was not part of a significant interaction with treatment or tree species, we proceeded to the next step.

Next, we visually examined the best-fit model by graphing it with time ( $t$ ) included as a first-, second-, or third-order polynomial, that is,  $a + bt$ ,  $a + bt + ct^2$ , or  $a + bt + ct^2 + dt^3$ . When two or three polynomial models appeared to be feasible fits we compared them quantitatively, again using the LRT, AIC, and BIC. If polynomials did not differ quantitatively we selected the lower-order model.

In the graphs shown in “Results” section, values plotted represent individual blocks. Different symbols are used only where there were significant differences among longevity, levels of diversity, or tree species as indicated in the figure legends; open circles represent treatments that did not differ significantly. To detect significant differences we conducted multiple pairwise comparison tests among least square means for each main variable in the model using a Tukey–Kramer correction and  $\alpha = 0.05$ . Where differences were significant, the relevant groups are represented by different symbols and lines, each portrayed using the most appropriate model determined by the statistical analysis. Lines are bounded by 95% confidence bands, and their convergence and divergence along the time trajectory indicates when treatments differed. Where ranges are given in the text they are the ranges in annual means from Table S1 or, when reference is made to temporal changes, the upper and lower bounds of the confidence bands on the graphs.

## RESULTS

Taken together, all the properties measured confirm the high fertility of the study-site soil, and its strong resistance to change over time. Significant changes in most soil variables in response to treatments were constrained to the surficial 10 cm, so results presented here focus on that depth. Magnesium, K, and SOC were significantly affected by treatments to a depth of 25 cm, and SOC was significantly affected by one treatment (slightly lower under unconstrained monocultures) to a depth of 70 cm. Only P showed a significant treatment effect at depth greater than 70 cm, where concentrations were significantly lower under *Hieronyma* than under *Cordia* or *Cedrela* (least square means over all 11 years of 9.1, 9.6, and 10.2 mg kg<sup>-1</sup>). Ranges of annual means for all variables and all depths are summarized in Table S1.

There were no significant interactions between tree species identity and life-form diversity, but two nutrients, Mg and P, had significant interactions between tree species and longevity. In the surface 10 cm there was only one significant interaction: Under *Hieronyma* and *Cordia* (but not *Cedrela*), Mg was significantly lower in stands of 1-year longevity than in stands of greater longevity. Other significant interactions between tree species and longevity were at depths 10–25 cm (lower Mg only under *Cordia*, 1-year longevity; higher P under *Hieronyma* and *Cedrela* stands of unconstrained longevity and under *Cordia* stands of 4-year longevity) and 25–70 cm (higher P under *Cedrela*, 1-year longevity and *Cordia*, 4-year longevity).

Soil variables followed different trajectories following the nutrient release that accompanied site preparation and subsequent leaching and plant uptake. Several variables decreased significantly over time in the surficial 10 cm: pH<sub>KCl</sub>, Mg, K, SOC, and N. Others—pH<sub>water</sub>, exchangeable acidity, Ca, and CEC<sub>e</sub>—increased then declined and stabilized during the last years. Concentrations of Na remained about 18 cmol<sub>c</sub> kg<sup>-1</sup> throughout the study. Phosphorus differed from the other variables; it was highly variable and increased in some treatments during the last years.

Of the 12 soil variables analyzed, 10 differed in response to stand longevity by the end of the study (only N and P did not); four responded to levels of diversity (K, Na, P, and N); and five responded to tree species identity (Mg, CEC, SOC, N, and P) (Table 1). When data for all 11 years were included in the statistical analyses, 6 of the 12 variables—pH<sub>water</sub>, Ca, Mg, K, SOC, and P—differed

**Table 1.** Soil Variables at End of Study, 0–10 cm

Variable	Stand longevity			Diversity		Tree species identity		
	1 year	4 years	Unconstrained	One tree species	Three life forms	<i>Hieronyma</i>	<i>Cedrela</i>	<i>Cordia</i>
pH <sub>water</sub>	<b>6.20<sup>a</sup></b>	<b>6.40<sup>b</sup></b>	<b>6.38<sup>b</sup></b>	6.38 <sup>d</sup>	6.36 <sup>d</sup>	6.27 <sup>f</sup>	6.36 <sup>f</sup>	6.37 <sup>f</sup>
pH <sub>KCl</sub>	<b>4.58<sup>a</sup></b>	<b>4.86<sup>b</sup></b>	<b>4.79<sup>b</sup></b>	4.79 <sup>d</sup>	4.86 <sup>d</sup>	4.76 <sup>f</sup>	4.73 <sup>f</sup>	4.82 <sup>f</sup>
Ca (cmol <sub>c</sub> kg <sup>-1</sup> )	<b>9.10<sup>a</sup></b>	<b>10.21<sup>b</sup></b>	9.90 <sup>a,b</sup>	9.90 <sup>d</sup>	10.66 <sup>d</sup>	9.98 <sup>f</sup>	10.41 <sup>f</sup>	9.51 <sup>f</sup>
Mg (cmol <sub>c</sub> kg <sup>-1</sup> )	<b>2.00<sup>a</sup></b>	<b>2.44<sup>b</sup></b>	<b>2.37<sup>b</sup></b>	2.37 <sup>d</sup>	2.43 <sup>d</sup>	<b>2.59<sup>h</sup></b>	<b>2.04<sup>f</sup></b>	<b>2.29<sup>g</sup></b>
K (cmol <sub>c</sub> kg <sup>-1</sup> )	<b>0.73<sup>a</sup></b>	<b>1.02<sup>b</sup></b>	<b>0.80<sup>a</sup></b>	<b>0.80<sup>e</sup></b>	<b>0.65<sup>d</sup></b>	0.85 <sup>f</sup>	0.80 <sup>f</sup>	0.76 <sup>f</sup>
Na (cmol <sub>c</sub> kg <sup>-1</sup> )	<b>0.19<sup>b</sup></b>	<b>0.14<sup>a</sup></b>	<b>0.17<sup>b</sup></b>	<b>0.17<sup>d</sup></b>	<b>0.21<sup>e</sup></b>	0.18 <sup>f</sup>	0.18 <sup>f</sup>	0.18 <sup>f</sup>
ExchAcid	<b>0.29<sup>b</sup></b>	<b>0.20<sup>a</sup></b>	<b>0.20<sup>a</sup></b>	0.20 <sup>d</sup>	0.22 <sup>d</sup>	0.21 <sup>f</sup>	0.21 <sup>f</sup>	0.26 <sup>f</sup>
CECe (cmol <sub>c</sub> kg <sup>-1</sup> )	<b>12.31<sup>a</sup></b>	<b>14.00<sup>b</sup></b>	13.22 <sup>ab</sup>	13.21 <sup>d</sup>	14.00 <sup>d</sup>	13.65 <sup>f</sup>	13.50 <sup>f</sup>	13.01 <sup>f</sup>
CEC (cmol <sub>c</sub> kg <sup>-1</sup> )	<b>34.3<sup>a</sup></b>	<b>35.8<sup>b</sup></b>	34.5 <sup>ab</sup>	34.5 <sup>d</sup>	35.8 <sup>d</sup>	<b>36.2<sup>g</sup></b>	35.2 <sup>fg</sup>	<b>33.8<sup>f</sup></b>
SOC (%)	<b>2.33<sup>a</sup></b>	<b>2.70<sup>b</sup></b>	2.58 <sup>ab</sup>	2.58 <sup>d</sup>	2.79 <sup>d</sup>	<b>2.88<sup>g</sup></b>	2.46 <sup>fg</sup>	<b>2.45<sup>f</sup></b>
N (%)	0.25 <sup>a</sup>	0.26 <sup>a</sup>	0.24 <sup>a</sup>	<b>0.24<sup>d</sup></b>	<b>0.29<sup>e</sup></b>	<b>0.24<sup>f</sup></b>	0.25 <sup>gf</sup>	<b>0.28<sup>g</sup></b>
P (mg kg <sup>-1</sup> )	16 <sup>a</sup>	18 <sup>a</sup>	15 <sup>a</sup>	<b>15<sup>e</sup></b>	<b>11<sup>d</sup></b>	<b>17<sup>g</sup></b>	<b>16<sup>g</sup></b>	<b>12<sup>f</sup></b>

Values are least square means of measurements at stand ages 9, 10, and 11 years. Statistically significant differences ( $P \leq 0.05$ ) are shown in bold; values within major groups (longevity, diversity, species) that share common superscript letters do not differ significantly. Least square means are shown because they account for potential imbalances due to occasional missing values and for variation due to other variables in the model.

significantly among treatments (Table S2), and these are the variables whose time courses are depicted in Figures 2, 3, and 4.

In almost all cases where longevity exerted a significant effect on a soil variable, it was the stands of intermediate longevity—4 years—that resulted in higher values (Table 1; Figure 2). Among the six variables in Figure 2, for example, there were two (pH<sub>water</sub> and Mg) for which the higher values of 4-year longevity stands did not differ significantly from stands of unconstrained longevity, but in the other four cases (Ca, K, SOC, and P) values in stands of 4-year longevity were significantly higher than those in stands of either shorter or greater longevity.

In contrast with the high values under stands of 4-year longevity, stands of 1-year longevity had the lowest values for five of the six variables in Figure 2. At the end of the study, those shortest longevity stands also had the lowest values for pH<sub>KCl</sub>, CECe, and CEC, and the highest value for exchangeable acidity (Table 1).

Stands of three life forms had higher concentrations of Ca and SOC than did equal-aged monocultures (Figure 3A, C), although differences were not significant during the last few years of the study. In contrast, K was highest in monocultures of unconstrained longevity, particularly during the middle of the study period, years 4–7 (Figure 3B).

The decline of K over time was more pronounced in both treatments of unconstrained longevity—monoculture and diverse—more so than in stands of 4-year longevity (compare Figures 2D and

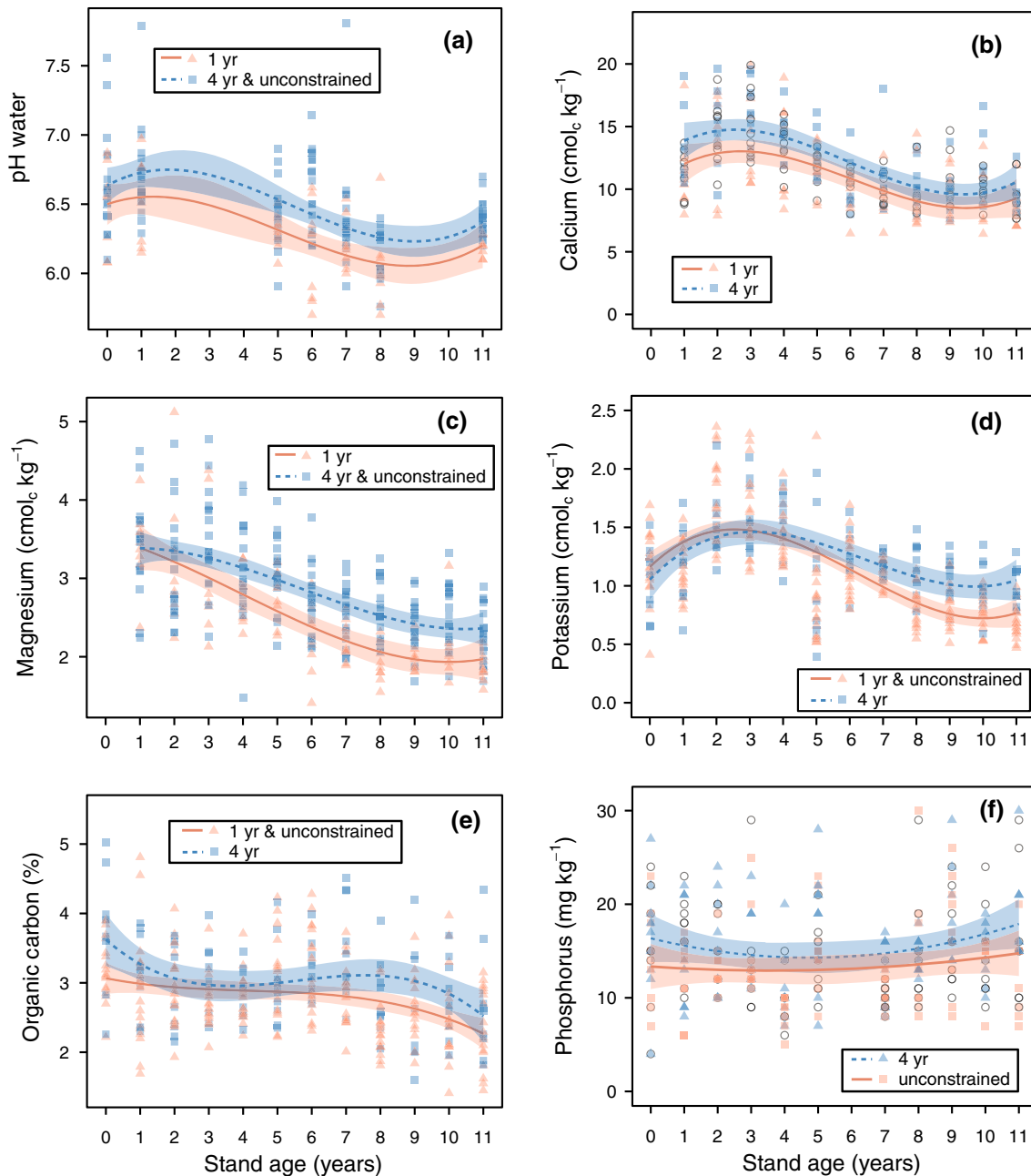
3B). The decline of K in stands of unconstrained longevity amounted to about 0.5 cmol<sub>c</sub> kg<sup>-1</sup>, or more than a third of the average initial concentration.

When considering data from all years, tree species significantly affected only Mg and P (Figure 4), although by the end of the study significant differences had developed among tree species for CEC, SOC, and N as well (Table 1). Concentrations of Mg declined under all three tree species, but most markedly under *Cedrela*, where they declined from about 3.5 to 2.0 cmol<sub>c</sub> kg<sup>-1</sup> over 11 years (Figure 4A).

The temporal dynamics of P in *Hieronyma* stands were distinctive: a decline during the first 4 or 5 years, followed by an upturn during the last five (Figure 4B). *Cordia* soil also declined in P during the first few years, but it then leveled off. Thus, by the end of the study P under *Hieronyma* had returned to its initial concentrations and was significantly higher than concentrations under *Cordia*.

Values of three variables—CEC, P, and N—were significantly different under *Cordia* at the end of the study (Table 1). The most striking difference was lower P, which was 4–5 mg kg<sup>-1</sup> lower under *Cordia* than under the other two tree species. The opposite happened with N, which by the end of the study was significantly higher under *Cordia* than under *Hieronyma*, although the values differed by only a modest amount (mean soil concentrations of 0.28 and 0.24%, respectively).

Cumulative deposits of organic matter on the soil surface differed by large amounts among stands of



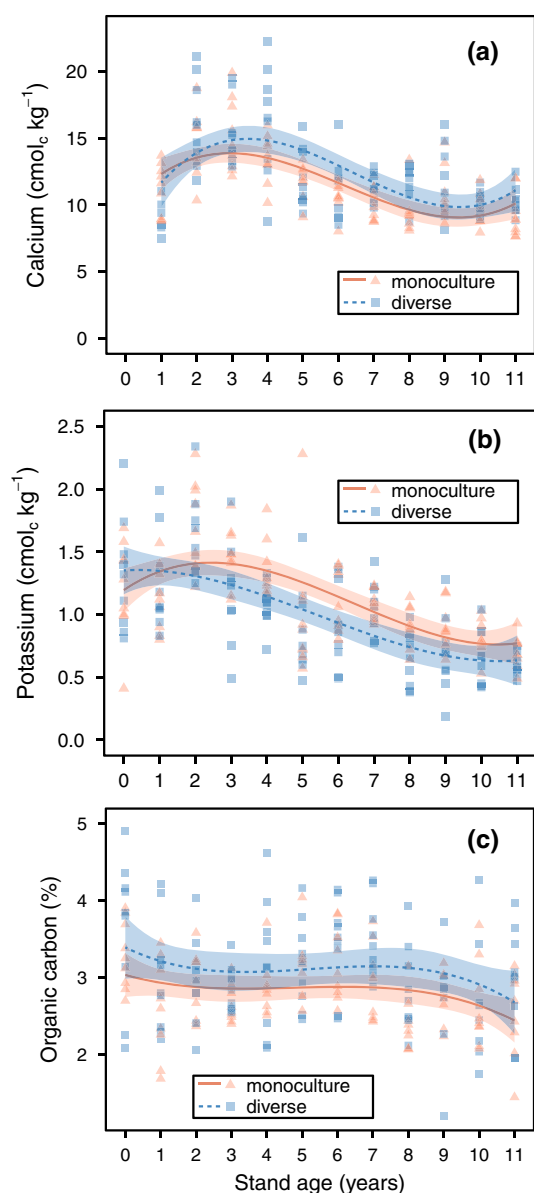
**Figure 2.** Effects of stand longevity on six soil properties, 0–10 cm. *Lines* are model-predicted values, and *shaded-band width* is scaled to 95% confidence limits. Density of symbol shading increases with number of overlain data points; *open circles* represent treatments that did not differ significantly.

different longevity (range 24–120 Mg ha<sup>-1</sup>), with stands of 4-year longevity returning substantially more organic matter than stands of either shorter or longer life span (Table 2). Also, the tree species differed in their organic-matter returns: the fast-growing, evergreen *Hieronyma* returned more organic matter than the other two species. Diversity, however, made little difference in total organic matter returns: monocultures and stands of three life forms returned about the same amount.

## DISCUSSION

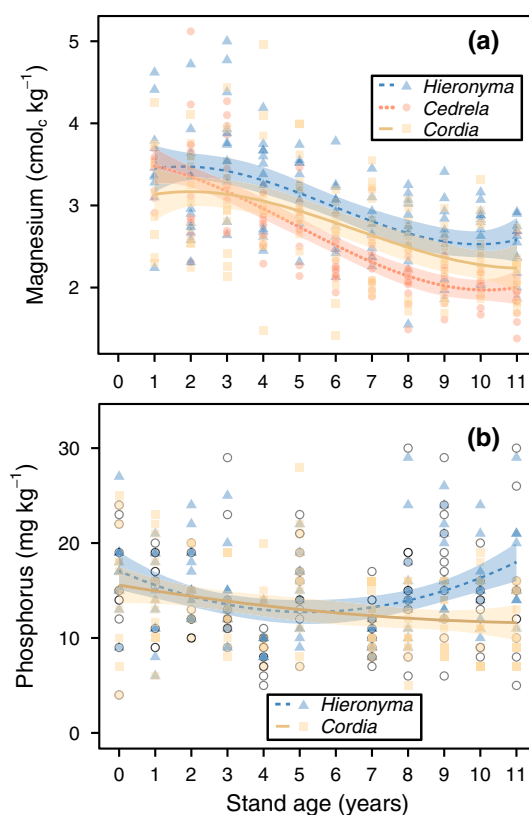
Soil nutrient concentrations reflect the sum of inputs and outputs. At our site, the principal input processes were release from organic matter (decomposition and leaching from tissues) and weathering of primary minerals; the principal outputs were deep infiltration and plant uptake. Other candidate processes—runoff, biomass removal, atmospheric deposition (Eklund and others





**Figure 3.** Effects of life-form diversity on three soil properties, 0–10 cm. *Lines* are model-predicted values, and *shaded-band width* is scaled to 95% confidence limits. Density of symbol shading increases with number of overlain data points.

1997), N-fixation—were known, or can safely be assumed, to be low. Following high concentrations that resulted from site preparation at the start of the experiments, base cations, especially Ca and Mg, declined in all plots during the first 8 years of the study, after which concentrations leveled off or began to increase. Elsewhere a prolonged decrease of exchangeable Ca after afforestation has been attributed to leaching losses (for example, Markewitz and others 1998) or to sequestration in vegetation (for example, Jobbágy and Jackson 2003).



**Figure 4.** Effects of tree species identity on two soil properties, 0–10 cm. *Lines* are model-predicted values, and *shaded-band width* is scaled to 95 per cent confidence limits. Density of symbol shading increases with number of overlain data points; *open circles* represent treatments that did not differ significantly.

Both mechanisms were important at our site, given that precipitation was 2–3 times greater than evapotranspiration (Bigelow and others 2004) and plant growth was very fast.

Values of most variables still indicated high soil fertility after 11 years of exposure to the treatments: near-neutral to slightly acid pH, high concentrations of base cations (especially Ca), extremely low concentrations of acid cations (Al + H), high CEC and  $\text{CEC}_e$ , and relatively high concentrations of P and SOC. This generalization regarding high fertility at the study's end held even for the short-longevity monocultures, which incurred the greatest losses of nutrients and SOC. Young allophanic Andisols are characterized by an abundance of amorphous clays (for example, allophane, imogolite, ferrihydrite), which can hinder organic matter decomposition through the formation of highly stable organic-mineral complexes and physical protection of organic matter in microaggregates (Torn and others 1997; Nanzyo 2002; Dahlgren and others 2004). In addition, the high

**Table 2.** Cumulative Organic Matter Returns to Soil Surface from Litterfall and Cuttings Over 11 years ( $\text{Mg ha}^{-1}$ )

Longevity	1 year	4 years	Unconstrained	Unconstrained
Diversity	One tree species	One tree species	One tree species	Three life forms
<i>Hieronyma</i>	32	144	121	116
<i>Cedrela</i>	20	107	70	77
<i>Cordia</i>	22	108	67	72
Mean	24 (88)	120 (62)	86 (0)	88 (0)

Values are means of three blocks. Parenthetical values are mean percentage of organic matter returns accounted for by end-of-cycle cutting.

Ca concentrations and relatively high P concentrations at the study site suggest the presence of Ca-rich volcanic glass and apatite (Dahlgren and others 2004). The soil proved remarkably resistant to loss of fertility, a characteristic of young allophanic Andisols that has been exploited by farmers for centuries.

### Effects of Stand Longevity

Fertility declined most in stands of shortest longevity (1 year). Leaching of divalent cations (Bigelow and others 2004) led to mild acidification (0.3 pH units) and a slight increase in exchangeable acidity from 0.16 to 0.29 in those short-lived, small-stature plant communities over the 11-year study period. Because extensive root systems never developed under the 1-year cutting regime, there was little opportunity for nutrient uptake and storage in plant tissues, and eventual return to the soil surface as litter.

The fertility decline observed in stands of 1-year longevity was expected, and we anticipated that changes in soil properties might continue to track the longevity gradient sequentially: 1 year > 4 years > 11 years. But that was not the case. Instead, the responses were more often parabolic or asymptotic. Values of soil properties in stands of 4-year longevity were generally higher than those in stands of 1-year longevity, and higher than, or not different from, values in stands of unconstrained longevity (see Tables 1, S2). A clear example was the response of SOC, which was lowest in the shortest and longest lived stands, and highest in stands of 4-year longevity; this confirms, over an 11-year period, the findings of a shorter-term study at the site mid-way through the experiment (Russell and others 2004).

The higher soil fertility in stands of intermediate-longevity almost certainly reflects large pulses of organic matter onto the soil surface every 4 years when the trees were cut: The cumulative return of organic matter to the soil surface (litterfall plus cut

biomass) in stands of 4-year longevity was about 1.4 times higher than litterfall in stands of unconstrained longevity and five times higher than soil inputs from litterfall plus cut biomass in stands of 1-year longevity (Table 2). Hurricanes, in comparison, typically produce a pulse of organic debris that is less than twice the annual litterfall (Lodge and others 1994; Herbert and others 1999; Ostertag and others 2003). Furthermore, freshly cut biomass contains higher concentrations of N, P, and K than do the senescent leaves and twigs captured by litter traps. In addition to the fertilization effect of nutrient-rich organic matter on the soil surface, leachates from the deposited organic matter can block phosphate sorption sites (Schreeg and others 2012), which may have led to the higher concentrations of P we observed in stands of 4-year longevity. Working in forested plots on an Oxisol to which fresh litter (containing a cumulative total of  $18 \text{ kg ha}^{-1}$  of P) was added for 3 years, Vincent and others (2010) observed a 103% increase in Bray-extractable P and a 16% increase in organic P in the surficial 2 cm. On the nutrient-rich soil of our study site, where growth was exceptionally rapid and biomass was not removed, monocultures of intermediate turnover (4 years) proved capable of sustaining soil fertility, but systems that turned over annually did not. It is clear that the return of organic matter is a key process in sustaining P cycles on tropical soils.

Our findings further indicate that the return of organic matter to the soil surface is important to other soil properties, in addition to P. Given equal harvest frequencies, plants that return substantial amounts of biomass to the soil surface (that is, crops of low harvest index) are more likely to sustain soil fertility than plants that return little biomass. Proponents of short-rotation woody crops as energy sources (for example, Jug and others 1999; Volk and others 2004) report little or no decline in soil fertility, but it is difficult to compare their findings with ours: They typically fertilize shortly after planting, remove biomass from the

site, and replace exported nutrients, whereas we left the biomass on the site and added no fertilizer. To some extent, however, leaving biomass on the soil compensates for biomass removal followed by fertilization. What is clear, both from our study and from very long-term agricultural studies (Soil Quality Institute 2001), is that fast-turnover monocultures do not sustain soil organic matter.

## Effects of Diversity

One of the most striking effects of added life forms was a reduction in K in the diverse-plot soil compared with the monoculture. Nevertheless, this decline was almost certainly a species effect, not an effect of diversity per se. The lower values of K in the diverse system were due to exceptionally high rates of K uptake by *Heliconia*, as illustrated by the following calculation. Concentrations of K in *Heliconia* leaves and stems were exceptionally high, averaging 2.5 and 5.1%, respectively, and above-ground biomass of *Heliconia* averaged 8.4 Mg ha<sup>-1</sup> (J. Ewel, unpublished data). These values yield a standing crop of K in *Heliconia* leaves and stems of 360 kg ha<sup>-1</sup>, which is substantially more than the average decline of K in diverse-system soil, which was about 0.25 cmol<sub>c</sub> kg<sup>-1</sup> (Figure 3B), or 83 kg ha<sup>-1</sup>. Similar depletion of soil K is known from plantations of banana (*Musa* spp.), a phylogenetic cousin of *Heliconia* (Lahav 1995). The singular role of *Heliconia*, our smallest stature species, demonstrates that dominance in biomass does not necessarily go hand-in-hand with dominance in biogeochemical cycling.

The greater retention of Ca in the diverse systems was likely caused by the palm, *Euterpe*. Roots of *Euterpe* extended deeper into the soil and were more concentrated at depth than those of the eudicots (Ewel and Mazzarino 2008), making it likely that palm roots could have retrieved Ca from greater depth than roots in the eudicot monocultures. Furthermore, the leaf area of the palm was extremely high, which led to increased evapotranspiration (Ewel and Bigelow 2011); greater evapotranspiration, in turn, would have reduced leaching losses and the dissolution of Ca compounds.

Concentrations of SOC were higher in the diverse systems than in monocultures. The amount of organic matter returned to the soil surface was about the same in monocultures and diverse communities (means of 86 vs. 88 Mg ha<sup>-1</sup>), so this does not account for the difference. A more likely contributor to SOC was fine roots. Russell and others (2004) reported more SOC, primarily as a

constituent of light particulate organic matter, under diverse plots containing *Cedrela* or *Cordia* than under their corresponding monocultures and attributed the difference to fine-root amounts and chemistry (for example, C:N). Others have reported a positive effect of diversity on SOC, and increased root biomass in more diverse communities has been identified as the mechanism (Fornara and Tilman 2008).

By the end of the study, concentrations of P were substantially lower, about 27% less, in the diverse systems than in monocultures (Table 1). This reduction in soil P in the diverse systems was almost certainly caused by plant uptake. The combination of tree plus monocots had higher net primary productivity than their corresponding monocultures (Ewel and Mazzarino 2008), and substantial P was required to drive that production.

For the most part, however, soil properties did not differ greatly in stands of unconstrained longevity whether they contained one life form or three. The lack of positive responses of soil nutrients to biodiversity that we observed is contrary to the expectations of 80 polled experts, a majority of who scored biodiversity as a positive influence on soil fertility (Quijas and others 2012). Although we agree that greater plant species richness is likely to augment SOC, which is linked to soil tilth and the storage and availability of nutrients, we suggest that greater plant species richness is just as likely to reduce soil concentrations of pedogenic nutrients—Ca, Mg, K, P—due to preferential uptake by particular species or as a consequence of biomass accrual. More diversity may help retain nutrients in the ecosystem, but not necessarily in the soil.

## Species Effects

Despite some interspecific differences in functional traits, the combination of shared traits among the species and high inherent fertility of a soil well buffered against change apparently mitigated most influences of tree species. Nevertheless, there were some differences attributable to tree species identity, and for the most part these effects are accounted for by litterfall. For example, *Hieronyma* produced the most litter, and its soil had higher Mg, extractable P, CEC, and SOC than soil under the other two tree species.

Soil Mg concentrations declined under all three tree species, but significantly more so under *Cedrela* than under the other two species. *Cedrela* Mg demand is lower than that of the other two species; mean annual leaf concentrations ranged from 0.41 to 0.88% in *Cordia*, 0.14 to 0.33% in *Hieronyma*,



and 0.14 to 0.19% in *Cedrela* (J. Ewel, unpublished data). Low uptake, coupled with comparatively modest litter return, precluded surface-soil enrichment of Mg under *Cedrela*. Limited inputs to the surface, coupled with leaching losses that did not differ significantly among species (Ewel and Bigelow 2011), resulted in the observed decline in Mg under *Cedrela*. The higher Mg demand of *Hieronyma* and *Cordia* was probably met through uptake by deep roots as documented for Ca by Dijkstra and Smits (2002).

There were interesting differences concerning N and P limitation among the species. *Hieronyma* had the lowest foliar N:P (~12–13), whereas *Cordia* had the highest (~16–18) (Ewel and Mazzarino 2008). *Cordia* had high concentrations of foliar P (somewhat higher than the other two species), but its foliar concentrations of N were extremely high, above 3% (Ewel and Mazzarino 2008), and rates of soil N mineralization under *Cordia* were higher than under *Hieronyma* (Ewel 2006). Thus, the P limitation of *Cordia* (inferred from its high foliar N:P) was probably due more to its unusually high uptake of N than to scarce soil P. Limitation of *Hieronyma* growth by N and *Cordia* growth by P is further reflected in the soil concentrations: lowest N values under *Hieronyma*, lowest P values under *Cordia*. But considering that the two species were on the same soil at the start of the experiment, how did these differences develop? Different mechanisms seem to have been involved. Soil under *Hieronyma* had significantly lower N mineralization rates than the other tree species (Ewel 2006), which would account for limited capacity to supply N. Furthermore, concentrations of P under *Hieronyma* (and to a lesser extent under *Cedrela*) were substantially higher during the last 3 years of the study than under *Cordia* (Table 1).

There are two plausible explanations for the higher concentrations of surface-soil P under *Hieronyma*. One of these is deep pumping, whereby roots take up nutrients (P in this case) from deep in the profile, which are later deposited on the soil surface in litterfall. Our evidence for this hypothesis is the significantly lower concentrations of P at soil depth greater than 70 cm under *Hieronyma* than under *Cordia* or *Cedrela*. A second possible explanation derives from the observation that increases in soil P were synchronous with a period of pronounced leaching loss of Ca under *Hieronyma*, which Ewel and Bigelow (2011) speculated might have been facilitated by acidic organic root exudates. Organic acids such as citrate and oxalate can form chelated compounds with Ca from apatite, resulting in the rapid release of P into the liquid

phase (Nakamaru and others 2000a, b). And even though apatite represents less than 0.3% of fresh volcanic materials, its weathering controls P availability in young Andisols (Dahlgren and others 2004). Is enhanced mineralization of apatite a quantitatively feasible explanation for the observed P enrichment? Yes: 3 g kg<sup>-1</sup> of apatite ((PO<sub>4</sub>)<sub>3</sub>Ca<sub>5</sub>OH) contains 93 mg kg<sup>-1</sup> of P, so release of the observed increase of 5 mg kg<sup>-1</sup> of P would have required weathering of only 0.027 g of apatite, or less than 1% of the initial amount.

## Temporal Trends

Overlying changes in soil properties induced by longevity, diversity, and species are temporal trends that can provide insights into the processes and mechanisms involved. Because of its broad importance to many variables that influence fertility, it is useful to focus on SOC. Although there were differences among treatments, SOC declined in all plots, even those that were never cut, despite their high rates of litter production. This phenomenon of sustained SOC decline following site conversion to plantations, despite high organic matter returns to the soil, is apparent in other tropical data (Sanchez and others 1985). The study most analogous to our treatments involved 3 years of litter addition to a forested Oxisol (Sayer and others 2011). Using a combination of isotopic signals and measurements of respiration, they were able to attribute the observed decline of SOC to a priming effect, whereby the breakdown of normally resistant organic matter is stimulated by the addition of easily decomposed organic matter (Kuzakov and others 2000), either roots (for example, Dijkstra and Cheng 2007) or litterfall (for example, Crow and others 2009).

The decrease in SOC was accompanied by a substantial loss of total N. Average N concentrations across plots of all three longevities declined over 11 years by 0.03, 0.04, 0.01, and 0.00% at depths 1–4, respectively, which translates to an average annual rate of 105 kg ha<sup>-1</sup>. This was 1.7 times larger than the annual NO<sub>3</sub><sup>-</sup>-N leaching loss from stands of 1-year longevity (62 kg ha<sup>-1</sup>), four times larger than leaching losses from stands of 4-year longevity (26 kg ha<sup>-1</sup>), and about ten times larger than the amount leached from stands of unconstrained longevity (7–13 kg ha<sup>-1</sup>) (Bigelow and others 2004; Ewel and Bigelow 2011). The discrepancy between decline in total N and N leaching losses increased with longevity, indicating that sequestration of N in biomass likely accounts for much of the difference. Another potential loss

pathway is denitrification. Laboratory incubations of study-site soil indicated that the potential for substantial nitrous oxide flux to the atmosphere is high if redox declines (Silver and others 2005) and, even though the soil was well drained, the topography was flat and water occasionally ponded on the surface.

In contrast to our findings on SOC, Russell and others (2007) found that SOC increased over 15 years under four of six tree species (including *Hieronyma*) in plantations on a nearby Oxisol that had previously been occupied by pasture for 30 years. Like us, however, they found that N decreased (Russell and Raich 2012). Based on stable C isotope concentrations in the soil, they proposed that the trees may have stimulated the decomposition of old soil organic matter through a priming effect, leading to an increase in soluble forms of N while having less effect on current organic matter inputs from the tree plantations. In our case, the previous vegetation was an abandoned, tree-invaded cacao plantation that was felled and burned before the experiment was installed; this might have contributed to an initial increase of SOC due to incomplete combustion, root disintegration, and charred-fragment incorporation (Ewel and others 1991). Another possible mechanism, derived by Paul and others (2002) from a synthesis of published reports on tree plantations, is that decreases in post-planting SOC reflect former land use, and that more time is needed to reach a new steady-state between residue inputs and decomposition. Considering the fate of old soil organic matter revealed by Russell and Raich (2012), we cannot discount this possible mechanism.

## CONCLUSIONS

Plant longevity exerts substantial influence on soil fertility, yet it is a neglected factor in the study of ecosystem functioning despite its widespread presence in natural and managed ecosystems. The key process in determining plant longevity effects on soil is nutrient sequestration in plant biomass and its return to soil surface. In addition to its soil-enriching properties, however, the deposition of fresh biomass can also stimulate declines in SOC, which has potential long-term consequences for soil fertility and release of otherwise recalcitrant C to the atmosphere. Study of the effects of plant-community longevity on soil properties across a range of climates, soils, and community types is clearly warranted.

Compared with the effects of plant longevity, effects attributable to life-form diversity and species

identity are relatively modest. Even when a mixture of species results in an effect, the cause may be linked to a single species and is not necessarily an outcome of diversity, as shown by our *Heliconia*-K findings. Tree species identity does affect soil properties, and we documented several instances of this: P depletion by *Cordia*; loss of Mg under *Cedrela*; and lowered rates of N availability but more P under *Hieronyma*. Those differences were probably caused by differences in nutrient demand, by N and P stoichiometry, by plant-tissue traits that influence rates of mineralization, and perhaps by deep pumping and organic acid exudation that accelerates apatite weathering.

Repeated sampling over time is advantageous in understanding changes in soil-plant interactions as species grow, exploit larger volumes of soil, and wax or wane in dominance. In our study, for example, measurements only at beginning and end would have led to the erroneous conclusion that cation depletion was inexorable, when in fact losses tapered off midway through the study and remained relatively stable thereafter. Two-point datasets do not reveal the full story.

Young allophanic Andisols are extremely well buffered against change, even when subjected to treatments as different as those we imposed, ranging from tall mixed-species stands to monocultures clear-cut annually. It is little wonder that these are among the most productive, intensively used, and sustainable agricultural soils in the world.

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**Table S1** Ranges of Annual Means<sup>a</sup> of Soil Properties

<b>Longevity</b>	<b>Life Forms</b>	<b>Depth</b> (cm)	<b>pH<sub>water</sub></b>	<b>pH<sub>KCl</sub></b>	<b>Ca</b> (cmol <sub>c</sub> kg <sup>-1</sup> )	<b>Mg</b> (cmol <sub>c</sub> kg <sup>-1</sup> )	<b>K</b> (cmol <sub>c</sub> kg <sup>-1</sup> )	<b>Na</b> (cmol <sub>c</sub> kg <sup>-1</sup> )
1 Year	tree	0-10	6.03-6.57	4.49-5.37	8.43-13.85	1.86-3.40	0.70-1.79	0.16-0.21
		10-25	6.27-6.64	4.69-5.08	7.93-10.96	1.85-2.72	0.77-1.54	0.19-0.26
		25-70	6.44-6.86	4.71-5.07	7.52-9.86	1.93-2.46	0.59-1.26	0.28-0.35
		70-120 <sup>b</sup>	6.59-7.01	4.79-5.20	7.20-11.13	1.90-2.52	0.39-1.25	0.31-0.39
4 Years	tree	0-10	6.07-6.78	4.78-5.62	9.40-16.32	2.30-3.54	0.98-1.60	0.11-0.20
		10-25	6.38-6.79	4.74-5.18	7.36-12.05	1.95-2.76	0.86-1.44	0.14-0.26
		25-70	6.50-6.87	4.62-5.33	7.63-10.24	1.86-2.52	0.48-1.31	0.31-0.32
		70-120 <sup>b</sup>	6.53-7.09	4.73-5.30	7.17-10.40	1.88-2.47	0.37-1.38	0.31-0.38
unconstrained	tree	0-10	6.18-6.65	4.71-5.28	9.20-15.19	2.23-3.45	0.70-1.70	0.14-0.21
		10-25	6.31-6.75	4.69-5.04	7.37-11.75	2.00-2.68	0.81-1.68	0.16-0.26
		25-70	6.41-6.85	4.58-4.97	7.42-10.78	1.86-2.22	0.71-1.28	0.32-0.37
		70-120 <sup>b</sup>	6.47-7.09	4.74-5.08	7.12-11.92	1.67-2.58	0.49-1.19	0.30-0.44
unconstrained	Tree + palm + herb	0-10	6.17-6.63	4.77-5.40	9.13-16.27	2.34-3.62	0.60-1.62	0.19-0.23
		10-25	6.42-6.78	4.70-5.18	6.71-11.83	1.99-2.96	0.63-1.49	0.21-0.26
		25-70	6.47-6.85	4.76-5.02	6.75-11.41	1.92-2.30	0.66-1.32	0.30-0.31
		70-120 <sup>b</sup>	6.59-7.05	4.77-5.14	6.27-11.49	1.77-2.35	0.58-1.70	0.28-0.39

<sup>a</sup>Maximum sample size = 11 years x 3 tree species x 3 blocks

<sup>b</sup>In one of three blocks sampling extended to 155 cm.

**Table S1** (continued)

<b>Exchangeable Acidity</b> (cmol <sub>c</sub> kg <sup>-1</sup> )	<b>CEC<sub>e</sub></b> (cmol <sub>c</sub> kg <sup>-1</sup> )	<b>CEC</b> (cmol <sub>c</sub> kg <sup>-1</sup> )	<b>SOC</b> (%)	<b>N</b> (%)	<b>P</b> (mg kg <sup>-1</sup> )
0.16-0.39	11.44-19.17	29.3-38.7	2.13-3.21	0.25-0.33	10-17
0.16-0.28	11.12-15.47	26.4-35.3	0.97-1.70	0.12-0.19	7-15
0.15-0.30	10.45-13.76	24.4-33.6	0.37-1.04	0.05-0.07	6-16
0.10-0.40	10.05-15.42	24.7-30.5	0.24-0.70	0.02-0.04	6-15
0.12-0.46	13.03-22.10	26.7-41.1	2.67-3.77	0.26-0.37	11-19
0.14-0.32	10.77-15.83	26.4-36.6	0.91-1.93	0.11-0.18	7-16
0.14-0.31	10.62-14.31	23.0-33.5	0.41-0.89	0.05-0.07	7-15
0.10-0.32	10.23-14.06	22.6-29.7	0.23-0.89	0.01-0.05	5-16
0.14-0.41	12.53-20.69	28.3-37.9	2.38-3.30	0.24-0.34	9-17
0.12-0.33	10.69-16.22	24.2-35.2	0.97-1.51	0.11-0.17	7-15
0.13-0.29	10.38-14.48	22.1-33.1	0.41-1.06	0.05-0.06	5-15
0.10-0.32	10.04-15.50	23.8-30.7	0.20-0.78	0.02-0.05	6-15
0.12-0.36	13.61-21.64	28.4-41.0	2.67-3.63	0.28-0.35	10-19
0.12-0.33	10.70-15.96	26.6-35.4	1.02-2.08	0.13-0.17	7-12
0.14-0.35	10.85-15.06	23.5-33.3	0.38-0.93	0.05-0.07	6-14
0.06-0.32	10.31-14.94	22.6-30.2	0.15-0.63	0.01-0.04	7-14



Table S2 Significant Differences in Soil Variables when Employing Data for Entire 11-year Time Course, 0-10 cm.

Variable	Stand longevity			Diversity		Tree species identity		
	1 year	4 years	unconstrained	one tree species	three life forms	<i>Hieronyma</i>	<i>Cedrela</i>	<i>Cordia</i>
pH <sub>water</sub>	<b>6.23<sup>a</sup></b>	<b>6.50<sup>b</sup></b>	<b>6.42<sup>b</sup></b>	6.42 <sup>d</sup>	6.48 <sup>d</sup>	6.39 <sup>f</sup>	6.40 <sup>f</sup>	6.49 <sup>f</sup>
Ca (cmol <sub>c</sub> kg <sup>-1</sup> )	<b>10.76<sup>a</sup></b>	<b>12.15<sup>b</sup></b>	11.43 <sup>a,b</sup>	<b>11.43<sup>d</sup></b>	<b>12.33<sup>e</sup></b>	11.65 <sup>f</sup>	11.48 <sup>f</sup>	11.87 <sup>f</sup>
Mg (cmol <sub>c</sub> kg <sup>-1</sup> )	<b>2.49<sup>a</sup></b>	<b>2.82<sup>b</sup></b>	<b>2.85<sup>b</sup></b>	2.85 <sup>d</sup>	2.94 <sup>d</sup>	<b>2.99<sup>h</sup></b>	<b>2.59<sup>f</sup></b>	<b>2.74<sup>g</sup></b>
K (cmol <sub>c</sub> kg <sup>-1</sup> )	<b>1.12<sup>a</sup></b>	<b>1.22<sup>b</sup></b>	<b>1.11<sup>a</sup></b>	<b>1.11<sup>e</sup></b>	<b>0.99<sup>d</sup></b>	1.14 <sup>f</sup>	1.11 <sup>f</sup>	1.08 <sup>f</sup>
SOC (%)	<b>2.75<sup>a</sup></b>	<b>3.05<sup>b</sup></b>	<b>2.82<sup>a</sup></b>	<b>2.82<sup>d</sup></b>	<b>3.09<sup>e</sup></b>	2.99 <sup>f</sup>	2.88 <sup>f</sup>	2.91 <sup>f</sup>
P (mg kg <sup>-1</sup> )	14 <sup>a,b</sup>	<b>16<sup>b</sup></b>	<b>13<sup>a</sup></b>	13 <sup>d</sup>	13 <sup>d</sup>	<b>15<sup>g</sup></b>	14 <sup>f,g</sup>	<b>13<sup>f</sup></b>