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Linking tree biodiversity to belowground process in a young tropical plantation: Impacts on soil CO_2 flux

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Abstract

This study examined the effect of tree species identity and diversity on soil respiration in a 3-year-old tropical tree biodiversity plantation in Central Panamá. We hypothesized that tree pairs in mixed-species plots would have higher soil respiration rates than those in monoculture plots as a result of increased primary productivity and complementarity leading to greater root and microbial biomass and soil respiration. In addition to soil respiration, we measured potential controls including root, tree, and microbial biomass, soil moisture, surface temperature, bulk density. Over the course of the wet season, soil respiration decreased from the June highs (7.2 ± 3.5 μmol $CO_2/(m^2\ s^{-1})$ to a low of 2.3 ± 1.9 μmol $CO_2/(m^2\ s^{-1})$ in the last 2 weeks of October. The lowest rates of soil respiration were at the peak of the dry season (1.0 ± 0.7 μmol $CO_2/(m^2\ s^{-1})$). Contrary to our hypothesis, soil respiration was 19–31% higher in monoculture than in pairs and plots with higher diversity in the dry and rainy seasons. Although tree biomass was significantly higher in pairs and plots with higher diversity, there were no significant differences in either root or microbial biomass between monoculture and two-species pairs. Path analyses allow the comparison of different pathways relating soil respiration to either biotic or abiotic controls factors. The path linking crown volume to soil temperature then respiration has the highest correlation, with a value of 0.560, suggesting that canopy controls on soil climate may drive soil respiration.

Keywords: Biodiversity; Carbon cycling; Ecosystem function; Soil respiration; Tropics

1. Introduction

Covering 40% of the world's land area, tropical systems house more than half of the terrestrial biomass and one third of soil carbon (C) while harboring as much as 65% of all species on earth (Buchmann et al., 2004; Lambertini, 2000). The tropics thus play a central role in the global C cycle (Knorr, 2000; Rayner et al., 2005). In particular, where there are high rates of land-use change, both biodiversity and terrestrial C reserves are decreasing. Until recently rising extinction rates and global climatic change have been studied separately but there is growing recognition of the potential feedbacks between these environmental perturbations (Chapin et al., 2000; Potvin et al., 2005; Sala et al., 2000; Thomas et al., 2004; Walther, 2003). Despite the importance of tropical systems most research integrating biodiversity and C cycling research has focused on temperate ecosystems neglecting the tropics (Raich and Schlesinger, 1992; Schimel et al., 2001).

The most current figures indicate that tropical land-use change has resulted in emission of CO_2 on the order of +1 to 2 Gt C $year^{-1}$ in the last decade (Houghton, 2005) and approximately 136 ± 55 Gt C $year^{-1}$ in terrestrial systems globally since the onset of the industrial revolution (Houghton, 1999). This amounts to roughly 20% of global greenhouse gas emissions (GHG). As a result of land-use changes including deforestation, biomass burning, plowing, and wetland drainage, terrestrial soils have historically released an estimated 40 Gt soil organic carbon, primarily via soil respiration (Houghton, 1999). Almost 10% of atmospheric CO_2 passes through soils each year (Raich and Potter, 1995). In terrestrial systems, soil respiration, the combined CO_2 efflux of microbial and roots respiration from soils, release 50–75 Gt C $year^{-1}$ to the

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atmosphere or 10 times the annual fossil fuel combustion. Thus, soil respiration is an important ecosystem C flux to the atmosphere that could be used as a good measure of ecosystem function (Catovsky et al., 2002).

There is ground to believe that plant diversity could have a direct impact on soil respiration. This is because vegetation affects soil respiration by influencing soil microclimate and structure, the quantity and quality of detritus supplied to the soil as well as the overall rate of root respiration (e.g. Raich and Tufekcioglu, 2000). Furthermore there is evidence that plant diversity might alter the diversity of soil microorganisms (Balvanera et al., 2006; Stephan et al., 2000; Zak et al., 2003) with further influences on soil respiration. In microcosms, Heemsbergen et al. (2004) manipulated the number of macro-detritivores, hence species richness, and the functional diversity, i.e., the number of species carrying different ecosystem functions. The study failed to report consistent diversity effect on soil respiration but found a net effect of diversity for functional dissimilarity with higher soil respiration in more dissimilar communities. Likewise, Hooper et al. (2005) suggested that soil processes might be more responsive to the functional characteristics of dominant species rather than to number of species.

We know of only a few experiments that have examined the relationship between plant diversity and soil respiration *in situ* (Craine and Wedin, 2002; Stocker et al., 1999; Wardle et al., 1999) and these studies report opposite results. The focus of our study was therefore to (1) identify the role of tree species identity and diversity on soil respiration rates at a young tree diversity plantation in Panamá, and (2) determine key biotic and abiotic controls on soil respiration rates. We hypothesized that greater tree diversity would increase tree productivity (Caspersen and Palcala, 2001), and thus carbon inputs into soils, leading to increased soil respiration rates via higher root and microbial biomass. We similarly anticipated that tree, root, and microbial biomass would be significant biotic controls while soil moisture and temperature would be significant abiotic controls.

2. Materials and methods

2.1. Site description

This study was conducted at a tree diversity plantation in Central Panamá (9°19′N, 79°38′W), which lies 55 km north of Panamá City. The plantation, known as the Sardinilla Project, is dedicated to understanding the complex links between ecosystem biogeochemical cycling, especially C cycling, land use, and biodiversity in tropical environments over the long term. The trees were planted in July 2001 using six native tree species: *Luehea seemanii* (Ls) (Triana and Planch), *Cordia alliodora* (Ca) (Ruiz and Pavon) Oken, *Anacardium excelsum* (Ae) (Bert. And Balb. ex Kunth) Skeels, *Hura crepitans* (Hc) L., *Cedrela odorata* (Co) L., and *Tabebuia rosea* (Tr) (Bertol.) DC. These species, of either ecological or economical importance, were chosen to represent a range of growth rates, from 2.3% to 9.1%, observed in the permanent plots at Barro Colorado Island (BCI), Panamá (Scherer-Lorenzen et al., 2005). The plantation is divided into twenty-four 45 m × 45 m plots including 1, 3, and 6 species plots replicated six times. There are two monocultures plots for each species, resulting in a total of 12 monoculture plots. Triplets were built in an additive manner with Ls or Ca (the fastest growing species on BCI), Ae or Hc, and Co or Tr (the slowest growing ones). The six-species plots maintain the same species composition. Trees were planted 3 m apart in each plot for a total of 225 trees per plot. Species were planted in a Latin square pattern in the three and six-species plots as described in Scherer-Lorenzen et al. (2005) (Fig. 1). Complementary six-species plots of 0.5 ha were planted at the same time on the perimeter of the main plantation to allow for destructive sampling methods in the future. At the time of this study, trees in the diversity plantations ranged between 2 m and 10 m in height.

Cm	Ca	Ls	Ae	Hc	Tr
Ca	Ls	Ae	Hc	Tr	Cm
Ls	Ae	Hc	Tr	Cm	Ca
Ae	Hc	Tr	Cm	Ca	Ls
Hc	Tr	Cm	Ca	Ls	Ae
Tr	Cm	Ca	Ls	Ae	Tr

Fig. 1. Latin square layout of six-species plots. Anyone individual will only have two species as neighbors. In the case of a Tr individual, it will only have Cm and Hc as neighbors in a six-species plot.

The dry season (January through March) and wet season (May through November) averages 25–50 mm and 250 mm of rain per month, respectively, measured at the nearby Buena Vista meteorological station. In 2004, the year we conducted our fieldwork, precipitation in March (dry season sampling period) and June (wet season sampling period) was 44 mm and 228 mm, respectively, at nearby BCI. Air temperature remained relatively constant between seasons in 2004. Average air temperatures on BCI in March and June were 27 and 26 °C, respectively (Paton, personal communication). The underlying geology consists of Tertiary limestone and other sedimentary rock. Soils are clayey Typic Tropudalfs and Aquic Tropudalfs (Potvin et al., 2004).

2.2. Soil respiration measurements

Soil respiration measurements were made using a closed chamber system and a PP Systems EGM-4 Environmental

infrared gas analyser. Soil CO_2 fluxes were measured within collars permanently inserted into the ground to 5 cm depth 1 month prior to sampling. The collars were located mid-way (1.5 m) between two trees, which are referred to as pairs. A plastic lid and the censor head capped the collars to form air-tight chambers during measurements. Davidson et al. (2002) recommend chambers 300–700 cm^2 in area to minimize the sampling artefact from high spatial variability in soil respiration. Due to the small size of the EGM chamber, we crafted a chamber out of PVC tubing (20.32 cm diameter, 10.16 cm height), increasing the total area of the chamber from the original 78 to 324 cm^2 and the total volume from 1178 cm^3 to 3293 cm^3. During the dry season when the soils cracked around the collar compromising the seal, nearby soil was spread over the outer perimeter of the collars. Respiration measurements were made between 7:00 h and 16:00 h during periods of no precipitation. Soil respiration was measured for 3 years old trees (i) within the biodiversity plots during the transition from the dry to the early wet season – the transition experiment –, (ii) within the complementary plot at the height of the wet season – the wet season experiment. We also measured soil respiration (iii) during the wet season for 6-year-old trees—the age experiment.

To test our first hypothesis, the transition experiment included the sampling of six monoculture pairs were selected among their corresponding monoculture plots and 12 two-species pairs were selected randomly from either the three or six-species plots (Appendix A). In the mixed-species plots, adjacent trees always belonged to two different species. The 12 two-species pair combinations represented the 12 pair combinations encountered in the six-species plots. For each monoculture and mixture, five pairs were selected randomly out of a subset of similar sized young trees (2–3 m height). All pair combinations were replicated five times, with the exception of AeLs and HcLs, which only had four replicates. There were five species used in the monoculture pairs (Ca was excluded because of high mortality) ($n = 25$). Thirty-four 2-species pairs were located in the three species plots, and 24 pairs in the six-species plots for a total of 83 collars. To capture seasonal changes in soil respiration, each collar was sampled up to twice a week over 4 weeks in March at the height of the dry season, and again in June at the onset of the wet season.

The wet season experiment tested our second hypothesis, examining biotic and abiotic controls on soil respiration. Control variables included soil temperature, moisture and bulk density, root biomass and density, microbial biomass, tree biomass, and tree crown volume. This experiment was conducted in the complementary plots to allow root excavation. It focused on Ae and Hc because of their importance to the forests ecosystems around the site. Monitoring of the Panamá Canal Watershed has shown that Ae and Hc ranked as two of the most important species in term of forest woody biomass (Heckadon-Moreno et al., 1999). We sampled Ae and Hc in monoculture and two-species pairs. In two-species pairs, Ae and Hc were paired with Ls and Tr species. Monoculture pairs were replicated five times ($n = 10$), while the unique species combinations in mixture were replicated twice ($n = 8$). Respiration measurements were recorded using the same methodology described above. Wet season measurements were conducted over three replicate runs. Each run lasted 3 months, with runs 1, 2, and 3 beginning on 8/17, 8/31, and 10/13, respectively. Intense sampling (2–3 times per week) occurred in the first 5 weeks of each run, and every 2–3 weeks after that for a total of 9 measurements per collar.

Finally the age experiment aimed at comparing the results obtained on 3 years old tree with those of larger, older tree. The comparison contrasted the Hc monoculture pairs (planted in 2001) in the complementary plot ($n = 5$) with a group of Hc pairs that were planted in 1998 as a preliminary trial in an adjacent pasture ($n = 6$). Soil respiration, soil moisture and temperature measurements, took place during run three only (October 2004).

2.3. Measures of environmental and architectural traits

For the first two experiments, soil temperature was taken during each respiration measurement at a depth of 5 cm. We also collected soil moisture data *in situ* with a Dynamax ML2x ThetaProbe moisture meter that measured volumetric water content. Due to technical difficulties, we were unable to collect soil moisture data from the end of March to the end of June. We measured soil bulk density at each collar in the biodiversity plots at the end of the June sampling period. Yearly measures of individual tree diameter were available for the trees used in the transition experiment. Therefore, we calculated relative growth rate (RGR) for 2004–2005 as an indicator of growth using tree diameter as the dependent variable: $\text{Ln}\ (\text{Diam}_{2005} - \text{Ln}\ \text{Diam}_{2004})/(t_{2005} - t_{2004})$, where t_{2004} and t_{2005} refer to the exact dates at which the diameters were measured as suggested by Condit et al. (2006). Diameter refers to either basal diameter (10 cm from the ground) when trees were <2 m tall or diameter at breast height when trees were >2 m. RGR was estimated only for trees that remained in the same height category in the 2004–2005 growing season. Because RGR was not measured for all the tree pairs in our dataset, the analysis RGR effects on soil respiration included a subset of the entire data set with Hc, Ls, and Tr monocultures ($n = 15$), 33 multi-species pairs from three-species plots and 24 multi-species pairs from six-species plots.

Biotic factors measured in the wet season experiment included root biomass and root density within the collars, microbial biomass, and tree pair biomass, and tree canopy volume. The biomass of each tree was estimated using height and basal diameter data collected in the 2004 dry season in species-specific allometric relationships (Coll et al., submitted for publication). In the analysis we summed the biomass of the two trees between which collars were located, thereafter referred to as tree biomass. Crown volume was calculated using the equation for the volume of a cylinder. Crown height was measured using an extended pole and the lateral span of each crown was measured in north–south and east–west directions. The crown radius was calculated by halving the average lateral span of each crown taken from the two directions. As for biomass we summed the crown volume of the two trees located

on each collar side and refer to it thereafter at crown volume. For root biomass, all roots greater than 5 mm up to a 10 cm depth were dried and weighed. Unfortunately, the very clayish soil made it impossible to retrieve and weigh roots less 5 mm. Root density was measured using a quadrate (12.5 cm × 12.5 cm) with grid lines running every 5 cm. The number of times that the roots intersected those grid lines constituted each collar's root density. Root measurements were made at the end of the 2004 growing season.

To measure microbial biomass, soil samples were taken immediately outside the perimeter of the collars in mid-August. Samples were shipped overnight to the University of Wisconsin (Madison, Wisconsin, U.S.A.) where they were homogenized and frozen before analysis. All glassware was baked at 475 °C for 4 h to remove any organic contaminants. Lipids were extracted, purified and identified from microbial cell membranes in 1-g samples of lyophilized soil using a hybrid lipid extraction based on a modified Bligh and Dyer (1959) technique, combined with fatty acid methyl ester analysis (FAME) as described by Microbial ID Inc. (Hayward, CA). Briefly, lipids were extracted from 4 g of freeze-dried soil using a chloroform–methanol extraction with a phosphate buffer (potassium phosphate (3.6 ml), methanol (8 ml), and $CHCl_3$ (4 ml)) in 25-ml glass tubes, shaken for 1 h and centrifuged. The supernatant was then decanted to 30-ml tubes and potassium phosphate buffer and chloroform were re-added and the tubes were vortexed for 30 s. The phases were allowed to separate overnight at room temperature. The top layer was aspirated off, saving the chloroform phase, and the volume was reduced in a RapidVap. We then followed the procedure for FAME as given by Microbial ID Inc.; sodium hydroxide was added for saponification and the solution was heated in a water bath for 30 min, followed by alkaline methanolysis. Fatty acids were analyzed using a Hewlett-Packard 6890 Gas Chromatograph equipped with a flame ionization detector and split/splitless inlet and a 25 m × 0.2 mm inside diameter × 0.33 μm film thickness Ultra 2 (5%-phenyl, 95% methyl) capillary column (Agilent) using hydrogen as the carrier gas, N as the make-up gas, and air to support the flame. Gas chromatograph conditions were set by the MIDI Sherlock program (MIDI Inc., Newark, DE). Peaks were identified by using bacterial fatty acid standards and Sherlock peak identification software (MIDI Inc., Newark, DE). Fatty acids were quantified by comparisons of peak areas from the sample compared with peak areas of two internal standards, 9:0 (nonanoic methyl ester) and 19:0 (nonadeconoic methyl ester), of known concentration. Total μmol/g soil was used as an index of microbial biomass (White et al., 1979; Hill et al., 1993; Zelles et al., 1992; Balser et al., 2005).

2.4. Statistical analyses

2.4.1. The transition experiment

The statistical analyses focused on differences either (1) among species, using monoculture tree pairs (the species effect), (2) between mixed and monoculture pairs (the pair effect), (3) among pairs located in monoculture, three-species, and six-species plots (the diversity effect). Analyses of variance with repeated measure on days (ANOVARs) were used to test the between subject effects of species (or pair or diversity), season and their interaction on soil respiration, moisture or temperature. Season tested for differences between March (dry season) and June (early wet season) in the main biodiversity plots. There were four sampling days in each month. The main within subject effect was days. Tukey pairwise comparisons were used as *post hoc* tests when necessary.

Analyses of covariance with repeated measurements (ANCOVAR) were used further to assess the importance of species (or pair or diversity) on soil respiration with tree biomass, soil temperature or moisture as a covariate. The ANCOVARs were run using temperature and moisture only for the early wet season because some covariates were not measured at all times. Finally, ANOVA was used to test the effect of either species or diversity on tree biomass and *t*-tests to examine the effect of pair on this trait. Averages are reported along with standard deviation for single measurements including tree, crown, and microbial biomass. For soil respiration, temperature, and soil moisture that were measured multiple times, standard errors are reported. Possible controls on soil respiration were tested using stepwise multiple linear regression analysis. Control variables (soil temperature, soil moisture, bulk density, tree pair biomass and RGR) were run against soil respiration. Model normality was assessed by testing the normality of model residuals using the Kolmogorov–Smirnov normality test with Lilliefors probability.

2.4.2. The wet season experiment

In the wet season, respiration rates were analyzed by ANOVAR to compare monoculture pairs of Ae and Hc and two-species pairs of Ae and Hc with Ls and Tr. Thus species and pair were the only between subject effect. Species effects compared same-species tree pairs (Ae vs. Hc) while the pair effect compared same-species pairs with two-species pairs. Unlike in the main experiment, monoculture and two species pairs occurred in the same plot. ANCOVAR were used to examine the importance of several possible covariates including soil temperature, moisture, bulk density, microbial biomass, root biomass and density, tree biomass and crown volume.

The wet season experiment was designed to better understand the controls on soil respiration in the plantation in the context of tree species and pair effects. Particular attention was given to biological contributors to soil respiration. We first used stepwise multiple regression analysis to determine the controls that explained the majority of the variation in soil respiration. Control variables tested included soil temperature, soil moisture, and soil bulk density and the biotic factors microbial biomass, root biomass and density, tree pair biomass and crown volume. Model normality was assessed by testing the normality of model residuals using the Kolmogorov–Smirnov normality test with Lilliefors probability.

Our second analysis of the controls on soil respiration was a path analysis, which is an analytical method based on multiple regression that allow to determine pathways contributing to correlations between traits and asses causal relationships

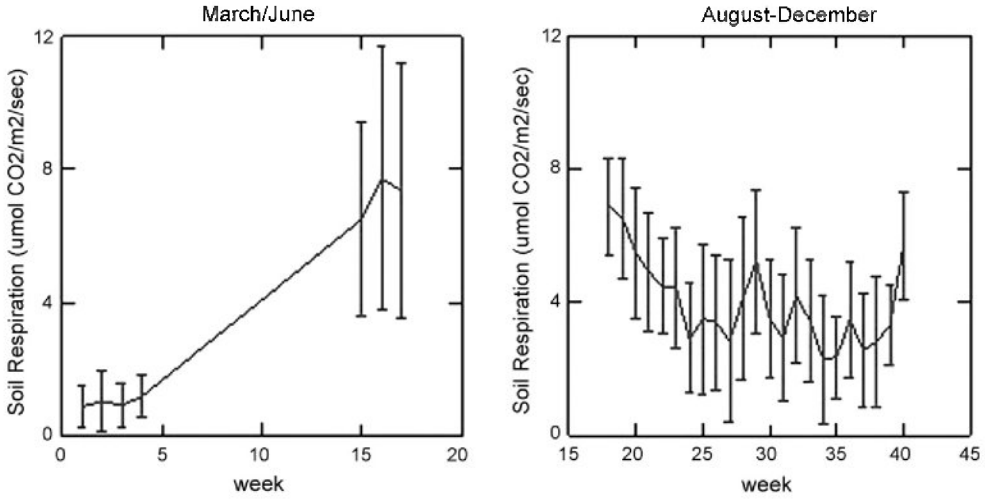

Fig. 2. Comparison of average soil respiration among tree pairs AeAe, HcHc, AeTr, HcTr, AeLs and HcLs in the (left) dry season (weeks 1–4) and early wet season (weeks 15–17), and (right) wet season (weeks 35–36) at the Sardinilla biodiversity plantation. Bars are standard deviation (S.D.).

(Legendre and Legendre, 1998). This statistical method thus provides a frame-work to integrate the various biotic and abiotic control of soil respiration and identify the most important causal relationship. Therefore, two path-analyses were calculated to differentiate between correlation and causation by partitioning standardized regression coefficients between soil respiration (dependent variable) and the biotic and abiotic factors (independent variables). The first path-analysis linked tree biomass first to root biomass and root biomass to microbes, while the second examined the link between tree biomass, canopy volume, and soil temperature and moisture. Variables were centered and standardized before running the multiple linear regression, which is necessary to calculate the path coefficients. The correlation between two variables one step apart, e.g. crown volume and soil respiration, can be calculated as $r_{13} = p_{13} + r_{23} \times p_{12}$ (Legendre and Legendre, 1998). All statistical analyses were done using SYSTAT (version 10.1).

2.4.3. The age experiment

The differences between old and young trees were analyzed by ANOVAR with repeated measures on time, i.e. days on which SR was measured on each collar.

3. Results

3.1. The transition experiment

Soil moisture doubled from the dry ($21.88 \pm 6.78\%$) to the early wet season ($44.87 \pm 4.78\%$) while soil temperature increased by a few degrees (27.48 ± 2.26 °C and 30.59 ± 2.26 °C (dry and early wet, respectively). A strong seasonal trend in soil respiration is evident by comparing the weekly soil respiration rates in the dry season (March), the dry to wet seasonal transition (June), and the wet season (August to December). Soil respiration was the highest during the seasonal transition (Fig. 2). The lowest rates of soil respiration were at the peak of the dry season (1.0 ± 0.7 μmol $CO_2/(m^2\ s^{-1})$). Over the course of the wet season, soil respiration decreased from the June highs (7.2 ± 3.5 μmol $CO_2/(m^2\ s^{-1})$) to a low of 2.3 ± 1.9 μmol $CO_2/(m^2\ s^{-1})$ in the last 2 weeks of October. During the dry to wet transition, season explained 73% ($F = 346.63$, $p < 0.001$), 88% ($F = 1073.68$, $p < 0.001$), and 89% ($F = 1344.40$, $p < 0.001$), respectively for models considering species, pair and diversity effects) of the variation in soil respiration.

The main effect of species, comparing soil respiration of monoculture pairs of six different species, was not significant during seasonal transition. In contrast, tree biomass differed significantly among species ($F = 8.21$, $p < 0.001$) with the largest pairs being Hc (Fig. 3). Tree biomass ranged from a high of 7.88 ± 3.18 kg for Hc to a low of 1.44 ± 0.93 kg for Ae (Table 1). Hc biomass was three times greater than Co and 5.5 times greater than Ae biomass. Relative growth rates (RGR) also differed among species, with Ls (0.62 ± 0.26) having significantly higher RGR than either Hc (0.32 ± 0.16) or Tr (0.33 ± 0.15) ($F = 7.20$, $p = 0.003$). However, even when tree biomass and RGR were considered as covariates, soil respiration did not show a significant species effect. ANCO-

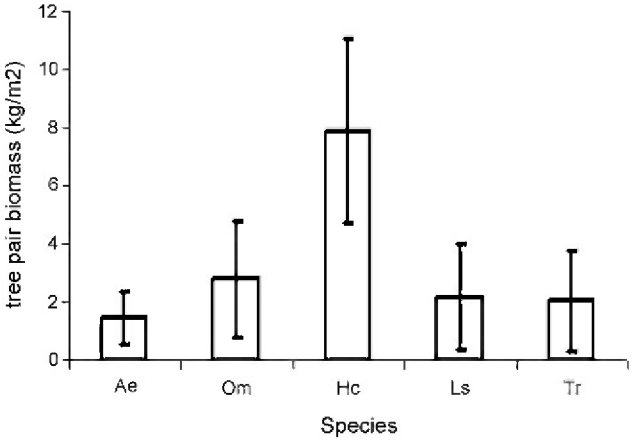

Fig. 3. Average tree pair biomass among monoculture pairs by species. Bars are S.D.

Table 1
Mean values and S.E. for soil respiration (μmol/(m^2 s^{-1}), tree biomass (kg/m^2) and relative tree growth rate (RGR)

Tree pairs	N	Soil respiration		Tree biomass	Tree growth	
		March	June		n	
Species comparison						
Ae	5	1.32 ± 1.0 a	9.12 ± 6.6 a	1.44 ± 0.9 b	–	–
Cm	5	1.14 ± 1.0 a	5.69 ± 1.4 a	2.78 ± 2.0 b	–	–
Hc	5	1.14 ± 0.6 a	7.10 ± 1.7 a	7.89 ± 3.2 a	5	0.32 ± 0.16 a
Ls	5	1.10 ± 1.1 a	5.37 ± 1.3 a	2.18 ± 1.8 b	5	0.62 ± 0.26 a
Tr	5	0.84 ± 0.8 a	6.18 ± 2.1 a	2.02 ± 1.7 b	5	0.33 ± 0.15 a
Pairs comparison						
Monoculture pairs	15	1.10 ± 0.87 a	6.95 ± 3.84 a	3.38 ± 3.28 a	15	0.43 ± 0.02 a
Two species pairs	30	0.88 ± 0.07 b	6.44 ± 1.63 a	5.11 ± 3.69 b	15	0.41 ± 0.06 a
Diversity comparison						
Pairs in monoculture plots	30	1.11 ± 0.90 a	6.70 ± 3.52	3.38 ± 3.28 a	15	0.41 ± 0.06 a
Pairs in 3 species plots	34	0.90 ± 0.65 b	7.24 ± 2.71	7.06 ± 6.59 b	33	0.43 ± 0.03 a
Pairs in 6 species plots	24	0.76 ± 0.64 b	6.23 ± 1.71	5.58 ± 4.44 a,b	24	0.43 ± 0.03 a

RGR values were available only for Hc, Ls, and Tr pairs. Letters represent significant differences among species.

VAR analysis of the early wet season found significant differences in soil respiration among species when soil bulk density was used as a covariate ($F = 4.66$, $p < 0.001$). Respiration rates ranged from 9.12 ± 6.61 μmol CO_2/(m^2 s^{-1}) for Ae pairs to 5.37 ± 1.29 μmol CO_2/(m^2 s^{-1}) for Ls pairs. At that time, soil temperature differed significantly among species ($F = 8.7$, $p < 0.001$) with Co collars having higher temperatures (33.16 ± 1.21 °C) than both Hc (29.99 ± 3.20 °C) and Tr collars (29.95 ± 3.20 °C) (Table 1).

The pair effect compared monoculture pairs and two-species pairs including Ae, Hc, Ls, and Tr and their combinations, AeHc, AeLs, AeTr, HcLs, HcTr, LsTr (see Section 2). On average over the seasonal transition, monocultures had slightly higher soil respiration than two-species pairs (1.10 ± 0.87 μmol CO_2/(m^2 s^{-1}) and 0.88 ± 0.07 μmol CO_2/(m^2 s^{-1})) (Table 1), but the difference was not statistically significant. The ANOVA, however, unveils a significant season by pair interaction ($F = 5.85$, $p = 0.02$) with two-species pairs exhibiting lower respiration then monoculture pairs in the dry season (Fig. 4). ANOVA analysis did reveal that the increase in soil respiration from the dry season to the early wet season was significantly greater in the mixed species pairs than the monoculture pairs ($F = 5.25$, $p = 0.025$). This change in soil respiration corresponds to significantly higher tree biomass ($t = -2.177$, $p = 0.042$) in two-species pairs (5.11 ± 3.69 kg) than in monoculture pairs (3.38 ± 3.28 kg). When either soil temperature or tree biomass were taken as covariates, ANCOVA unveiled significant pair effect ($F = 7.62$, $p = 0.007$), i.e., species pairs in monoculture plots showed differences in soil respiration compared to multi-species mixtures. RGR was also a significant covariate in the dry season ($F = 7.02$, $p = 0.01$) although inclusion in the ANOVA did not improve the pair effect.

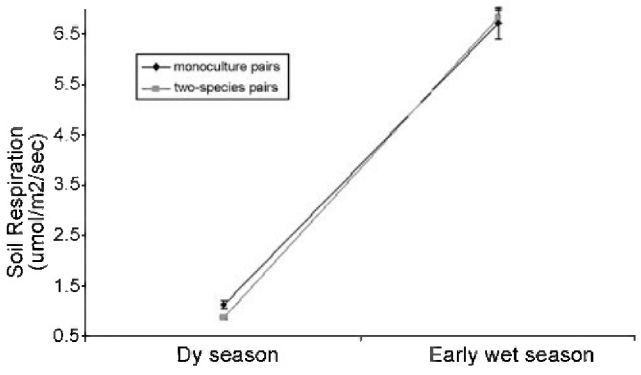

Fig. 4. Average soil respiration in the dry and early wet season for monoculture and two-species pairs. Bars are S.E.

The diversity effect compared trees growing in plots of varying tree diversity, i.e., in monoculture, three-species, and six-species plots. The ANOVAR uncovered significant effect of diversity ($F = 3.55$, $p = 0.031$) and significant interaction between plot and season ($F = 3.08$, $p = 0.049$). During the dry season, soil respiration rates in the monoculture pairs were 31% higher than those of the pairs in three- and six-species plots (Table 1, Fig. 5). In the early wet season however, soil respiration was highest at collars in the three-species plots. Between the dry and the early wet season, soil respiration measured in three and six-species plots increased by a factor of 7 while that of monocultures increased only by a factor of five. ANOVA analysis indicated that the change in soil respiration from the dry season to the early wet season was significantly higher for pairs in the three-species plots than pairs in the monoculture plots ($F = 4.54$, $p = 0.014$). Of all the abiotic and biotic covariates, soil bulk density ($F = 4.4$, $p = 0.015$) and tree biomass ($F = 3.8$, $p = 0.023$) were significantly different among diversity levels. Soil bulk density was higher in three species than in the six-species plots while pairs in the three species plots had twice the biomass of pairs in the monocultures (Fig. 6).

Linear regression indicated that, in the dry season, temperature was the only significant predictor, varying with soil respiration (Log(soil respiration) = −0.023 temperature + 0.533; adj. $r^2 = 0.04$, $p = 0.05$). In the early wet season, tree pair biomass was the only significant predictor, varying with soil respiration (Log(soil respiration) = 0.07 bio-

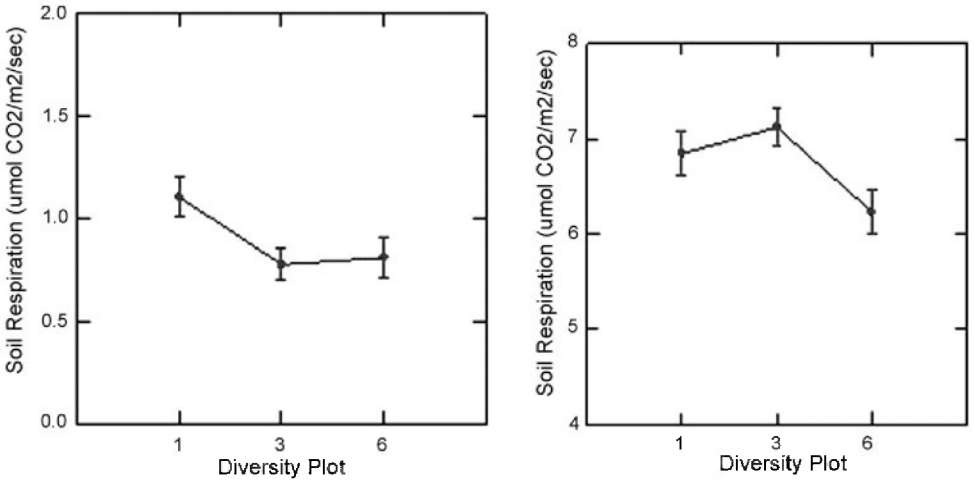

Fig. 5. Least square means for soil respiration in the dry season (left) and early wet season (right) for pairs in monoculture, three-species, and six-species plots. Bars are S.D. Note different *y*-axis.

mass + 0.58; adj. $r^2 = 0.07$, $p = 0.009$). In both analysis however, the r^2 values are very low thus indicating highly variable responses and a very weak explanatory power suggesting that factors, other then those measured in our experiment must control soil respiration.

3.2. The wet season

With or without covariates, the main effect of species, comparing Ae and Hc, was never significant during the wet season. Microbial biomass in Hc (0.35 ± 0.04 μmol lipids/g) was similar to that in Ae monocultures (0.28 ± 0.13 μmol lipids/g soil). No other covariates, whether biotic or abiotic, showed any significant differences between species.

In the wet season, the pair effect considered a reduced set of species mixed (see Section 2): Ae and Hc monocultures were compared with AeLs, AeTr, HcLs, and HcTr mixtures. The pair effect was highly significant ($F = 8.88$, $p = 0.014$) without covariates, accounting for 32% of the variability in soil respiration. Monocultures had higher soil respiration than two-species pairs (3.9 ± 0.24 μmol $CO_2/(m^2\ s^{-1})$ and 3.1 ± 0.28 μmol $CO_2/(m^2\ s^{-1})$. The only significant covariates were soil surface temperature and soil moisture, accounting for 7% and 3% of the variability, respectively. We failed to find any significant differences in root biomass, root density, average crown and tree biomass for between monoculture and mixed pairs (Table 2).

To shed light on the mechanisms through which tree diversity affects soil respiration we conducted both linear regression and paths analyses on the wet season dataset. In the wet season, a combination of crown volume and soil temperature explained the majority of the variation in soil respiration (adj. $r^2 = 0.29$, $p = 0.01$). Crown volume was entered as the first explanatory variable in the stepwise multiple regression and explained 16% of the variability (Table 3).

Path analysis focused more closely at the biotic and abiotic pathways that control soil respiration. The first pathway focused on possible biotic controls of respiration while the second one examined abiotic ones (Fig. 7). Correlation

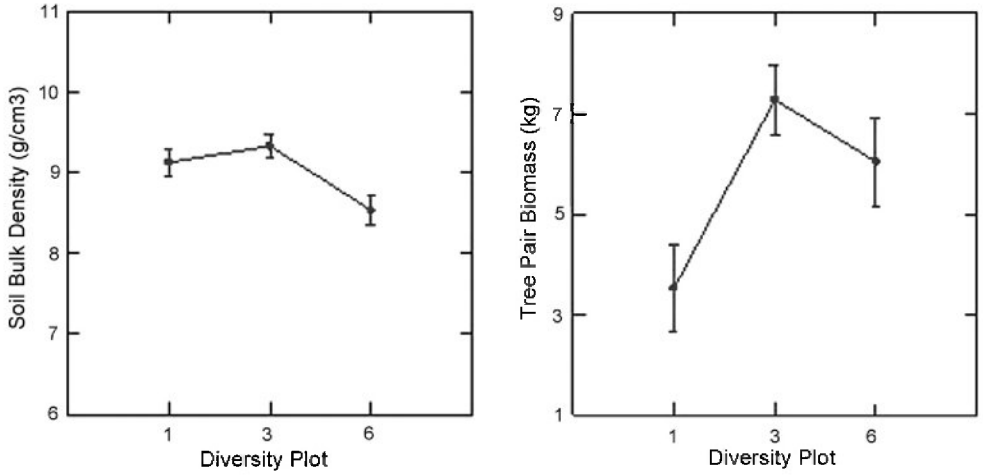

Fig. 6. Least square means for soil bulk density (left) and total tree biomass (right) for pairs in monoculture, three-species, and six-species plots. Bars are S.D.

Table 2
Mean values and standard errors for the abiotic and biotic covariates measured in the wet season on (i) monoculture and mixed tree pairs of young trees as well as on (ii) old trees

Trait	Monoculture	Mixed	Old
Soil temperature (°C)	29.7 ± 0.5	28.1 ± 1.0	27.9 ± 0.5
Soil moisture (%)	46.5 ± 1.1	45.7 ± 1.3	45.7 ± 0.6
Root biomass (g/m^2)	0.733 ± 1.499	0.375 ± 0.762	9.71 ± 13.93
Root density (/m^2)	2.800 ± 5.007	1.750 ± 4.950	15.2 ± 3.5
Crown volume (kg)	1.19 ± 1.86	0.89 ± 1.00	n.a.
Tree biomass (kg)	2.06 ± 1.96	1.42 ± 7.991	n.a.

Table 3
Stepwise linear regression of tree pair soil respiration (μmol/(m^2 s^{-1}) against average crown volume (kg) and soil temperature (°C) for the wet season

Effect	Coefficient	SE	Std Coefficient	p
Constant	−1.557	0.93	0.00	0.115
Crown Volume	0.121	0.044	0.588	0.016
Temperature	0.064	0.032	0.438	0.061

Adj. r^2 for model is 0.29, $p = 0.01$.

coefficients are presented next to each term described the nature and strength of the relationship as well as its significance. In the biotic path analysis, the strongest pathways that we observed were those between tree and root biomass and between root and microbial biomass. The total correlation between root biomass and soil respiration can be calculated as the sum of the direct of root biomass on soil respiration and its indirect effect mitigated by microbial biomass. That correlation was estimated to be 0.103. The second path analysis examined the relationship between tree crown volume and soil respiration mediated by soil temperature and moisture. The three significant effects in the analysis were tree biomass to crown volume, crown volume to soil temperature and soil temperature to soil respiration. The total correlation between crown volume and soil respiration mitigated by soil temperature was of 0.560 while it dropped to 0.315 if mediated by soil moisture.

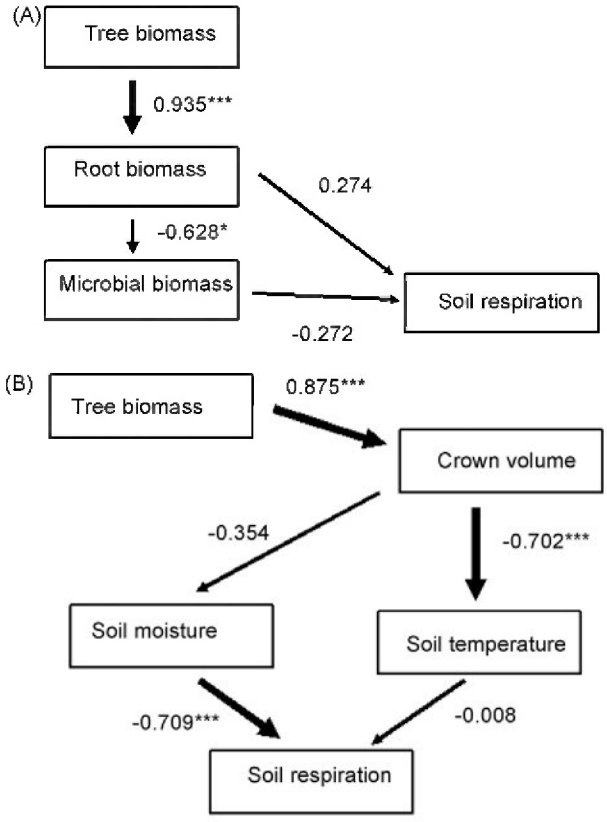

Fig. 7. Path analysis examining (A) biotic and (B) abiotic controls of soil respiration. The analysis used only wet season data from monoculture pairs in order to have a full range of independent variables. The thickness of the line represents the strength of the interactions. The numbers on the diagram are the path coefficients and significance levels are ***$p < 0.001$ and *$p < 0.05$.

3.3. The age experiment

Because we worked on trees that had a maximal height of 3 m, we were concerned that herbaceous vegetation could dwarf the effect or tree root respiration. We therefore compared the 3-year-old Hc pairs with 6-year-old Hc pairs from an adjacent stand. These older trees had significantly higher root density ($p = 0.041$, $t = -2.964$, d.f. = 4). The average root biomass within a collar was more then 10 times larger for the 6-year-old trees (Table 2) but the difference was not statistically significant because of the large variation among individual trees. Because of their dense tree crowns, the soil was bare under the old trees. Despite these differences, the effect of age on soil respiration rates was not statistically significant.

4. Discussion

Overall, the soil respiration rates at the Sardinilla plantation are within the range of rates reported from other studies in the tropics. Average soil respiration rates observed in this study ranged from 7.2 ± 3.5 μmol CO_2/(m^2 s^{-1}) in the wet season to 1.0 ± 0.7 μmol CO_2/(m^2 s^{-1}) in the dry season, which are consistent with those reported by Schwendenmann et al. (2006) for different land-cover types in Central Panamá (5.1–8.1 μmol CO_2/(m^2 s^{-1}). Soil respiration rates in other plantation systems range from 2.23 ± 0.15 μmol CO_2/(m^2 s^{-1}) in a Puerto Rican plantation (Li et al., 2005) to 5.4 μmol CO_2/(m^2 s^{-1}) in a Hawaiian plantation (Giardina and Ryan, 2002). In comparison to their temperate counterparts, tropical systems report consistently higher annual soil respiration rates. Hibbard et al. (2005) compiled a list of published daily soil respiration rates from temperate ecosystems in the northern hemisphere. Combining soil respiration data from evergreen needle leaf forest, mixed evergreen/deciduous forest, deciduous broadleaf forest and woodland/savanna yielded an average daily flux of 2.1 μmol CO_2/(m^2 s^{-1}).

4.1. Seasonal trends and controls of soil respiration

Of the main effects tested in this experiment, season had the greatest effect on soil respiration rates, accounting for 89% of the variation. The observed seasonal trend is similar to that reported for tropical forest (Davidson and Trumbore, 1995; Kiese and Butterbach-Bahl, 2002). However, differences in soil

respiration from the dry to wet season were considerably more pronounced at Sardinilla with a percent increase of 600% compared with the tropical rainforest site that showed a 50% increase in soil respiration (Kiese and Butterbach-Bahl, 2002). Sardinilla had both lower soil respiration in the dry season and higher soil respiration in the wet season. Seasonal effects on respiration in this study corroborated the findings of Wilsey et al. (2002) who reported similar increases in ecosystem respiration rates from 2.38 ± 1.04 μmol $CO_2/(m^2\ s^{-1})$ in the dry season to 9.40 ± 1.8 μmol $CO_2/(m^2\ s^{-1})$ in the wet season in a nearby pasture. In Sardinilla, environmental factors played an important role in soil respiration rates. We believe that extremely low soil moisture during the dry season reduces the respiration of microbes and tree roots. Numerous studies in the tropics have linked seasonal trends in soil respiration to changes in soil moisture (Adachi et al., 2005; Buchmann et al., 2004; Feigl et al., 1995; Holt et al., 1990; Kiese and Butterbach-Bahl, 2002). In the dry season, soil respiration is so depressed that it is very difficult to relate it to either tree characteristics or biotic factors.

A main objective of this study was to identify the key biotic and abiotic controls of soil respiration. Plant roots, and soil micro- and macrofauna are responsible for soil respiration. The size of these biological pools (i.e root biomass, microbial biomass) (Benasher et al., 1994; Smith and Johnson, 2004; Franklin and Mills, 2003) as well as carbon supply (i.e. SOM, litter inputs, photosynthates from photosynthesis) (Fang et al., 1998; Rey et al., 2002; Epron et al., 2004; Janssens et al., 2001) and environmental factors such as temperature and soil moisture influence the rates at which these biological components respire. Our data suggest that trees' influence on soil respiration becomes significant in the early wet season when soil respiration is positively related to tree biomass and continues to be important through the wet season, when crown volume also positively relates to soil respiration. The mechanism by which larger trees with larger canopies produce greater soil respiration is highlighted in our path analysis. As trees become bigger, crown volume increases and might decrease soil temperature and increase soil moisture. These slight changes in soil physical characteristics in turn reduce soil respiration rates. Additionally, a larger canopy could also reflect higher photosynthesis rates and thus C supplies to roots, which could in turn increase rates of root respiration (Janssens et al., 2001) and microbial respiration through root exudation of photosynthates (Bardgett et al., 1999; Mikola and Setala, 1998; Zak et al., 1994).

It is important to note, however, that even though trees play an important role in soil respiration, the variables we used (i.e. tree biomass and canopy volume) only explained 8% and 16% of the variation in soil respiration, respectively. A stronger relationship between canopy volume and soil respiration and not biomass and soil respiration in the wet season likely reflects the fact that canopy volume is a better indicator of current photosynthesis and tree activity than biomass which is a cumulative effect of tree activity over many years.

The low explanatory power of either biomass or canopy volume may indicate that other biological components dominate soil respiration at Sardinilla. Microbial activity and/or macrofauna activity may make up the largest component of soil respiration at the site. Although microbial biomass was not a significant predictor this may also be because biomass is a poor reflection of actually biological activity. The heterotrophic component of soil respiration in the tropics ranges 27–76% (Subke et al., 2006). Silve et al. (2005) found that heterotrophic respiration dominated in lowland tropical forest ranging for 62–76% of total soil respiration.

Our primary objective in this study was to determine the effect of tree diversity on soil respiration. We anticipated that greater tree diversity would increase tree productivity (Caspersen and Palcala, 2001), and carbon inputs into soils, leading to increased soil respiration rates either through increase root respiration and/or increased microbial respiration as a result of increased C supply to the rhizosphere. While tree biomass was in fact greater in pairs located in three- and six-species plots and lowest in monoculture (Fig. 6), and tree growth has similarly been found to be higher in these mixed species plots relative to monocultures (Potvin and Gotelli, 2008), dry season soil respiration rates showed an opposite trend. We attribute the lack of congruence between tree productivity and soil respiration in the dry season to the dormancy of both plants and microbes during that time, which would mask a tree diversity effect. The differences that were detected in the dry season could be the result of higher earthworm biomass in monoculture versus mixed-species pairs. Sarlo (2006) measured earthworm biomass in the same diversity plos of the Sardinilla plantation at the time when we carried out our experiment. These results indicate higher earthworm biomass in monoculture pairs of Hc, Ls, and Tr than their two species combinations (HcLs, HcTr, LsTr).

The transition from the dry season to the early wet season provides evidence of a tree diversity effect. The greatest increase in soil respiration from the dry to early wet season was in three-species plots, which also had the highest tree biomass. Our wet season experiment indicates, tree effects become more obvious further into the wet season with a significant positive relationship between crown volume and soil respiration. Thus, we might anticipate a continued increase in the three species plots relative to the monocultures as the wet season continues. Knowledge from the path analysis in combination with our diversity results suggests diversity increases tree growth and size yielding larger canopies, which in turn reduced temperatures and increase soil moisture. The changes to soil climate likely provide a more preferred climate for soil microbes. The poor relationship between soil microbial biomass and soil respiration may indicate that these changes to soil climate likely effect rates of microbial respiration but not the amount of microbes in soils. While the wet season experiment found higher biomass and soil respiration in monoculture pairs, the experiment was not able to separate monoculture and mixed pairs into different plots and draw off the strong block design of the main experiment and as such, monoculture pairs may have benefited from the proximity of neighboring species.

Our study highlights the complexities both of ecosystem level diversity effects and soil systems. There are often numerous processes and mechanisms operating at any given time that may either enhance or mask ecosystem processes. Our study indicates that soil contributions to ecosystem productivity may differ between seasons and, when not taken into account, may result in either over- or underestimation of net ecosystem productivity. While tree diversity clearly influences ecosystem carbon cycling at Sardinilla, the effects on soil respiration clearly differ across seasons. Future research into tree diversity effects on soils should not focus solely on growing season effects and should include numerous abiotic and biotic measures to understand the mechanism by which tree diversity alters soils, including soil macrofauna.

5. Conclusion

Our results suggest that tree diversity affects soil respiration in two ways: (1) by increasing tree biomass, and (2) decreasing earthworm biomass in mixed versus monoculture pairs. The first pathway supports our hypothesis of larger trees increasing C supplies to roots and microbes. Evidence of this pathway was found in the early wet season as the largest relative change in soil respiration from the dry to wet season corresponded to pairs in the three species plots with the highest tree biomass.

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Appendix A. Tree pair distribution among diversity plots

Plot	Pairs	Collar replicate
T1	Co, Ca	1,2,3,4
	Ca, Hc	1,2
T3	Co, Ls	1,5
	Ae, Co	1,2,3,4,5
T4	Co, Ls	2,3,4
	Co, Hc	1,2,3,4,5
	Hc, Ls	1,2,3,4,5
T5	Ca, Hc	3,4,5
	Hc, Tr	5
T6	Ae, Tr	1,2,3,4,5
A3	Co, Ca	5
	Co, Tr	2,3
	Ae, Ls	2,4
	Hc, Tr	3,4
A4	Co, Tr	1,4,5
	Ca, Ls	1,2,3,4,5
	Ae, Ls	1,3,5
	Ae, Hc	1
	Hc, Tr	1,2
A5	Ae, Hc	2,3,4,5
Ae2	Ae	1,2,3,4,5
Ca1	Ca	1,2,3,4,5
Co2	Co	1,2,3,4,5
Hc1	Hc	1,2,3,4,5
Ls1	Ls	1,2,3,4,5
Tr2	Tr	1,2,3,4,5

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