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Coordination of aboveground and belowground responses to local-scale soil fertility differences between two contrasting Jamaican rain forest types

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There is growing interest in understanding how declining soil fertility in the prolonged absence of major disturbance drives ecological processes, or 'ecosystem retrogression'. However, there are few well characterized study systems for exploring this phenomenon in the tropics, despite tropics occupying over 40% of the Earth's terrestrial surface. We studied two types of montane rain forest in the Blue Mountains of Jamaica that represent distinct stages in ecosystem development, i.e. an earlier stage with shallow organic matter and a late stage with deep organic matter (hereafter 'mull' and 'mor' stages). We characterized responses of soil fertility and plant, soil microbial and nematode communities to the transition from mull to mor and whether these responses were coupled. For soil abiotic properties, we found this transition led to lower amounts of both nitrogen (N) and phosphorus (P) and an enhanced N to P ratio. This led to shorter-statured and less diverse forest, and convergence of tree species composition among plots. At the whole community (but not individual species) level foliar and litter N and P diminished from mull to mor, while foliar N to P and resorption efficiency of P relative to N increased, indicating increasing P relative to N limitation. We also found impairment of soil microbes (but not nematodes) and an increasing role of fungi relative to bacteria during the transition. Our results show that retrogression phenomena involving increasing nutrient (notably P) limitation can be important drivers in tropical systems, and are likely to involve aboveground–belowground feedbacks whereby plants produce litter of diminishing quality, impairing soil microbial processes and thus reducing the supply of nutrients from the soil for plant growth. Such feedbacks between plants and the soil, mediated by plant litter and organic matter quality, may serve as major though often overlooked drivers of long term environmental change.

At local spatial scales (tens to hundreds of meters), variability in soil fertility, notably the availability and supply of nutrients, is a fundamental driver of both aboveground and belowground community and ecosystem properties (Vitousek 2004). It has frequently been proposed that the aboveground and belowground ecosystem components show coordinated responses to soil fertility, because fertility governs the quality of resources that plants return to the belowground subsystem, and regulates the composition and activity of soil organisms that govern the supply of nutrients from the soil for plant growth (Berendse 1998, Wardle et al. 2004a, van der Putten et al. 2013). However, the evidence for coordination between the two components is mixed. For example, some studies have shown that nitrogen (N) addition can impede plant litter decomposition when added at levels known to enhance plant growth (Fog 1988, Carreiro et al. 2000), and plant production and litter decomposition can show contrasting responses to both N and phosphorus (P) fertilization (Hobbie and Vitousek 2000). Further, while some studies have found plant and microbial communities to show a coupled response to nutrient addition (Suding et al. 2008), others have found plants and microbes to respond to nutrient addition independently of each other (Wardle et al. 2013) or to respond to nutrient addition in similar ways in only some environmental settings (Sundqvist et al. 2014). Hence, the view that aboveground and belowground subsystems display simple and coordinated responses to variation in nutrient availability (Wardle et al. 2004b) appears to have mixed support.

The evaluation of how aboveground and belowground components of ecosystems respond to soil fertility in natural ecosystems is arguably done most effectively by comparing sites that are close to one another and which differ in nutrient availability but which have the same climate, parent material and topography. Such comparisons are scarce because of problems with potentially confounding factors. Some of the most effective comparisons have involved the use of retrogressive chronosequences (Walker and Syers 1976, Vitousek 2004, Wardle et al. 2004b, Peltzer et al. 2010). These chronosequences consist of sites that differ in their

stages of ecosystem development, and for which limitation by nutrients (and notably the limitation of P relative to N) increases over the time frame of several centuries to millennia (Peltzer et al. 2010). Only a handful of retrogressive chronosequences have been well characterized, and these include examples in temperate (Richardson et al. 2004), Mediterranean-type (Laliberté et al. 2012), boreal (Wardle et al. 2012) and montane tropical (Vitousek 2004) ecosystems. Few studies have explicitly considered both aboveground and belowground community responses to changes in soil fertility during retrogression; some have found coordinated responses (Williamson et al. 2005, Doblas-Miranda et al. 2008) while others have not (Wardle et al. 2012). Further, despite the tropics occupying 40% of the Earth's land surface, these studies have been performed mostly in boreal and temperate ecosystems, with almost nothing known about whether similar responses occur for tropical systems outside of Hawaii (Peltzer et al. 2010).

In the present study we considered replicated forest plots that have a comparable climate, topography and parent material in a montane tropical rainforested area in the Blue Mountains of Jamaica (Grubb and Tanner 1976, Tanner 1977). This area consists of several patches of each of two types of forest on ridge tops that are on 'mull' and 'mor' soil (sensu Muller 1884), i.e. 'mull' and 'mor' forest (sensu Tanner 1977), often adjacent or within 100 m of each other. Here, the mor soil consists of a thick uppermost layer of humus (usually >20 cm deep) while mull soil consists of organic material mixed into the soil and without a thick humus layer (Tanner 1977). The vegetation composition differs greatly between the two forest types, and the mor forest is shorter statured and with a much deeper and more acidic humus layer than is the mull forest (Tanner 1977, 1980). Soils in the mor forest also contain lower levels of available nutrients (on a per area basis) and support slower rates of those soil processes that enhance N availability when compared with the mull forest (Tanner 1977, Brearley 2013); further, litter bag studies show that mass loss from decomposition of tree litters placed in mor forest plots occurs more slowly (Tanner 1981). The mull forest represents an earlier stage of ecosystem development than the mor forest, and when mor forest vegetation and humus is removed (Sugden et al. 1985) or when fresh mineral soil in mor forest is exposed by uprooting of canopy trees following hurricane damage (Bellingham et al. 1995), the newly exposed surface is colonized by tree species that are characteristic of the mull forest but absent in the mor forest. As such, the mor forest patches represent the stage that the mull forest patches are likely to reach if soil profiles were not disturbed, and ecosystem retrogression was therefore able to proceed (Grubb and Tanner 1976). The patchiness of the forest may also be reinforced by chance colonization of ridge-crest sites by tree species that can form mor humus and alter their local environment (through production of acidic, nutrient-poor litter), in turn favoring mor-forming species and disfavoring many species that dominate on mull soils (Grubb and Tanner 1976, Tanner 1977).

We explored differences between six mull and six mor plots for several aboveground and belowground properties, to test the following three hypotheses which are based on our understanding of ecosystem retrogression (Peltzer et al. 2010). 1) Soil abiotic properties: soils in the mull plots will have higher amounts of the most biologically available forms of N and P, and a greater ratio of N to P, relative to the mor plots. This is based on the expectation that retrogression is characterized by decreasing plant-available nutrients and increasing limitation of P relative to N (Wardle et al. 2004b, Peltzer et al. 2010). 2) Aboveground properties: in addition to having a shorter stature, trees in mor plots will produce leaves and litter with lower N and P concentrations and greater N to P ratios than those in mull plots. Further, resorption of both foliar N and P prior to leaf senescence will be greater in mor plots, and P will be resorbed more than N in these plots. These differences are expected both at the individual species and whole plot levels, and are expected to reflect the differences in soil fertility between the mull and mor plots. 3) Soil biological properties: soils in the mor plots will support lower densities of soil primary decomposers (bacteria and fungi) and nematodes that feed on bacteria, fungi and each other, relative to the mull plots. Further, we expect that the ratio of fungi to bacteria and fungal-feeding to bacterial-feeding nematodes to be greatest in the mor plots, given that infertile ecosystems promote the fungal-based energy channel that promotes more conservative nutrient cycling (Coleman et al. 1983, Wardle et al. 2004a). Answering these questions in combination will inform on how local scale variability in soil fertility in tropical forests affects key aspects of both the aboveground and belowground components of ecosystems, the degree to which these components show coordinated responses to soil fertility and may feed back to one another, and ultimately the mechanistic basis by which forested ecosystems may respond to environmental change over time scales of centuries to millenia.

Methods

Study system, plots and soil sampling

The study was conducted on ridge forest in the western Blue Mountains of Jamaica (18°05′N, 79°39′W), between Belle Vue Peak (1822 m) and John Crow Peak (1762 m). The annual rainfall averages 2500–3000 mm year^{-1} (Kapos and Tanner 1985) and the mean monthly maximum temperatures range from 18.5 to 20.5°C, and minimum temperatures from 11 to 12°C (Tanner 1980). The region is in the Atlantic hurricane belt, and hurricane eyes pass over or within 15 km of the Blue Mountains every 25 years (Tanner and Bellingham 2006). The ridge includes several patches of both 'mull' and 'mor' forest. Soils in mull forest are characterized by having a thin O-horizon (<2 cm thick) and a well-developed A-horizon with a high organic matter content mixed into it (i.e. with $>30\%$ soil organic matter) (Plice 1946, Grubb and Tanner 1976). Soils in mor forest are characterized by a well-developed O-horizon dominated by organic material. The underlying mineral soil does show features of an A-horizon, but visible signs of E-horizon formation can be seen in the surface mineral soil (FAO/UNESCO 1988). Previous measurements in this study system reveal that for the mor forest soil carbon (C) concentration is 47% in the O-horizon (0–30 cm depth) and between 18% for 30–45 cm depth and 5% for 45–60 cm (Tanner 1977). Meanwhile C concentration for the mull forest soil is 29% for 0–8

cm depth, 18% for 8–11 cm and 1% for 11–68 cm (Tanner 1977). Mineral soils are derived from granodiorite, andesites and sedimentary rock, and are loams (Hafkenscheid 2000). The forests, through being on a ridge, are free draining and very rarely and only locally become waterlogged (Grubb and Tanner 1976, Tanner 1977).

For the present study, we selected six patches of mull forest and six of mor forest along the ridge at altitudes between ca 1500–1625 m, based on known vegetation composition of the two forest types (Tanner 1977). Within each patch we set up a 10×10 m plot between 16 and 23 September 2011, and all measurements and sampling were performed at that time. One each of these mull and mor plots are the same as those used for previous work in this system (Tanner 1977, 1980, 1981). All plots were at least 60 m from the next nearest plot, and the total area containing the plots was ca 1600×100 m (16 ha). The parent material underlying the plots is mainly derived from metamorphosed Cretaceous sediments and granodiorite. Parent material and topography are comparable between the two forest types.

Within each plot one composite soil sample (i.e. humus and/or mineral soil) was collected to 10 cm depth at the time of plot measurement. This was done by selecting four points (one in the center of each quadrant of the plot) and for each point using a trowel to collect soil to that depth; all soil within the plot was bulked. The depth of the humus layer was also measured at each point using a ruler. All soil samples were packaged at field moisture levels in double plastic bags, tightly positioned together in a single insulated box with minimal extra space, and sent by courier to Sweden where they were kept at 4°C before analyses were performed. There was a two week delay between collection in Jamaica and analysis in Sweden for reasons beyond our control, and as is characteristic for studies that have collected soils from remote locations and shipped them to laboratories elsewhere, we assume that any temperature changes in the samples during transportation would have been equivalent for all samples and would not have introduced treatment bias.

Abiotic soil properties

A subsample of each soil sample was sieved to 4 mm for measurement of abiotic properties. These included pH in a KCl extract, loss on ignition as a measure of soil organic matter (SOM) using a muffle furnace (360°C, 24 h), concentrations of total C, nitrogen (N) and stable N isotopes determined by combustion (with an elemental analyser connected with a mass spectrometer), phosphorus (P) determined by colorimetry on an auto-analyzer III after Kjeldahl digestion, and ammonium, nitrate and phosphate (following extraction with 1 M KCl) by colorimetry as above. Here, natural abundances of ^{15}N were expressed in per mil (‰) deviation from the international standard, i.e. atmospheric N. Ratios of C to N, C to P and N to P were calculated from the total C, N and P values. Lower natural abundance values of ^{15}N are typically associated with more conservative nutrient cycling and greater nutrient limitation (Menge et al. 2011, Brearley 2013). To characterize soil P composition, we performed a five-step sequential extraction for each soil sample as described by Hedley et al. (1982) and modified by Binkley et al. (2000) and Giesler et al. (2004); this provides a direct estimate of the five different operationally-defined P pools of contrasting lability. These include membrane-extractable inorganic P (P_i), $NaHCO_3$-extractable P_i and organic P (P_o), and NaOH-extractable P_i and P_o and HCl-extractable P. Membrane-extractable P_i and $NaHCO_3$-extractable P_i and P_o are considered to be more labile than NaOH and HCl extractable P (Giesler et al. 2004).

All concentrations of total soil C, N and P, and for all forms of both N and P, were expressed on both a per unit soil weight basis and a per area basis to 10 cm soil depth. To determine the latter requires a measure of soil bulk density; we calculated bulk density (g cm^{-3}) for each soil sample from the following equation based on the total C concentration of soils previously collected from this study system (Tanner and Bellingham, 2006), i.e.

$$\text{bulk density} = 0.998 \times \text{EXP}(-0.054 \times \text{soil C}); \; R^2 = 0.939.$$

Plant variables

For each plot, the diameter at breast height (DBH) of each stem with a DBH greater than 5 cm was measured and identified to species. The diameter of each stem was then converted to aboveground biomass by using allometric relationships developed in this study system by Tanner (1980). This biomass data was used to determine standing biomass of each woody species in the plot, as well as total biomass and the Shannon–Wiener diversity index. The total species richness of the measured stems was also determined.

For each of the dominant and subordinate but abundant woody plant species in each plot, foliar and litter samples were collected; a mean of 8.2 species were sampled per plot which on average comprised a total of 89.4% of the total woody plant biomass. For each species at least 25 fully expanded live leaves were collected from the canopy using a long handled pruner; we sampled only the most recently produced fully expanded leaves on each branchlet. At least 25 freshly fallen dead leaves were collected for the same species from the litter layer. For each species, the mean oven-dry weight per live leaf and per dead leaf was determined (for use in nutrient resorption calculations) and the total N and P concentrations measured by micro-Kjeldahl analysis; leaf and litter N to P ratios were determined from these values. For each species in each plot, we also determined resorption efficiency of both N and P as the percentage resorption during leaf senescence (Killingbeck 1996). Because substantial leaf mass loss can occur during senescence which needs to be corrected for when values of resorption efficiency are calculated, we used the measurements of mean live leaf mass and mean dead leaf mass for each sample to provide this correction (van Heerwaarden et al. 2003). As such, percent resorption efficiency for both N and P was calculated as:

$$\text{percent efficiency} = 100 \times ((\text{MLM} \times \text{CL}) - (\text{MDM} \times \text{CD}))/(\text{MLM} \times \text{CL})$$

where MLM is mean live leaf mass, MDM is mean dead leaf mass, CL is the concentration of N or P in live leaves, and CD is the concentration of N or P in dead leaves.

For each plant nutrient measure in each plot (i.e. foliar and litter N, P and N to P ratio, and N and P resorption) we calculated a plot-level abundance weighted measure by using the following equation according to Garnier et al. (2007):

$$\text{Plot-level measure} = \sum_{i=1}^{n} p_i \times \text{nutrient}_i$$

where p_i is the biomass of species i as a proportion of the total biomass for all species collected in that plot, and nutrient$_i$ is the value of the plant nutrient measure for species i. We also repeated these calculations but without abundance-weighting (so that all species were weighted equally) to provide a plot-level unweighted measure for each variable. Comparison of weighted and non-weighted plot-level nutrient measures enables assessment of the role of dominant versus subordinate species in determining these measures (Mason et al. 2012, Kichenin et al. 2013).

The height of the forest canopy was measured at four positions within each plot, by measuring the length of the pruner pole needed to sample canopy foliage.

Soil biological variables

A 4 mm sieved subsample of the soil sample collected from each plot was used for determination of soil microbial variables. We measured substrate-induced respiration (SIR; a relative measure of active microbial biomass) as described by Anderson and Domsch (1978) and modified by Wardle (1993). Briefly, a 3 g (dry weight) subsample of soil was amended to 150% moisture content (dry weight basis), amended with 30 mg glucose, placed in a 130 ml airtight vessel, and incubated at 22°C. Evolution of CO_2 between 1 h and 4 h was then determined by injecting 1 ml subsamples of headspace gas into a gas analyzer, and used as a measure of SIR. We also measured the composition of microbial phospholipid fatty acids (PLFAs) for assessing the microbial community by using the method of Bligh and Dyer (1959) as modified by White et al. (1979), and used by Sundqvist et al. (2014); different PLFAs represent different subsets of the soil microbial community. For each soil, the abundance of each fatty acid extracted was expressed as relative nmoles per g of dry soil using standard nomenclature. The PLFAs i15:0, a15:0, i16:0, 16:1ω9, 16:1ω7t, 16:1ω7c, i17:0, a17:0, cy17:0, 18:1ω7 and cy19:0 were used to indicate relative bacterial biomass, the PLFA 18:2ω6 was used to indicate relative fungal biomass and the PLFAs 10Me17:0 and 10Me18:0 were used to indicate relative actinomycete biomass. The PLFAs used for calculation of total branched PLFAs (i.e. gram positive bacteria) were i15:0, a15:0, i16:0 and i17:0, while those used to determine total cyclic PLFAs were cyc17:0 and cyc19:0. For each soil sample we expressed SIR and PLFA concentrations per unit soil weight, per unit SOM, and per unit area to 10 cm depth using the soil bulk density measures described above. Further, for each sample we calculated the Shannon–Wiener diversity index to represent the diversity of all PLFAs, and the ratio of fungal PLFAs to the sum of fungal plus bacterial PLFAs to represent the fungal to bacterial ratio.

An unsieved 100–150 g (wet weight) subsample of each soil sample was used to characterize the soil nematode community, by using a sugar flotation method. The nematodes were heat-killed, and fixed using 35% formaldehyde diluted to 4%. Subsequently approximately 200 nematodes per sample were identified to family level, and placed into five functional feeding groups following Yeates et al. (1993), i.e. bacterial feeders, fungal feeders, plant feeders, omnivores and predators. For each soil sample nematode densities were expressed per unit soil weight, per unit SOM, and per unit area to 10 cm depth as described above. For each sample we also used this data to determine the richness of nematode families, nematode diversity (Shannon–Wiener index), and the ratio of fungal feeding nematodes to fungal plus bacterial-feeding nematodes.

Data analysis

All aboveground and belowground response variables were analysed using one-way ANOVA (using STATISTIX ver. 10.0) with each plot as a replicate to test for differences between mull and mor forests; data were transformed if needed to conform to ANOVA assumptions. Further, differences between mor and mull plots for the community composition for trees (species biomass data), PLFAs and nematode families were each analyzed using principal component analysis (PCA), using CANOCO ver. 4.5 (ter Braak and Šmilauer 2002). To determine whether community composition for each of these three groups was significantly different between mor and mull plots, we used redundancy analysis (RDA) with Monte Carlo permutation tests (999 unrestricted permutations), using CANOCO ver. 4.5. All analyses for PCA and RDA analyses were run using proportional biomass or abundance data. As a measure of β-diversity for each of the tree, PLFA, and nematode community data sets, we calculated the inverse of the percentage similarity index:

$$\text{dissimilarity} = \sum_{i}^{N} \min(x_i y_i)$$

where x_i and y_i is the proportional abundance density (N_i / N, $N = \Sigma(N_i)$) of the i-th taxon in the two communities being compared (Lepš et al. 2001). We calculated 'overall' β-diversity for mull plots as the mean percentage dissimilarity of each mull plot with all other mull plots, and for mor plots as the mean percentage dissimilarity of each mor plot with all other mull plots.

Results

Soil abiotic variables

Humus depth was shallower in the mull than mor plots (mean ± SE: mull: 1.7 ± 0.5 cm; mor: 21.3 ± 2.9 cm; $F_{1,10} = 43.8$, $p < 0.001$). The pH in the top 10 cm of soil was greatest in the mull plots (mull: 4.46 ± 0.10; mor: 3.58 ± 0.06; $F_{1,10} = 58.3$, $p < 0.001$), as was soil bulk density (mull: 0.463 ± 0.032 g cm^{-3}; mor: 0.064 ± 0.001 g cm^{-3}; $F_{1,10} = 148.6$, $p < 0.001$). Levels of SOM were significantly greater in the mor than mull plots on a concentration basis (mull: 35.6 ± 3.0%; mor: 94.5 ± 0.9%; $F_{1,10} = 344.9$, $p < 0.001$) and significantly greater for the mull than mor plots on a per unit area basis to 10 cm depth (mull:

16052 ± 447 g m^{-2}; mor: 6105 ± 88 g m^{-2}; $F_{1,10} = 475.6$, $p < 0.001$).

The concentration of total C and N was greatest in mor plot soil, while that for P was greatest in mull plot soil (Fig. 1). On a per area basis to 10 cm depth, total C, N and P were all substantially greater in the mull than mor plots (Fig. 1). Meanwhile, the ratios of total C to N, C to P and N to P were all considerably greater in the mor than mull plots (Fig. 1). The $\delta^{15}N$ values of soil were greatest in the mull plots (mull: 2.38 ± 0.41‰; mor: –1.73 ± 0.24‰; $F_{1,10} = 74.6$, $p < 0.001$).

Mull plots had substantially more soil nitrate both on a per soil weight and per unit area basis than mor plots, while mor plots had substantially more ammonium per soil weight (Table 1). Soil phosphate was greater (but marginally not significantly so at $p = 0.05$) in the mor than mull plots both per unit soil weight and per unit area. Amongst the Hedley fractions, concentrations of $NaHCO_3$-extractable P_i and P_o were significantly higher in the mor than mull plots whereas NaOH-extractable P_o was higher in the mull than mor plots, when expressed per unit soil weight (Table 1). Meanwhile, all Hedley fractions except membrane-extractable P_i were considerably higher in the mull than in the mor plots on a per unit soil weight basis (Table 1).

Plant variables

Total tree aboveground biomass did not differ significantly between the mull and mor plots, but canopy height and tree species richness and diversity (Shannon–Wiener index) were all significantly less in the mor plots (Table 2). Further, of the 12 tree species that occurred most frequently in the mull

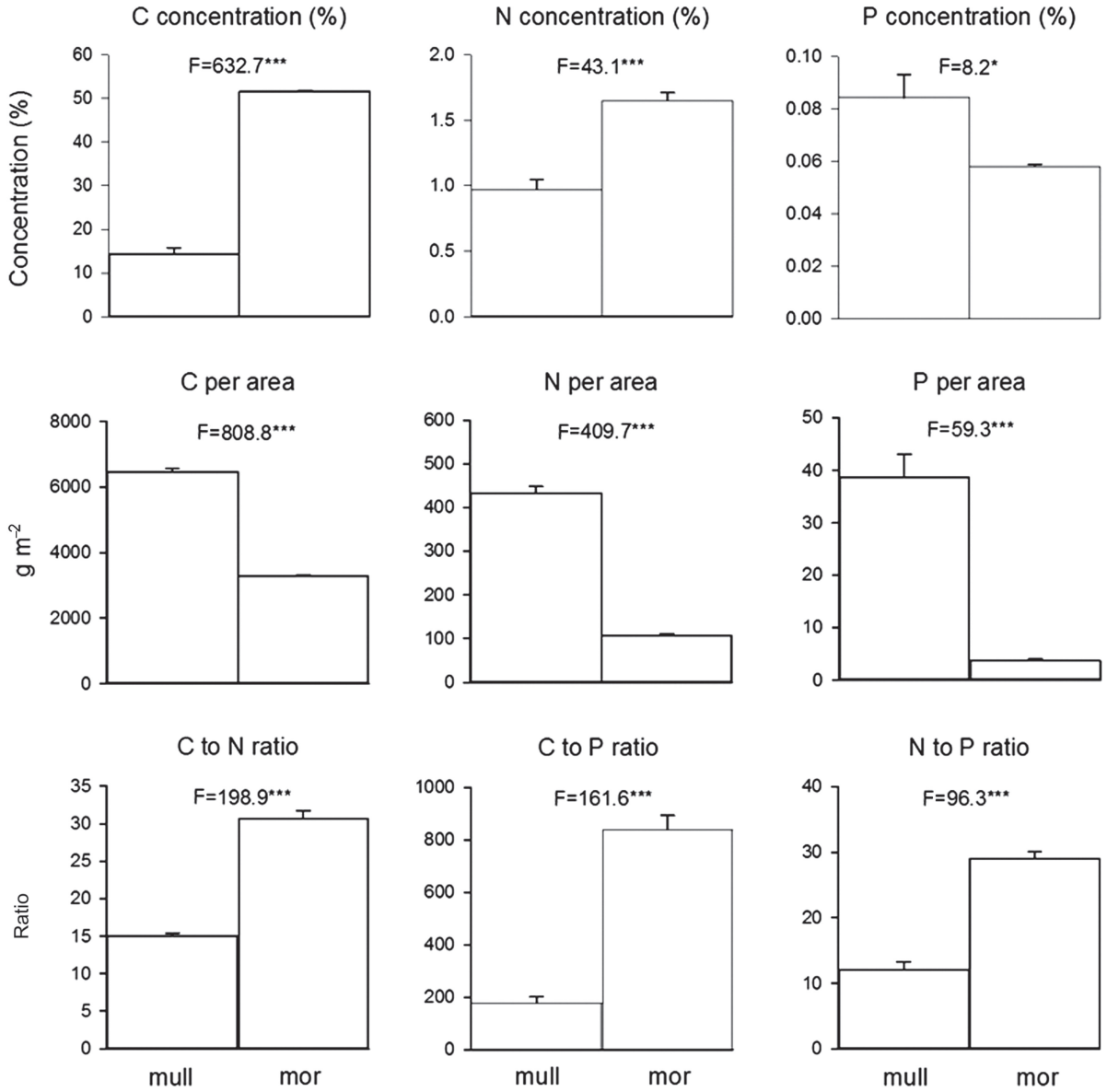

Figure 1. Soil carbon (C), nitrogen (N) and phosphorus (P) expressed both as a concentration and per unit area, and ratios of soil C to N, C to P and N to P. Values are means and standard errors. Note that the vertical axis scale varies among different variables. F-values are from one-way ANOVAs comparing mull and mor plots following ln-transformation of data; degrees of freedom are 1,10. *, **, ***indicate that the means for mull and mor plots differ at 0.05, 0.01 and 0.001, respectively.

Table 1. Chemical forms of soil nitrogen and phosphorus expressed both per unit soil weight and per unit area to 10 cm depth in mull and mor plots. Values are means ± standard errors (n = 6). For the Hedley fractionation data, HCl–extractable P_i was below detection limit for all samples and is thus not shown. Bold indicates statistically significant differences between mull and mor at p = 0.05.

	Per unit soil weight			Per unit area		
Measure	Mull	mor	F- and p- value[a]	mull	mor	F- and p- value[a]
	($\mu g\ g^{-1}$ soil)			($mg\ m^{-2}$)		
Ammonium	**1.69 ± 1.38**	**7.38 ± 1.09**	**10.5 (0.009)**	82.6 ± 67.4	47.6 ± 7.0	0.3 (0.617)
Nitrate	**20.19 ± 2.75**	**0.03 ± 0.03**	**53.8 (<0.001)**	**900.7 ± 87.5**	**0.2 ± 0.2**	**105.8 (<0.001)**
Phosphate	0.007 ± 0.004	0.485 ± 0.223	4.7 (0.056)	0.311 ± 0.211	3.097 ± 1.406	3.8 (0.079)
Hedley fractionation data[b]	($\mu g\ g^{-1}$ soil)			($g\ m^{-2}$)		
Membrane-extractable P_i	0.7 ± 0.3	31.2 ± 15.2	4.0 (0.072)	0.03 ± 0.01	0.23 ± 0.11	3.1 (0.104)
$NaHCO_3$-extractable P_i	**19.8 ± 3.3**	**39.0 ± 2.5**	**21.2 (0.001)**	**0.91 ± 0.16**	**0.29 ± 0.02**	**15.4 (0.003)**
$NaHCO_3$-extractable P_o	**33.3 ± 8.6**	**56.5 ± 3.9**	**6.0 (0.034)**	**1.47 ± 0.30**	**0.42 ± 0.03**	**11.8 (0.006)**
NaOH-extractable P_i	117.0 ± 2.7	105.5 ± 2.1	0.7 (0.432)	**5.32 ± 0.55**	**0.79 ± 0.05**	**66.7 (<0.001)**
NaOH-extractable P_o	**582.1 ± 68.3**	**380.5 ± 27.5**	**7.5 (0.021)**	**26.3 ± 2.97**	**2.89 ± 0.26**	**62.1 (<0.001)**

[a]F-values are from one way ANOVA with 1,10 degrees of freedom
[b]P_i = inorganic phosphorus, P_o = organic phosphorus

and/or mor plots, four had significantly higher biomass in the mull plots, and four had significantly higher biomass in the mor plots (Table 2). The PCA revealed large compositional differences between mull and mor plots (Fig. 2a), and the redundancy analysis revealed these differences to be highly statistically significant (F-ratio = 10.1, p = 0.002, proportion of total variation explained = 50.3%). Values for β-diversity were greater in the mull than mor plots (0.61 ± 0.02 and 0.31 ± 0.01, respectively).

Table 2. Data on tree biomass, canopy height, species richness and diversity (Shannon–Wiener index), and biomass of species occurring most frequently in mull and/or mor plots. Values are means ± standard errors (n = 6). Bold indicates statistically significant differences between mull and mor at p = 0.05.

Response variable	Mull plots	Mor plots	Test statistic and p-value[a]
Total biomass ($kg\ 100\ m^{-2}$)	2420 ± 295	1847 ± 153	3.0 (0.116)
Canopy height (m)	**13.0 ± 0.8**	**8.0 ± 0.5**	**23.6 (<0.001)**
Species richness per 100 m^2	**18.0 ± 1.3**	**10.0 ± 0.6**	**30.0 (<0.001)**
Shannon–Wiener index	**2.11 ± 0.09**	**1.75 ± 0.08**	**8.6 (0.015)**
Species biomass ($kg\ 100\ m^{-2}$)			
Alchornea latifolia	315 ± 141	333 ± 90	0.1 (0.715)
Chaetocarpus globosus	**0 ± 0**	**189 ± 172**	**10.8 (<0.001)**
Clethra occidentalis	**425 ± 125**	**121 ± 28**	**4.3 (0.034)**
Clusia havetioides	**0 ± 0**	**46 ± 37**	**8.9 (<0.001)**
Cyrilla racemiflora	**32 ± 79**	**347 ± 13**	**9.6 (<0.001)**
Eugenia virgultosa	**100 ± 40**	**1 ± 1**	**7.1 (<0.001)**
Lyonia octandra	**0 ± 0**	**612 ± 103**	**10.8 (<0.001)**
Pittosporum undulatum	46 ± 25	13 ± 6	1.0 (0.318)
Podocarpus urbanii	374 ± 212	3 ± 2	3.3 (0.074)
Sideroxylon montanum	**284 ± 231**	**0 ± 0**	**8.9 (<0.001)**
Solanum punctulatum	**213 ± 128**	**0 ± 0**	**8.9 (<0.001)**
Vaccinium meridionale	45 ± 63	101 ± 84	2.4 (0.130)

[a]Kruskall–Wallis test statistic for species biomasses, $F_{1,10}$ from ANOVA for all other variables

Community level measures of foliar and litter N and P were always greater in the mull than mor plots regardless of whether or not they were abundance-weighted, and these differences were significant at p = 0.05 with only one exception (Fig. 3). Community-level foliar N to P ratios were greater in the mull than mor plots but this was significant at p = 0.05 only when measures were not abundance-weighted. In contrast, community level litter N to P ratios were greater in the mor than mull plots but this was significant at p = 0.05 only when measures were abundance-weighted. Community measures of N resorption did not differ significantly between mull and mor plots but community measures of P resorption were greater in the mor plots; these were significant at p = 0.05 when measures were abundance-weighted but marginally non-significant when unweighted (Fig. 3).

At the individual species level, foliar N and P both varied at least two-fold among species in both the mull and mor plots (Supplementary material Appendix 1 Table A1). Of the four most widespread species, foliar N was significantly greater in the mull plots at p = 0.05 for *Clethra occidentalis* and marginally non-significantly greater for *Alchornea latifolia*. Foliar P did not differ significantly between mull and mor plots for any species. All four species had a higher foliar N to P ratio in the mull plots, and significantly so at p = 0.05 for three of them. Litter N varied at least three-fold and P varied at least seven-fold among species in both the mull and mor plots (Supplementary material Appendix 1 Table A2). Litter N, P and N to P ratios for the four most widespread species never differed significantly between mull and mor at p = 0.05, but there were marginally non-significant greater values in mull plots for litter N for two species and for litter N to P for one species. Resorption of N and P varied substantially among species in both mull and mor plots, with values for N resorption ranging from below zero to over 70%, and those for P resorption ranging from below zero to over 85% (Supplementary material Appendix 1 Table A3). Resorption of N did not differ between mull and mor plots for any of the four most widespread species, but P resorption was significantly greater at p = 0.05 in the mor plots for

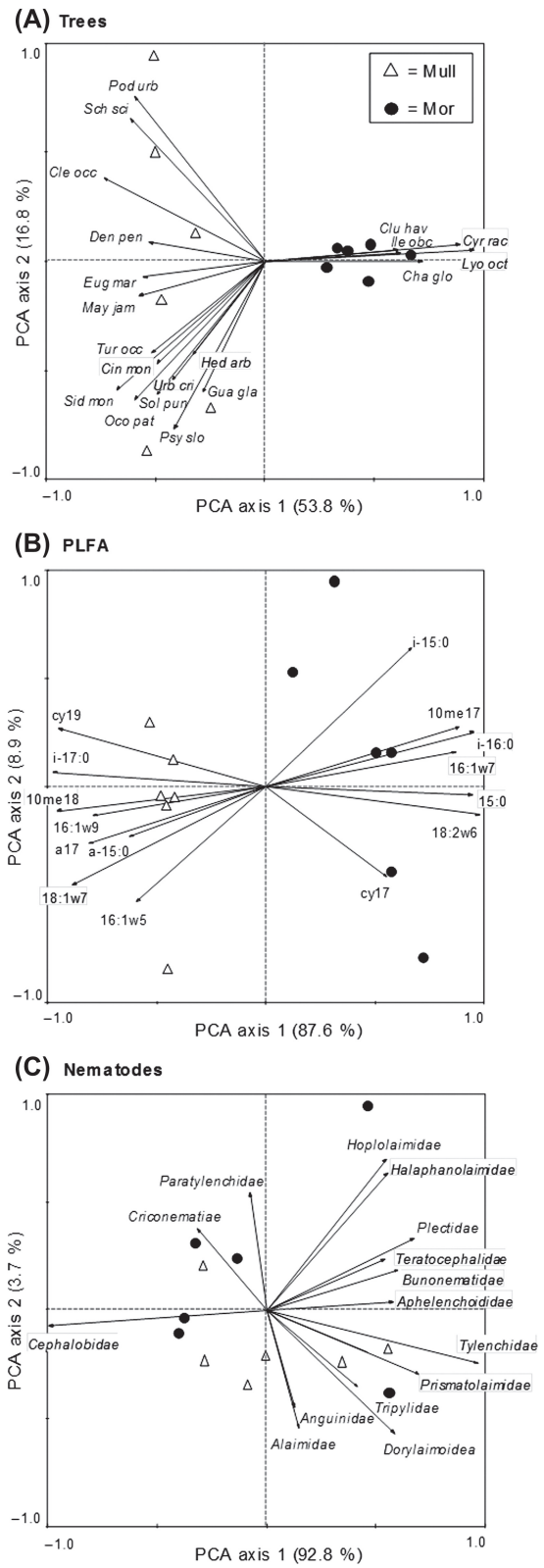

Figure 2. Species–sample bi-plots resulting from principal component analysis of the community composition of tree species (A), soil microbes (phospholipid fatty acids or PLFAs) (B) and soil nematode families (C). Percentages along the axes correspond to the amount of explained variation in community composition. Each point indicates one mor or mull plot. For clarity, only the best fitting tree and nematode taxa are plotted. Abbreviations for tree species: *Cha glo* = *Chaetocarpus globosus*, *Cin mon* = *Cinnamomum montanum*, *Cle occ* = *Clethra occidentalis*, *Clu hav* = *Clusia havetioides*, *Cyr rac* = *Cyrilla racemiflora*, *Den pen* = *Dendropanax pendulus*, *Eug mar* = *Eugenia marshiana*, *Gua gla* = *Guarea glabra*, *Hed arb* = *Hedyosmum arborescens*, *Ile obc* = *Ilex obcordata*, *Lyo oct* = *Lyonia octandra*, *May jam* = *Maytenus jamaicensis*, *Oco pat* = *Ocotea patens*, *Pod urb* = *Podocarpus urbanii*, *Psy slo* = *Psychotria sloanei*, *Sch sci* = *Schefflera sciodaphyllum*, *Sid mon* = *Sideroxylon montanum*, *Sol pun* = *Solanum punctulatum*, *Tur occ* = *Turpinia occidentalis*, *Urb cri* = *Urbananthus critoniformis*.

A. latifolia and marginally non-significantly greater for *Pittosporum undulatum*.

Soil biotic variables

Measures of SIR (i.e. active microbial biomass) were significantly greater at $p = 0.05$ in mor than mull soil on a per unit soil weight basis and greater in mull than mor soil on a per unit area basis; SIR was also marginally non-significantly greater in mull than mor soil on a per unit weight SOM basis (Fig. 4). For PLFA data expressed on a per unit soil weight basis, fungal and branched bacterial PLFAs were significantly greater in mor than mull soil and no other PLFA group differed between the two soil types. All PLFA groups significantly differed between the mull and mor soil when expressed either on a per unit SOM basis or per unit area (to 10 cm depth) basis; in all but one case (i.e. fungal PLFAs per unit SOM) the highest values occurred for the mull plots (Fig. 4). The ratio of fungal to bacterial PLFAs and diversity of PLFAs (Shannon–Wiener index) were both greatest for the mor soils (Table 3). The PCA revealed large compositional differences in PLFA composition between mull and mor plots (Fig. 2b), and the redundancy analysis revealed these differences to be highly statistically significant (F-ratio = 41.3, $p = 0.002$, proportion of total variation explained = 80.5%). Values for β-diversity were higher in the mull than mor plots (0.09 ± 0.01 and 0.05 ± 0.01 respectively).

For all nematode feeding groups, numbers per unit soil weight were greater for the mor than mull plots, and these differences were significant at $p = 0.05$ for all groups except the predators (Fig. 5). The same trend occurred when nematodes were expressed per unit OM, but here differences between mull and mor plots were significant only for bacterial-feeders, with differences for fungal-feeders and omnivores being marginally non-significant. There were no significant differences between mull and mor plots for any feeding group when densities were expressed per unit area, although densities of predators were marginally non-significantly greater for mull soils (Fig. 5). The ratio of fungal-feeding to bacterial-feeding nematodes and nematode diversity (Shannon–Wiener index) did not differ between mull and mor plots, but mor soils supported a greater richness of nematode families than did mull soils (Table 3). The PCA did not reveal any compositional differences in nematodes between mull and mor plots (Fig. 2c), and this was supported by the redundancy analysis (F-ratio = 0.3, $p = 0.630$, proportion of total variation explained = 2.5%). Values for β-diversity were lower in the mor than mull plots (0.31 ± 0.03 and 0.38 ± 0.04 respectively).

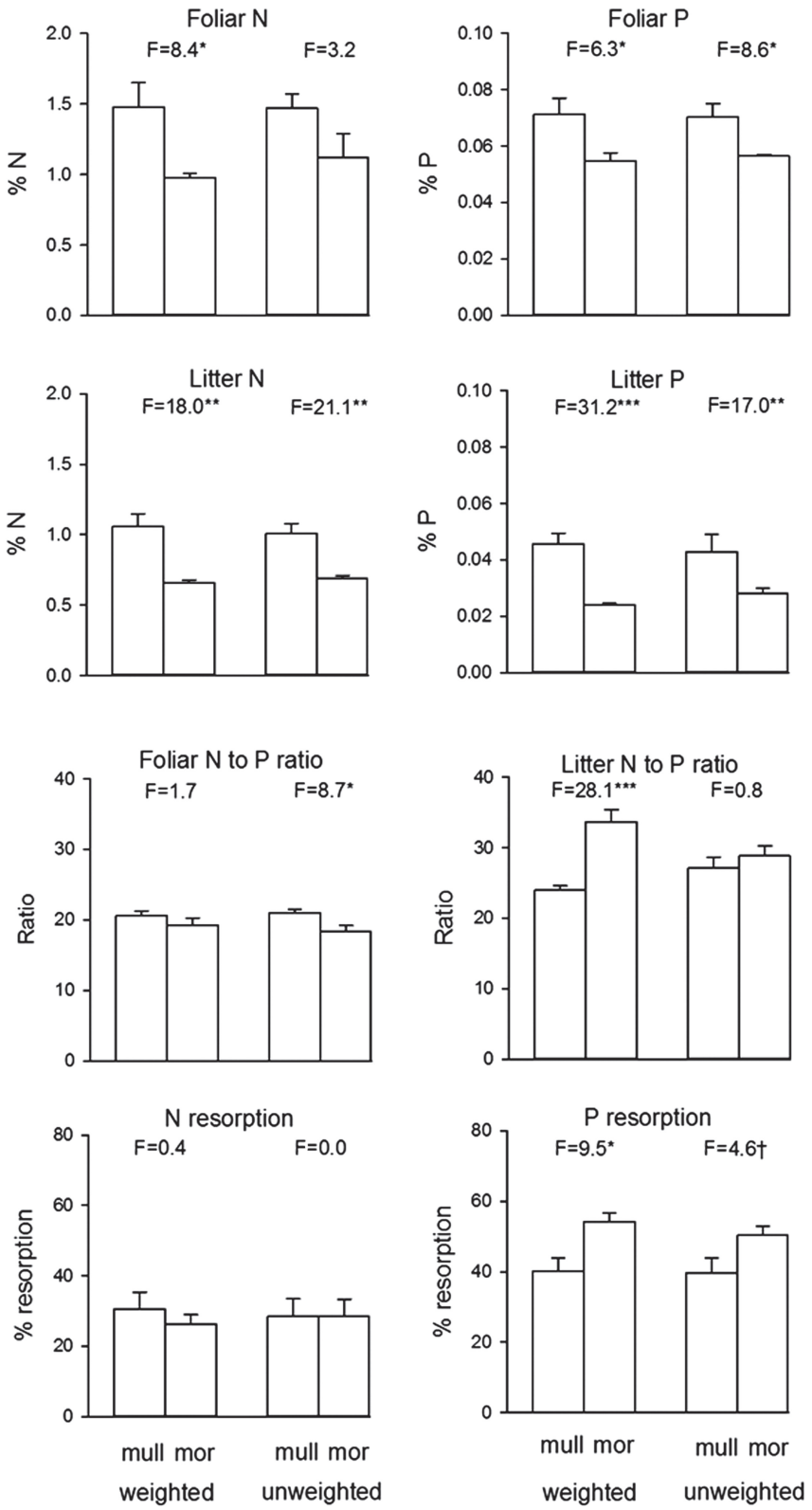

Figure 3. Abundance-weighted and unweighted whole plot level measures of foliar and litter nitrogen (N), phosphorus (P) and N to P ratios, and N and P resorption during leaf senescence. Values are means and standard errors. F-values are from one-way ANOVAs comparing mull and mor plots; degrees of freedom are 1,10. †, *, **, ***indicate that the means for mull and mor plots differ at 0.10, 0.05, 0.01 and 0.001, respectively.

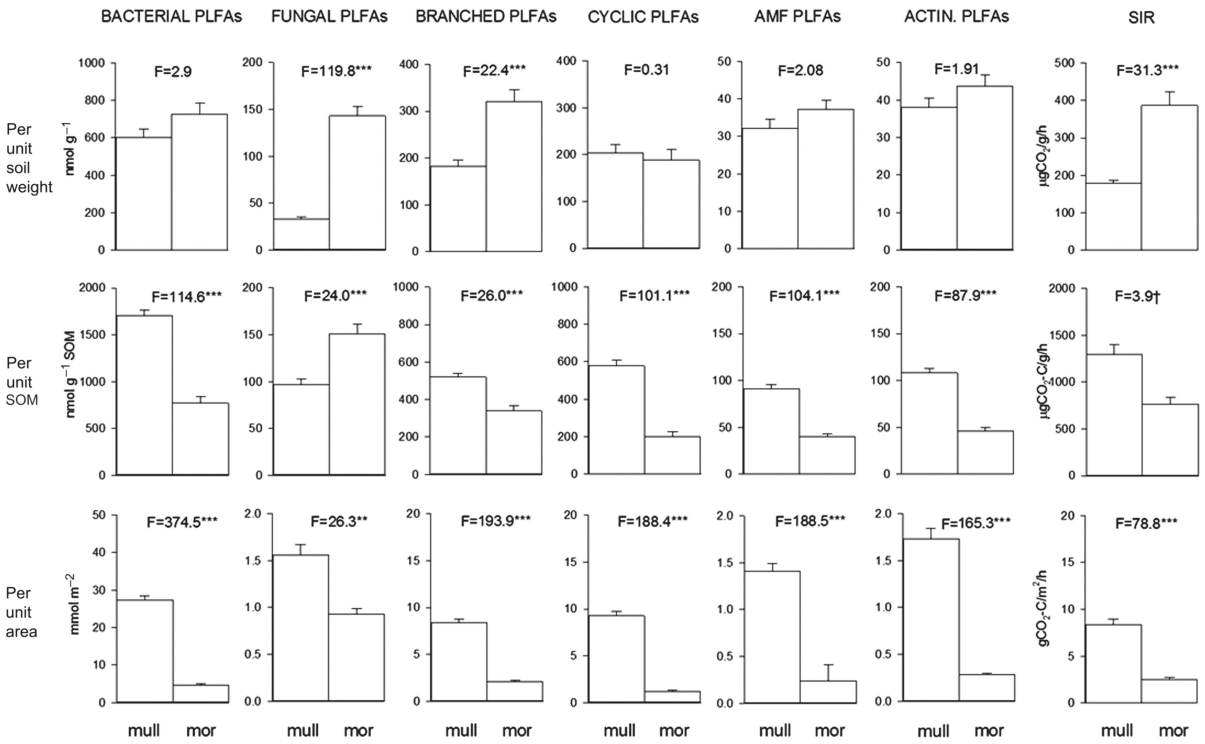

Figure 4. Measures of soil microbes measured as phospholipid fatty acids (PLFAs) and substrate-induced respiration (SIR), expressed per unit soil weight, per unit soil organic matter (SOM), and per unit area to 10 cm depth. AMF = arbuscular mycorrhizal fungi; ACTIN = actinomycetes. Values are means and standard errors. Note that the vertical axis scale varies among different variables. F-values are from one-way ANOVAs comparing mull and mor plots; degrees of freedom are 1,10. †, *, **, ***indicate that the means for mull and mor plots differ at 0.10, 0.05, 0.01 and 0.001, respectively.

Discussion

We found that the transition from mull to mor stands involves changes both belowground and aboveground that are characteristic of retrogression or soil aging. These include diminished soil fertility, reduced forest stature and diversity, reduced nutrients in foliage and litter at the whole community (though usually not the individual species) level, and lower densities of microbes (though not nematodes) per unit soil C and per unit area. We now discuss these results and their significance for understanding how local scale variability of soil fertility in tropical forests affects key aspects of both the aboveground and belowground subsystems.

We found several changes in soil abiotic properties from mull to mor that are mostly consistent with changes expected during retrogression. These are in line with mineral nutrient data reported from this system by Tanner (1977), and with our first hypothesis. First, we showed that mor soils have a higher N to P ratio than mull soils, in line with what occurs during retrogression in other systems (Wardle et al. 2004b, Peltzer et al. 2010). This is likely because N (which can be fixed biologically) can be replenished while P (which is derived from parent material) cannot (Vitousek 2004). In our study system, N_2-fixing trees are very scarce, but it is known for other montane tropical forests that free living N_2-fixing bacteria, such as those associated with dead leaves, can fix appreciable amounts of N (Crews et al. 2000). Second, we showed a marked increase in SOM depth, which is likely to stem from less decomposer activity (Fig. 4) and lower quality litter entering the decomposer subsystem (Fig. 3). This is indicative of a shift of C storage from vegetation to longer term organic matter pools in the soil (Peltzer et al. 2010). Third, we found that concentrations of nitrate and total P diminished from mull to mor. Conversely, the concentrations of total N, ammonium, phosphate and of two of the three most labile forms of P from the Hedley

Table 3. Community–level variables for the soil microflora using phospholipid fatty acid (PLFA) data, and nematode fauna, in mull and mor plots. Values are means ± standard errors (n = 6). Bold indicates statistically significant differences between mull and mor at p = 0.05.

Response variable	Mull plots	Mor plots	F- and p-value[a]
Ratio of fungal to fungal + bacterial PLFAs	**0.054 ± 0.002**	**0.169 ± 0.019**	**37.2 (<0.001)**
Ratio of FF to FF + BF nematodes[b]	0.086 ± 0.031	0.050 ± 0.013	1.2 (0.299)
Diversity (Shannon–Wiener index) for PLFAs	**2.28 ± 0.01**	**2.36 ± 0.01**	**24.1 (<0.001)**
Diversity (Shannon–Wiener index) for nematode families	1.20 ± 0.23	1.36 ± 0.37	0.1 (0.728)
Richness of families for nematodes	**6.00 ± 0.63**	**8.66 ± 0.76**	**7.2 (0.024)**

[a]Derived from one-way ANOVA; degrees of freedom are 1,10
[b]FF = fungal-feeders; BF = bacterial-feeders

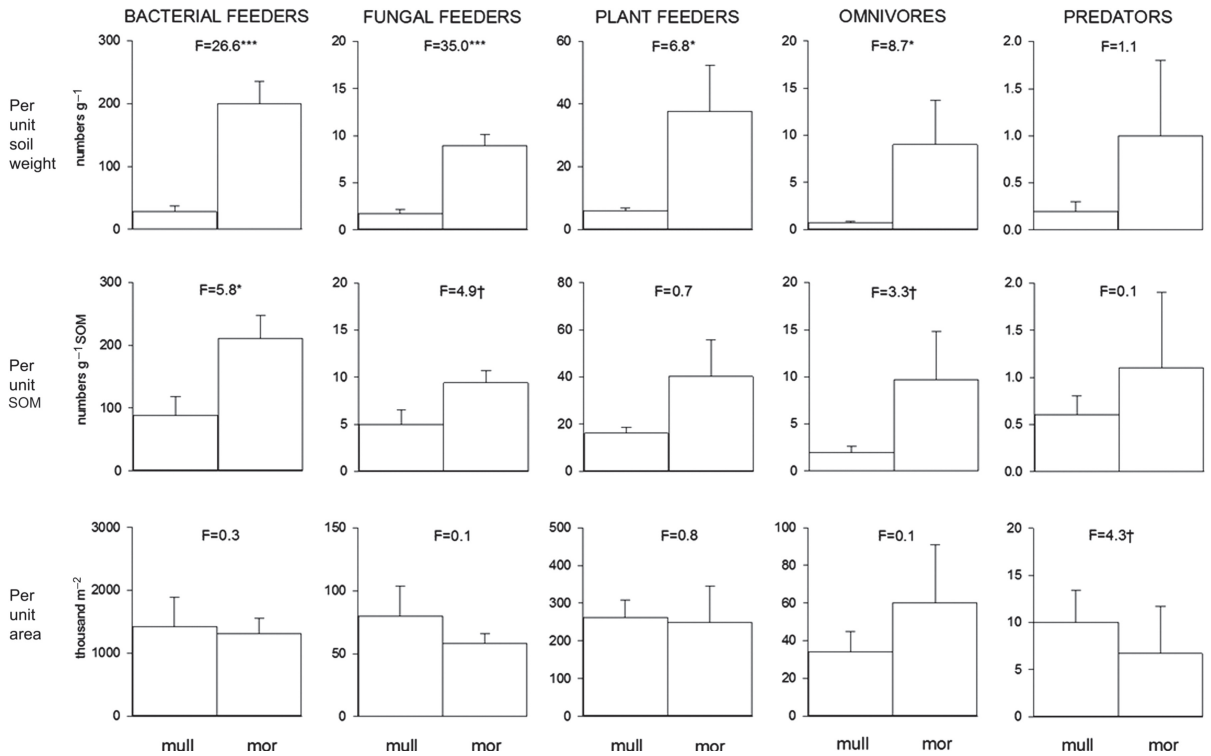

Figure 5. Densities of major functional groupings of soil nematodes, expressed per unit soil weight, per unit soil organic matter (SOM), and per unit area to 10 cm depth. AMF = arbuscular mycorrhizal fungi; ACTIN = actinomycetes. Values are means and standard errors. Note that the vertical axis scale varies among different variables. F-values are from one-way ANOVAs comparing mull and mor plots following ln-transformation of data; degrees of freedom are 1,10. †, *, **, ***indicate that the means for mull and mor plots differ at 0.10, 0.05, 0.01 and 0.001, respectively.

fractionation increased, but this was mostly due to the greater amount of organic matter in the mor soil, and when data are expressed per unit area to adjust for this, most of these measures decreased. Further $\delta^{15}N$ values were lower in the mor plots, in line with what has been shown for both this system (Brearley 2013) and other retrogressive sequences (Selmants and Hart 2008, Menge et al. 2011), and is consistent with more closed N cycling through diminished N availability in the mor sites. In total, our results provide evidence that as mull plots transition to mor plots over time, there are distinct decreases in N and P availability in the top 10 cm of the soil layer (where most plant rooting occurs) and reduced total P relative to total N.

The changes that occurred in abiotic soil properties from the mull to mor transition had important effects on forest stand characteristics. Although mor plots did not have significantly less biomass than mull plots they were significantly shorter, as expected for forests undergoing retrogression (Crews et al. 1995, Richardson et al. 2004). Further, there were large compositional differences, with both less α-diversity and β-diversity in mull than in mor plots. This arises because the mull plots have a much larger potential pool of tree species (Tanner 1977), with different subsets of this pool establishing on different plots, but with these plots supporting fewer species from a smaller species pool as they transition to mor plots over time. The fewer species that can establish on mor plots leads to convergence of species composition and thus less variation of composition among mor than among mull plots (Walker and del Moral 2003, Walker et al. 2010). Our findings are consistent with work from some other chronosequences that show a smaller potential species pool and thus reduced tree diversity as retrogression proceeds (Wardle et al. 2008), despite total α-diversity (including understory species) frequently increasing (Laliberté et al. 2013).

We found our hypotheses regarding changes in foliar and litter N and P characteristics to be more consistently supported at the whole community level than at the individual species level. At the community level, we found both foliar and litter N and P to be less on the mor than the mull plots, in line with the reduced soil fertility in these plots. We also found two lines of evidence for greater limitation by P than by N in the mor plots. First, the litter N to P ratio was greater in the mor plots though only for abundance-weighted measures (and with a weak but significant trend in the opposing direction for the foliar N to P ratio when abundance weighting was not performed). Second, community-level foliar resorption values for P but not for N were greater in the mor than mull plots. These findings are broadly in line with other studies showing community-level measures to reflect increasing P relative to N limitation as retrogression proceeds (Richardson et al. 2005, Wardle et al. 2009, Hayes et al. 2014). Further, with the exception of the litter N to P ratio, we found comparable differences in N and P characteristics between the mull and mor plots regardless of whether or not the community-level measure was abundance weighted, meaning that dominant and minor species contribute similarly to these differences (Mason et al. 2012,

Kichenin et al. 2013). At the community level, our results show that the greater limitation of both N and P during retrogression, and the greater limitation of P relative to N, leads to the return to the decomposer subsystem of litter that has poorer quality and with an elevated N to P ratio.

However, when foliar and litter N and P characteristics for each of the four species that occurred commonly on both mull and mor plots was considered, the trends identified at the whole community level for were mostly unsupported. Consistent with Tanner (1977), we found foliar N and P levels within species to be rather unresponsive to the transition from mull to mor, suggesting a rather low plasticity at the individual species level. This is in line with other work along retrogressive chronosequences (Lagerström et al. 2013) and other gradients of soil fertility (Kichenin et al. 2013) in revealing that traits of individual species can show contrasting responses both to each other and to whole community measures. These various responses emerge because of the complex nature of interactions and consequences for nutrient acquisition among coexisting species (Kichenin et al. 2013). Our results also contrast with some studies that have pointed to a strong role of intraspecific variation in determining trait values at the whole community level (Albert et al. 2010, Violle et al. 2012). The fact that we find clear responses of foliar and litter characteristics at the whole community but not individual species level emerges because differences between mull and mor plots appear to be driven by genera that occur largely only in the mull plots (e.g. *Solanum*, *Eugenia*) or only in the mor plots (e.g. *Clusia*, *Lyonia*, *Vaccinium*, *Chaetocarpus*), and therefore by turnover of species between the mull and mor plots (Wardle et al. 2009).

We found that while microbial measures as assessed by the SIR and PLFA techniques were enhanced in the mor plots when expressed per unit soil mass, this arose simply through the mor soils containing more SOM; when data was expressed per unit SOM (or per unit area) the microflora was impaired, in line with our third hypothesis. This is reflective of SOM being of lower quality in the mor than the mull plots (Insam and Domsch 1988). Further, we found the ratio of fungal to bacterial biomass to increase from mull to mor, in line with what has been shown during retrogression for some other chronosequences (Williamson et al. 2005, Wardle et al. 2012). This is also consistent with our third hypothesis, and is indicative of lower resource quality and more conservative nutrient cycling in the mor soil (Coleman et al. 1983, Wardle et al. 2004a). We did not, however, find nematode groups to be impaired in mor relative to mull soils, and indeed the reverse was sometimes true even when densities were expressed per unit SOM. This is likely to be due to greater soil moisture availability resulting from higher organic matter levels in the mor soil creating a microclimate that is more conducive for nematodes (which require moisture for motility and feeding; Bakonyi et al. 2007), and with this effect counteracting any effect of lower fertility in the mor soil. The deeper organic matter layer in the mor plots, and probably therefore a greater diversity of microhabitats, could also help explain the higher diversity of both microbial PLFAs and nematodes in the mor plots despite plant diversity being less. In total, the data for the primary decomposers (microbes) is strongly indicative of poorer resource quality in the mor plots, which may arise both from diminishing soil fertility exerting direct effects and indirect effects via poorer quality of plant litter entering the soil. This will in turn lead to reduced microbial activity, reduced mineralization of nutrients for plant growth, and impaired decomposition leading to build up of soil organic matter.

We note that while there has been a growing interest in identifying and interpreting retrogressive chronosequences from around the world (Peltzer et al. 2010), with one exception all described examples are from the temperate or boreal zones. Our work, alongside that from Hawaii (Vitousek 2004), suggests that the type of retrogressive phenomena identified elsewhere also occurs in tropical systems at least in areas relatively unimpacted by humans. This is consistent with suggestions that controls of N relative to P availability, and the ecological consequences of this, are governed by similar biogeochemical processes in vastly differing climatic regions, even if the time scale involved may vary (Wardle et al. 2004b, Peltzer et al. 2010). While we are unable to identify the precise time frame over which this retrogression occurs (attempts to use ^{14}C dating on soil organic matter were unsuccessful, presumably because of soil bioturbation), the size and structure of the trees suggest that this process occurs at least over the timeframe of centuries, probably longer.

Our results provide evidence for the type of feedback mechanism between the aboveground and belowground subsystems proposed for this study system by Grubb and Tanner (1976), and which operates in a comparable manner to that previously shown for a fire-driven retrogressive chronosequence in boreal forest (Wardle et al. 2012). In such a feedback, a decreased availability of nutrients (notably P) over time would lead to diminished soil fertility, and replacement of plant species that produce high quality litter with those that produce poorer litter. The poorer quality litter entering the decomposer subsystem would in turn impair microbial activity and contribute to reduced mineralization of nutrients required for plant growth and consequently a build-up of organic matter. Over a time scale from centuries to millennia, this reduction in nutrient supply would lead to retrogressive ecosystems characterized by reduced vegetation stature and productivity. Most studies on plant–soil feedbacks have considered only plant associations with soil organisms that interact with their roots in the short term, rather than with the decomposer subsystem over much larger spatial and temporal scales (Wardle et al. 2012, van der Putten et al. 2013). As such, study systems such as the one investigated here can be used to inform on likely mechanisms through which feedbacks between the plant community and the belowground subsystem, mediated by plant litter and organic matter quality, can contribute to ecosystem succession and (over sufficient timescales) ecosystem retrogression. More broadly, greater consideration of these sorts of feedbacks delivers the potential to better understand drivers of ecosystem change in forested ecosystems over the time scale of centuries to millennia, including those drivers resulting from human-driven global change phenomena.

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Supplementary material (available online as Appendix oik.01584 at <www.oikosjournal.org/readers/appendix>). Appendix 1.