

1 Tanner responses to comments by W Wieder.

2 1) Comment.

3 “Was soil mineral mass measured in each plot, in each treatment, or in a single pit (like bulk
4 density)”

5 Response

6 Soil mineral matter was calculated for each plot and soil depth from soil carbon concentration
7 (mineral matter is total soil mass minus twice soil carbon content). Bulk density was measured for
8 every plot for 0-5 cm depth; below 5 cm we used the bulk density from one soil pit (lines 146-151 in
9 the manuscript).

10 2) Comment.

11 “More broadly, the emphasis placed on soil mineral mass to extrapolate findings seems somewhat
12 surprising,”

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14 Response

15 The emphasis on expressing soil carbon per mineral mass is to deal with the (general) problem that
16 as soil organic matter changes the bulk density changes, so sampling to the same depth will not be
17 comparing like with like. This is well known problem - Powlson et al 2011 say “The principle is that an
18 equal mass of organic-matter-free mineral soil should be sampled between the treatments or times
19 being compared.” For this reason in our study in Panama we expressed carbon relative to an
20 unchanging mineral mass. It is also an easy calculation to make and can often be made
21 retrospectively on published data. It was not done to get round a problem of non-significant results.

22

23 3) Comment.

24 “If data are available to make an extrapolation of Fig 3 with depth on the X axis it would be much
25 more valuable for studies trying to quantify or model changes in soil C stocks, as information about
26 mineral mass is typically lacking or not considered.”

27 Response

28 Fig 4 shows the cumulative (with depth) mineral matter and soil depth in the control plots, down to
29 about 93 cm. An e mail exchange with the referee clarified that he wanted a second axis In Fig 3
30 showing the soil depth in the control plots – we have done this. We disagree with the comment that
31 “information about mineral matter is typically lacking”, because if samples have data on soil carbon
32 per dry soil mass, then the mineral matter is easily calculated (as total mass minus twice soil carbon -
33 there will be a small error because soil organic matter is not exactly twice soil carbon, but the effect
34 will be trivial.)

35 4) Comment.

36 “I recall publications from some of the temperate DIRT plots (e.g., Lajtha references in the paper)
37 showed changes in different soil C fractions. I assume similar data are not available for this study,
38 but I wonder if consideration of C stabilization mechanisms and soil mineralogical conditions could

39 help explain some of the differences between temperate and tropical sites. Is it worth a brief
40 discussion on this point (e.g. expanding / developing the paragraph that begins on line 202)?”

41 Response

42 Other researchers are working on this in the experiment. As we present no data on carbon fractions
43 in this paper we think it best to leave discussion of that subsequent manuscripts.

44 5) Comment.

45 “The authors (justifiably) seem keen on their soil P results, which are interesting and relevant (line
46 262). Is it possible to extrapolate findings for P, similar to the soil C figure 3, making this a multi-
47 panel figure?”

48 Response

49 It is not sensible to express cumulative Mehlich P per cumulative mineral mater (in an analogous
50 way to cumulative carbon per cumulative mineral matter in Fig. 3) because a substantial (but
51 unknown) amount of Mehlich P comes from organic matter. Soil matter is either organic or mineral
52 and we plot one against the other in Fig. 3; Mehlich P is different - it comes from both mineral and
53 organic matter.

54 6) Comment.

55 “The discussion starts off with the introduction of new results. I appreciate the authors wanting to
56 focus readers’ attention on these findings, but feel like results (Figs 3 & 4) are best introduced in the
57 results, not discussion section of a paper”

58 Response

59 We disagree. The ‘results’ are concentrations of carbon per mass. We then use those results to
60 calculate concentrations of carbon per mineral matter.

61 7) Comment.

62 “Finally, calling out the small plots from the Costa Rican study seems a bit unjustified in a single
63 paragraph subsection of the discussion. Granted the authors make a good point about the
64 appropriate size of experimental plots, but I think Leff and co-authors (2012, cited in the paper)
65 acknowledge the limitation of their small plots. If the authors want this section to remain they
66 should more broadly discuss other litter manipulation studies, not just the Costa Rican site.”

67 Response

68 We are not making any personal points here, but we do think that there is a real issue about the size
69 of experimental plots affecting the qualitative patterns of results. Specifically, small (3 x 3 m) litter
70 removal and addition plots might be local cold spots and hot spots that will affect the responses. The
71 pattern of results from small plots might be the OPPOSITE of those from large plots. For example,
72 small litter addition plots might cause extra root growth into local patches of soil with extra
73 nutrients, but large litter addition plots (45 x 45 m) might cause reduced root growth because the
74 whole tree is receiving extra nutrients and ‘can afford’ to reduce root growth and put more into
75 shoot growth, in other words, a completely opposite pattern of results caused by differences in
76 experimental design. We simply want to point out that the design of these experiments might well
77 affect the pattern of results. If there were lots of experiments like this we could look for patterns,
78 but there aren’t many.

79 To address the reviewer’s comment, we have changed the last line to “small hot and cold spots may
80 not represent what would happen in plots on the scale of the large trees - as pointed out by Leff et al
81 2012.”

82 8) Technical corrections:

83 Comment. Introduction: specific values for C pools, turnover times, and fractions seem
84 unnecessarily detailed (lines 33, 36). More broadly the introductions reads a bit like a bullet
85 point of disconnected ideas. This is a stylistic concern, not a scientific one.

86
87 Response. As Wieder says this is stylist – we think this is clear and informative
88

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91 Comment. Throughout, check that abbreviations are defined before they are used in the
92 text (eg. LR and LA line 55, GFP line 251).

93
94 Response. We have changed all ‘LR’ to ‘litter removal’ and all ‘LA’ to ‘litter addition’. We
95 have reworded the text so that GFP is no longer used.

96
97
98 Comment. Line 66-68, This is unclear P mineralization (0-2 cm) in LR plots met 20% of NPP
99 needs, or the decline in P mineralization would have met this demand?

100
101 Changed to “mineralization of organic phosphorus (P) (inferred from the decrease in the
102 concentration of organic P) in the top 2 cm of soil during three years of litter removal was
103 calculated to be sufficient to supply 20% of the P needed to sustain forest growth”

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105 Comment. Line 76. This study looked at net nitrification and should be Wieder et al. 2013 (i
106 before e).

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108 Response. Added ‘net’ and corrected spelling of Wieder.
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110
111 Comment. Line 89. Awkward. Forest productivity isn’t mitigated, but increases in terrestrial
112 C storage can mitigate atmospheric CO2 accumulation.

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114 Response. Changed to “can thus be considered as partial mitigation of atmospheric CO₂
115 accumulation through increased forest productivity”

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118 Comment. Line 210. Awkward, maybe insert ‘a’ here: In a deciduous forest in MA. . .
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120 Response. Changed to “In a deciduous forest in”
121

122 Comment. Line 307. What is meant by ‘polluted’ sites? Is this sites receiving large amounts
123 of N, P or micronutrient deposition (is the later actually a real a thing)? Is this just to say that
124 litter manipulations aren’t identical to CO₂ enrichment alone, because they also serve as
125 nutrient manipulations that modify ecosystem dynamics?

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Response. This site is not receiving large amounts of N or P (though N input is increasing Hietz et al 2011 Science 334, 664). Our comparisons are based on N & P inputs in polluted sites in USA and Europe. We have added ‘temperate’.
We don’t mention micronutrients in the Conclusions – so we ignore that part of the comment.

Biogeosciences Discuss. of Tanner at al. “Changes in soil carbon and nutrients”
Author responses to reviewer 2

Comment “I would appreciate seeing a comparison of results using more traditional ways of measuring soil C (e.g., fraction of dry mass) and the approach utilized here. Given its novelty, mineral mass is of limited utility when comparing to other studies.”

Response

Tanner did a calculation (using the data in the supplementary material) of the changes in concentration over the top 20 cm of soil. Litter removal soil shows a 1.9% fall in concentration and litter addition a 2.0% increase in C concentration. This compares with 1% per year using the ‘new’ calculation based on the same amount of mineral matter. We put a sentence about this into the discussion in the revised ms. “These changes are about c. 1% per year; in contrast if we calculate the change based on a fixed depth of 20 cm, ignoring changes in bulk density, we get a change of about 2% per year. Thus ignoring the changes in bulk density results a misleading doubling of the estimated rate of change.”

Comment

Technical comments: Please clarify abbreviations: The LA and LR

Response. LA and LR now written out in full everywhere. L- and L+ now changed to litter removal and litter addition.

Comment

The sentence that begins on line 75 is awkward - perhaps a better way of saying this is that "After 2.5 years of litter manipulation in Costa Rica, surface soils (0-10 cm) had lower nitrification in both litter removal and addition treatments..."

Response

We ask to keep our original wording. We deliberately put “In Cost Rica” first in the sentence to mark the fact that we are moving on in the discussion from Panama to Costa Rica. If we start with “After 2.5 years of litter manipulation” it could be taken to mean that we are still discussing Panama.

Comment

“On line 89, the carbon that stays in soil and litter crop does not mitigate increased forest productivity”

Response.

I could not find this. Anyway, in our revised ms we use ‘mitigate’ only once
“The increase in C in the mineral soil and the litter standing crop following litter addition was statistically significant in the top 20 cm of the soil, suggesting that any increased litterfall as a result of increased atmospheric CO2 and/or temperature could result in a substantial increase in soil C and therefore partially mitigate the increase in atmospheric CO2.”

Comment

215 I appreciated the improvements to the figures in response to previous comments. The figures could
216 be strengthened by including notations to depict which litter effects were significantly different from
217 controls. While this information is largely contained in the text, including this in the figures would
218 help if the images were ever reproduced for other uses.

219 **Response.**

220 In Figs 1 & 2 we plot means and confidence errors if errors don't overlap means are significantly
221 different; we say which are significant in the text. We make comparisons between litter removal and
222 litter addition, as well as between each treatment and control, showing both types of comparison on
223 the figure would clutter up the diagrams, so I drew a new figure for the supplementary material
224 showing just those elements that were significantly different, and just down to 30 cm; I also added a
225 second supplementary Table with the means and 95% confidence intervals for the data in Figs 1 & 2.

226

227 End of comments and responses.

228

229 Comparison of original ms submission and revised version

230 **Title:**

231 **Changes in soil carbon and nutrients following six years of litter removal and addition in a tropical**
232 **semi-evergreen rain forest.**

233

234 **Authors**

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240 **Abstract**

241 Increasing atmospheric CO₂ and temperature may increase forest productivity, including litterfall,
242 but the consequences for soil organic matter remain poorly understood. To address this, we
243 measured soil carbon and nutrient concentrations at nine depths to 2 m after six years of continuous
244 litter removal and litter addition in a semi-evergreen rain forest in Panama. Soils in litter addition
245 plots, compared to litter removal plots, had higher pH and contained greater concentrations of: KCl-
246 extractable nitrate (both to 30 cm); Mehlich-III extractable phosphorus and total carbon (both to 20
247 cm); total nitrogen (to 15 cm); Mehlich-III calcium (to 10 cm); Mehlich-III magnesium and lower bulk
248 density (both to 5 cm). In contrast, litter manipulation did not affect ammonium, manganese,
249 potassium or zinc, and soils deeper than 30 cm did not differ for any nutrient. Comparison with
250 previous analyses in the experiment indicates that the effect of litter manipulation on nutrient
251 concentrations and the depth to which the effects are significant are increasing with time. To allow
252 for changes in bulk density in calculation of changes in carbon stocks, we standardized total carbon
253 and nitrogen on the basis of a constant mineral mass. For 200 kg m⁻² of mineral soil (approximately
254 the upper 20 cm of the profile) about 0.5 kg C m⁻² was 'missing' from the litter removal plots, with a

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308 similar amount accumulated in the litter addition plots. There was an additional 0.4 kg C m⁻² extra in
309 the litter standing crop of the litter addition plots compared to the control. This increase in carbon in
310 surface soil and the litter standing crop can be interpreted as a potential partial mitigation of the
311 effects of increasing CO₂ concentrations in the atmosphere.

312

313 1 Introduction

314 Tropical forests and their soils are an important part of the global carbon (C) cycle, because they
315 contain 692 Pg C_v equivalent to 66 % of the C in atmospheric CO₂ (Jobbagy and Jackson 2000).
316 Carbon in tropical forest soils is dynamic; Schwendenmann and Pendall (2008) reported a turnover
317 time of 15 years for the 'slow' pool of soil C_v comprising 38% of the total soil C_v in the top 10 cm of
318 soil in semi-evergreen rain forest on Barro Colorado Island, Panama (61% of total soil C was 'passive'
319 with a turnover time of the order of a thousand years). Turner et al. (2015) reported an approximate
320 25% increase in soil C from one dry season to the next wet season in the top 10 cm of soil on the
321 Gigante Peninsula in Barro Colorado Nature Monument, Panama, at a site close to the current litter
322 manipulation experiment. Thus, there is the potential for the amount of C in tropical soils to change
323 over only a few years, with potentially important consequences for atmospheric CO₂ concentrations.

324 Atmospheric CO₂ concentrations have been steadily increasing for decades and, one of the
325 effects of this could be widespread increases in forest growth (Nemani et al. 2003) and, as a result,
326 increased litterfall. There are few experimental studies of the effects of elevated CO₂ on forest
327 growth. Körner (2006) reported that elevated CO₂ caused increased litterfall in one of three studies
328 in steady-state tree stands in temperate forests, but there have been no such studies in the tropics.
329 Thus the potential exists for increased CO₂ to increase forest growth and litterfall – though we do not
330 know how widespread and how large any increase in litterfall might be, especially in the tropics.

331 Soil C has been shown to respond to experimental changes in litter inputs. In three studies in
332 temperate forests in the USA, litter removal always resulted in lower soil organic carbon, but litter
333 addition had much more variable effects, increasing in one (Lajtha et al. 2014a), not changing in the
334 second (Bowden et al. 2014) and decreasing in the third (Lajtha et al. 2014b). The single study from
335 the tropics, in lowland rain forest in Southwestern Costa Rica, reported decreased soil C in litter
336 removal plots and increased soil C in litter addition plots (Leff et al. 2012). It is therefore likely that
337 soil C will increase in many, but not all, forests as a result of increased litter input.

338 The relative importance of aboveground or below ground inputs as sources of soil organic
339 matter has been reassessed in the last decade (Schmidt et al. 2011). Recently it was shown that 50-
340 70 % of the soil organic matter in boreal coniferous forest is from roots and root associated micro-
341 organisms (Clemmensen et al. 2013). The origin of the soil organic matter is thus a question of the
342 relative contributions of above-ground and below-ground inputs. Litter manipulation experiments
343 can provide insights into this issue by controlling one source of C input – aboveground litterfall.

344 Soil nutrients as well as C can change as a result of increasing or decreasing litter inputs and
345 are important because they will potentially affect soil fertility. In Panama, mineralization of organic
346 phosphorus (P) (inferred from the decrease in the concentration of organic P) in the top 2 cm of soil
347 during three years of litter removal was calculated to be sufficient to supply 20% of the P needed to
348 sustain forest growth – there were corresponding increases in organic P in litter addition plots, and
349 total nitrogen (N) showed a similar pattern (Vincent et al. 2010). 'Available' nutrients, including KCl-
350 extractable ammonium (NH₄) and nitrate (NO₃), and Mehlich-III extractable P, potassium (K), calcium
351 (Ca), magnesium (Mg), and micronutrients all changed over 4 years in the upper 2 cm of soil as a

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419 result of litter manipulation (Sayer and Tanner 2010). After six years of litter manipulation surface
420 soils (0-10 cm) had lower NO₃ and K in litter removal plots, and higher NO₃ and Zn in litter addition
421 plots; other nutrients were not significantly affected (Sayer et al. 2012). In Costa Rica after 2.5 years
422 of litter manipulation surface soils (0-10 cm) had lower net nitrification in both litter removal and
423 addition treatments, while NH₄ concentrations were significantly lower in litter removal plots (NH₄
424 was 83-91% of the extractable N; Wieder et al. 2013). Thus, several soil nutrients in surface soils
425 change following litter manipulation, but there is no consistent pattern for N, very little data for P or
426 cations (the latter were not reported for the Costa Rican experiment), and no data for soils deeper
427 than 10 cm.

428 Here we report results from the Gigante Litter Manipulation Plots (GLiMP) experiment over
429 a much greater soil depth (0–200 cm) for total C, N, and P, and extractable ('plant-available') N, P, K,
430 Ca, Mg, manganese (Mn), and zinc (Zn), measured after 6 years of continuous litter transfer. In
431 addition, we present a new way of expressing soil C (relative to the unchanging mineral mass), which
432 allows us to calculate overall changes in soil C and other elements independently of changes in bulk
433 density. Our objective was to describe changes in C and nutrient concentrations in the full soil profile
434 and to calculate C budgets to discover to the fate of the increased C input in litter addition plots. In
435 particular, we aimed to calculate the proportion of the added C that remains in the soil and the litter
436 standing crop, and can thus be considered as partial mitigation of atmospheric CO₂ accumulation
437 through increased forest productivity due to increased atmospheric CO₂ and temperature –
438 mitigation because C that is not in the soil will be in the atmosphere as extra CO₂. No other study has
439 tried to quantify the fate of C in organic matter added to tropical forest soils, though a study of
440 agricultural soil in temperate UK calculated that about 2.4% of organic matter in annual additions of
441 farmyard manure was still in the soil after 120 years (Powlson et al. 2011).

442 2 Materials and methods

443 The litter manipulation experiment is located in old-growth semi-evergreen lowland tropical forest
444 on the Gigante Peninsula (9°06'N, 79°54'W), part of the Barro Colorado Nature Monument in central
445 Panama. The experiment is located on the upper part of the landscape, where soils are Oxisols (Typic
446 Kandiudox). Surface soils have a pH of 4.5–5.0, low 'available' P concentrations, but high base
447 saturation and cation exchange capacity. Annual rainfall on nearby Barro Colorado Island (c. 5 km
448 from the study site) is 2600 mm and average temperature is 27°C. There is a strong dry season from
449 January to April, with approximately 90 % of the annual precipitation during the rainy season.

450 The experiment consists of fifteen 45-m x 45-m plots within a 40-ha area of old growth
451 forest. In 2001 all 15 plots were trenched to a depth of 0.5 m to minimize lateral nutrient and water
452 movement via the root/mycorrhizal network; the trenches were double-lined with plastic and
453 backfilled. Beginning in January 2003, litter (including branches <20 mm in diameter) was raked up
454 once a month in five plots, resulting in low, but not entirely absent, litter standing crop (litter
455 removal plots). The removed litter was immediately spread on five further plots (litter addition
456 plots), with five plots left as controls (CT plots). Treatments were assigned on a stratified random
457 basis using total litterfall per plot in 2002 (i.e. the three plots with highest litterfall were randomly
458 assigned to treatments, then the next three and so on) (Sayer et al. 2007). The plots were
459 geographically blocked, litter from a particular litter removal plot was always added to a particular
460 litter addition plot and there was a nearby control plot.

461 Soils samples were collected in January 2009, the early dry season, using a 7.6 cm diameter
462 constant volume corer for the top 20 cm of soil and 7 cm diameter auger from 20 – 200 cm. Fresh
463 soils were extracted for NO₃ and NH₄ within 2 hours of sampling in a 2 M KCl solution, with detection

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595 by automated colorimetry on a Lachat Quikchem 8500 (Hach Ltd, Loveland, CO). Phosphorus and
596 cations were extracted within 24 h in Mehlich III solution and analyzed by inductively coupled
597 plasma optical emission spectrometry (ICP-OES). Soil pH was measured on a 1:2 fresh soil solution in
598 distilled water.

599 Dried (22C x 10 d) and ground soil was analyzed for total C and N by combustion and gas
600 chromatography on a Flash 1112 analyzer (Thermo, Bremen, Germany). Total P was determined by
601 ignition at 550°C for 1 h and extraction for 16 h in 1 M H₂SO₄, with detection by automated
602 molybdate colorimetry at 880 nm using a Lachat Quikchem 8500 (Hach Ltd, Loveland, CO).

603 Nutrient data was analysed using mixed effects models, with ‘litter treatment’, ‘depth’, and
604 their interaction as fixed effects, and ‘plot’ as a random effect. Where nutrient concentrations varied
605 non-linearly with depth, we used splines with two or three knots. Some nutrients showed severe
606 heteroscedasticity, and we accounted for this in the model by using ‘variance covariates’, which
607 model the variance as a function of one or more of the effects in the model (Pinheiro and Bates
608 2000; Zuur et al. 2009). For all nutrients, depth was modelled as a numeric predictor and log
609 transformed prior to analysis. We performed model selection based on likelihood ratio tests and
610 Aikake Information Criterion with correction for small sample sizes (AICc, Burnham and Anderson
611 2002). We derived P-values for fixed effects by comparing null models to full models using likelihood
612 ratio tests. Final models were refitted using restricted maximum likelihood estimation (REML) (Zuur
613 2009). Where the treatment * depth term was significant, we refitted the model omitting either the
614 litter addition treatment or the litter removal treatment to assess the contribution of each of the
615 treatments (litter addition and litter removal) to the overall interaction term. Analyses were done in
616 R version 3.1.2.

617 Amounts of soil total C and N were also calculated relative to soil mineral mass to allow
618 comparisons between the treatments where bulk density and soil depth was changing due to
619 removal and addition of litter; soil in litter removal plots was shrinking and had increasing bulk
620 density, soil in litter addition plots was increasing in depth and had lower bulk density. Expressing
621 potentially changing elements relative to unchanging mineral mass allows for change to be
622 expressed against an unchanging reference; it is analogous to expressing soil water relative to soil
623 dry mass rather than soil fresh mass. Soil organic C with depth was calculated for each plot by fitting
624 a line to cumulative soil organic C (Y) against cumulative soil mineral mass (X). Bulk density data
625 were measured for each plot only in the top 0-5 cm for soil. Below that we used bulk density data for
626 one pit only. Bulk density below 10 cm depth does not vary much across the site; data for four soil
627 pits (not in any of the plots) have a coefficient of variation of about 10 % for soils from 10 - 20 cm
628 deep and 3 % for soils from 20-50 cm deep), whereas coefficients of variation of bulk densities in
629 surface 0-5 cm soils were higher: control 12 %, litter addition 15 % and litter removal 4.9 %. Bulk
630 density data were used to estimate approximate soil depth for control plots in Figs. 3 and 4.
631 Statistical comparisons of modelled cumulative total C against cumulative mineral matter were
632 compared by bootstrapping, using R version 3.1.2.

633

634 **3 Results**

635 Soils in litter addition plots, compared to litter removal plots, had significantly lower bulk density
636 (both to 5 cm) and higher NO₃ and pH (to 30 cm), P_{Meh} and total C (both to 20 cm), total N (to 15 cm),
637 Ca (to 10 cm), and Mg (to 5 cm) and (Fig. 1 and 2 and Tables S1 and S2). There were fewer
638 differences when compared to control soils: litter addition soils had higher concentrations of P_{Meh}

683 (to 20 cm), NO₃ (to 15 cm), Ca (to 10 cm), and pH (to 10 cm). **Nutrient concentrations in litter**
684 **removal soils** were not significantly lower than those in controls. Nutrient concentrations in soils >
685 30 cm deep did not differ significantly for any nutrient. Thus, in some way total C, total N, NO₃, P_{Meh},
686 Ca and Mg were significantly affected by litter removal or addition, but K, Mn, NH₄, Zn and were not;
687 effect sizes (log response ratio for 0-5 cm soils) decreased from 0.81 for NO₃, to 0.39 for Ca, 0.27 for
688 Zn, 0.20 for P_{Meh}, 0.20 for Mg, 0.15 for C_{tot}, 0.11 for N_{tot}.

689 All nutrients decreased in concentration with increasing soil depth. In control soils,
690 concentrations at 50–100 cm compared to 0–5 cm were: NH₄ 50 %, Mg 37 %, P_{tot} 36 %, K 32 %, P_{Meh}
691 25 %, NO₃ 24 %, N_{tot} 12 %, Ca 11 % and C_{tot} 11 %; NO₃ was only 24 % of the total inorganic N in
692 controls (mean over all depths) (Figs 1 and 2 and Table S1). Concentrations of most elements
693 continued to decrease below 100 cm deep in the soil; those from 150–200 cm were about half those
694 from 50–100 (ranging from 14% for Ca to 81% for NH₄, Table S1).

695 Soil bulk density in the top 5 cm was significantly lower in **litter addition** than **litter removal**,
696 though neither was significantly different from the controls. Soil C stocks standardized to a
697 consistent mineral mass (*i.e.* that in the control plots) was significantly greater in **litter addition**
698 compared to **litter removal** to about 10 cm deep in the soil (Fig. 3 and 4). Total N per mineral mass of
699 soil was also significantly greater in **litter addition** than **litter removal** in approximately the top 10 cm
700 of soil. In contrast, C:N ratios changed little with depth; in control soils, C:N was about 10.5 near the
701 surface and 10.0 at 150–200 cm, in **litter removal** plots, C:N was 10.5 at the surface and 10.3 at
702 depth, while **litter addition** soils were more variable, with C:N being 11.7 at the surface and about
703 10.0 at 150–200 cm deep.

704

705 4 Discussion

706 4.1 Soil carbon dynamics

707 The amount of C ‘missing’ from **litter removal** and ‘extra’ in the **litter addition** over about the
708 top 20 cm of soil (from calculations based on C per mineral matter), six years after (January 2009)
709 litter removal and addition started, was about 0.5 kg C m⁻² (Fig. 3). **These changes are about c. 1%**
710 **per year; in contrast if we calculate the change based on a fixed depth of 20 cm, ignoring changes in**
711 **bulk density, we get a change of about 2% per year. Thus ignoring the changes in bulk density results**
712 **a misleading doubling of the estimated rate of change.** The similarity of the losses from **litter**
713 **removal** and gains in **litter addition probably** has different causes: **we speculate that** losses from the
714 soil in the **litter removal** plots are due to respiration being greater than additions; we did not
715 physically remove organic matter from the mineral soil. **We further speculate that increases** in C in
716 the mineral soil in the **litter addition** plots are a result of infiltration of dissolved and **particulate**
717 organic matter draining from the litter standing crop, and/or changes in root exudates; increases in
718 root growth are not the explanation – root growth was lower in **litter addition** plots (Sayer et al.
719 2006).

720 In addition to the extra soil C in the **litter addition** plots, the litter standing crop **was** also
721 **larger in litter addition plots. In** September 2005 (2.8 years after litter manipulation started) there
722 was **an additional** 0.4 kg C m⁻² in the Oi and Oe layers compared to control plots (Sayer and Tanner
723 2010) and data from 2013 show that **litter standing crop was** at about this level (C. Rodtassana,
724 **University of Cambridge, unpublished data**). Together this extra 0.9 kg C m⁻² in the **litter addition** soil
725 and litter standing crop is about 30 % of the 3 kg C m⁻² in litter added to the **litter addition** plots over
726 6 years (litterfall is c. 1 kg m⁻² yr⁻¹, c. 45 % is C, times 6 years). This increase in C in surface soil and the

829 litter standing crop could be interpreted as *potential* partial mitigation of the effects of increasing
830 CO₂ concentrations in the atmosphere, though any increases in litterfall due to increased CO₂ will be
831 less than our experimental doubling. For example, a free air CO₂ experiment in 13-year old loblolly
832 pine plantation in North Carolina USA reported a 12% increase in litterfall over 9 years (Lichter et al.
833 2005, 2008).

834 The increases in soil C in our litter addition plots (c. 1% per year, of total C to c. 20 cm depth)
835 are much smaller than those reported in the other study of litter manipulation in tropical forest
836 (lowland rain forest in Southwestern Costa Rica) where two years of litter removal reduced soil C
837 concentration in the top 10 cm of soil by 26 %, and doubling litter increased soil C by 31 % (Leff et al.
838 2012). In three temperate forest studies, rates of change in soil C were small, but they were
839 measured over much longer periods. In north central USA, soil C content decreased by 44 % in litter
840 removal plots and increased by 31 % in double litter plots over a 50-year period (Table 2 Lajtha et al.
841 2014a). In Pennsylvania, USA, 20 years of removing litter reduced soil C by 24%, although the
842 corresponding litter doubling had no effect (Bowden et al. 2014). In a deciduous forest in
843 Massachusetts, USA, 20 years of litter removal also reduced mineral soil C (by 19%), but litter
844 addition also resulted in lower mineral soil C (by 6%, Lajtha et al. 2014b). Differences between
845 forests in the effect of litter addition on soil organic matter could be partly due to differences in
846 priming of pre-existing soil organic C resulting in no, or small, increases in soil C in double litter plots.
847 Priming might be greater in N limited temperate forests remote from atmospheric N pollution,
848 because one cause of priming is mining of soil organic matter for N by microbes stimulated by
849 additions of litter with low N concentrations (relative to soil organic matter) (e.g. Nottingham et al.
850 2015). It is therefore likely that many, but not all, forests will show increased C in soils as a result of
851 increased litter input.

852 Soil C might on average originate predominantly from roots rather than shoots (Rasse et al.
853 2005) and that may be the case in our soils in Panama because although changes in litter inputs have
854 caused changes in soil C they are small – approximately 1% of total soil C per year, compared to the
855 'normal' turnover of C of 25% (0-10 cm soil) within 6 months (as calculated from changes in C
856 concentration from wet season to dry season; Turner et al. 2015) and an annual turnover of about
857 7% based on incorporation of ¹³C into soils over decades (Schwendenmann and Pendall 2008).
858 Turnover rates of soil C are also high in other tropical forests; for example, in Eastern Brazil 40-50 %
859 of the C in the top 40 cm of soil had been fixed in about 32 years (Trumbore 2000). In Panama the
860 much greater rates of turnover of soil C as compared to changes caused by litter removal and
861 addition suggest that the main source of soil organic matter (over months to a few years) is roots,
862 root exudates and mycorrhizal fungi. Nevertheless, changes in above ground litter input are still
863 important, because they have resulted in overall decreases and increases in soil C.

864

865 4.2 Litter manipulation - depth of effects,

866 Effects of litter removal and addition differed among nutrients and were strongest near the soil
867 surface, with no significant differences below 30 cm. The strength of the effects and the depth to
868 which they were significant are increasing with time. Four years after the start of litter manipulation
869 six nutrients showed significant effects in the upper 2 cm of soil (NO₃, NH₄, P_{Meh}, K, Ca, Mg), whereas
870 only NO₃ and Ca showed significant effects from 0-10 cm (Sayer et. al 2010). After 6 years, in the
871 early dry season 2009 (current paper), effects were seen to greater depths: NO₃ was higher to 30 cm
872 and P_{meh}, to 20 cm in litter addition plots. Over time significant differences have become apparent

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1099 for more nutrients and to greater depth in the soil; these differences were caused by differences in
1100 litter input.

1101 The concentrations of NH_4 and NO_3 are usually only measured in surface soils in tropical rain
1102 forests, perhaps because N is generally thought not to limit growth in such forests. However,
1103 fertilization with N and K together increased growth of saplings and seedlings in the Gigante
1104 Fertilization Project, which is adjacent to our litter manipulation experiment in Panama (Wright et al.
1105 2011). Relevant concentrations of NH_4 and NO_3 are also difficult to measure since they change
1106 rapidly over only a few hours (Turner and Romero 2009); extractions for the current paper were
1107 done within two hours of collecting soils. In our litter manipulation experiment, NH_4 accounted for
1108 76% of the sum of NH_4 and NO_3 (mean over all depths in controls plots) and decreased less with
1109 depth than NO_3 (at 50-100 cm NH_4 was about 50 % of surface values whereas NO_3 was about 25 %).
1110 In the nutrient addition experiment, Koehler et al. (2012) reported that NH_4 also decreased less with
1111 depth (at 200 cm it was 41 % of surface soils) than NO_3 (to 17 % of surface soils), and that NH_4 was
1112 the dominant form of total inorganic N (about 80 %) – the same patterns as in our litter
1113 manipulation experiment. Nitrogen dynamics in soils have also been measured in a litter
1114 manipulation experiment in Costa Rica (Wieder et al. 2013), where nitrification rates were lower in
1115 both jitter removal and jitter addition plots and extractable NH_4 was significantly lower in jitter
1116 removal plots. This contrasts with our results of greater NO_3 in jitter addition compared to jitter
1117 removal and no effect on NH_4 ; the differences between the experiments might be due in part to,
1118 different soils and a wetter climate in Costa Rica (c. 5 m rain per year, c.f. 2.6 in Panama). Thus, soil
1119 N dynamics differ somewhat between the only two tropical litter manipulation experiments, but in
1120 both NH_4 was the dominant form of inorganic N, and in both total inorganic N decreased in jitter
1121 removal plots and increased in jitter addition plots (though differences were not always statistically
1122 significant).

1123 The 'available' forms of P are also not often reported for the deeper horizons of tropical
1124 forest soils, despite the fact that P is usually regarded as the most likely limiting nutrient in such
1125 forests (Tanner et al. 1998 and Cleveland et al. 2011) and has been shown to limit fine litter
1126 production in the adjacent nutrient addition experiment (Wright et al. 2011). Mehlich P and total P
1127 both decreased with depth in control soils in our litter manipulation experiment (at 50-100cm
1128 concentrations were 25 and 29 % of those at 0-5 cm); in jitter removal soils the decrease was less
1129 steep (37 % and 36 %). Jitter addition increased Mehlich P in the surface soils (though total P was not
1130 significantly greater), indicating increased P availability, which is consistent with the finding that
1131 jitter addition decreased the strength of phosphate sorption in these soils (Schreeg et al. 2013). Thus
1132 for P, potentially the most commonly limiting nutrient in tropical rain forest soils, six-years of
1133 continuous removal and addition of litter in our experiment has reduced and increased 'available' P
1134 down to 20 cm in the soil.

1135 The relative amounts of exchangeable cations and their change with depth in the control
1136 plots of the Panamanian litter manipulation soils are similar to patterns in other tropical forest soils.
1137 In our experiment, Ca concentrations (in centimoles of charge) are about twice those of Mg in
1138 surface soils (though below 30 cm Mg to Ca ratios exceed 1); K concentrations are usually less than 5
1139 % of the total exchangeable bases. With increasing depth, Ca, Mg and K concentrations all decrease,
1140 with Ca decreasing more than Mg or K. Other tropical forest soils are similar: in 19 profiles
1141 throughout Amazonia the sum of base cations (Ca, Mg, K) was usually dominated by exchangeable
1142 Ca (11 cases) or Ca was equal to Mg (4 cases), and both Ca and Mg mostly decreased with depth,
1143 while K was in low or in trace concentrations in all profiles (Quesada et al. 2011). In Hawaii (Porder
1144 and Chadwick 2009), much younger soils (11,000 BP on lava), with much higher concentrations of

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1185 Ca, Mg and K than Panama and Amazonia, showed similar patterns: Ca was the dominant cation, K
1186 was usually less than 5 % of the sum of exchangeable Ca, Mg and K, and all cations decreased with
1187 depth at the wetter sites (but not in the drier sites). Thus, in most wet tropical forest soils, Ca is the
1188 most abundant cation and most cations decrease with depth. Litter addition in Panama increased Ca
1189 and Mg concentrations in the surface soils and thus steepened the depth gradient, whereas litter
1190 removal decreased Ca and Mg and therefore decreased the gradient; K was at much lower
1191 concentrations (as in Amazonia and Hawaii) and was not affected by [litter addition](#) and [litter](#)
1192 [removal](#) even in 0-5 cm soils.

1193 **4.3 Design of litter manipulation experiments**

1194 The design of litter manipulation experiments needs to be carefully considered when
1195 evaluating their results. [The strength](#) of [the effect](#) of litter manipulation [on soil C](#) in Panama [was](#)
1196 [much less than that](#) in Costa Rica, [but the](#) Panama [and](#) Costa Rica experiments are very different in
1197 spatial scale. Plots in Panama are large, 45 x 45 m, those in Costa Rica are small, 3 x 3 m. The small
1198 plots are 'hot' and 'cold' spots relative to large individual tree crown areas (and likely tree root
1199 areas); crowns of the largest trees in lowland rain forests are commonly 25 m in diameter, so a 3 x 3
1200 m plot is 2 % of that area. These differences in experimental design and their effects on the pattern
1201 of the results should be considered when trying to understand ecosystem level processes; small hot
1202 and cold spots may not represent what would happen in plots on the scale of the large trees, [as](#)
1203 [pointed out by Leff et al. \(2012\)](#).

1204

1205 **5 Conclusions**

1206 The increase in C in [the mineral soil and the](#) litter standing crop following litter addition was
1207 statistically significant in the top 20 cm of the soil, suggesting that any increased litterfall as a result
1208 of increased [atmospheric CO₂ and/or temperature](#) could result in a substantial increase in soil C and
1209 therefore partially mitigate the increase in atmospheric CO₂. However, the current experiment
1210 added much more litter than might be produced by an increase in CO₂ of [, say,](#) 200 ppm, and added
1211 more nutrients than might occur even in [temperate](#) polluted sites. Thus new experiments are
1212 required to investigate the effects of more realistic increases in litterfall using litter with low nutrient
1213 concentrations.

1214 Supplementary material

1215 [R code for models used to estimate of means and confidence intervals](#)

1216 [Supplementary](#) Table S1 with full original data from soil analyses

1217 [Supplementary](#) Table S2 Model estimates of concentrations (from Sheldrake)

1218 [Supplementary Figure 1. Expanded versions of parts of Figures 1 & 2 showing significant differences.](#)

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1221 experiment from 2001-2009; A Vincent for helping to maintain the experiment from 2003-2005. T.
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1268 [We thank D. Agudo and T. Romero for doing the laboratory work and J. Rodriguez for collecting the](#)
1269 [samples in the forest.](#) S.J. Wright has been a frequent source of help for many aspects of the
1270 experiment.

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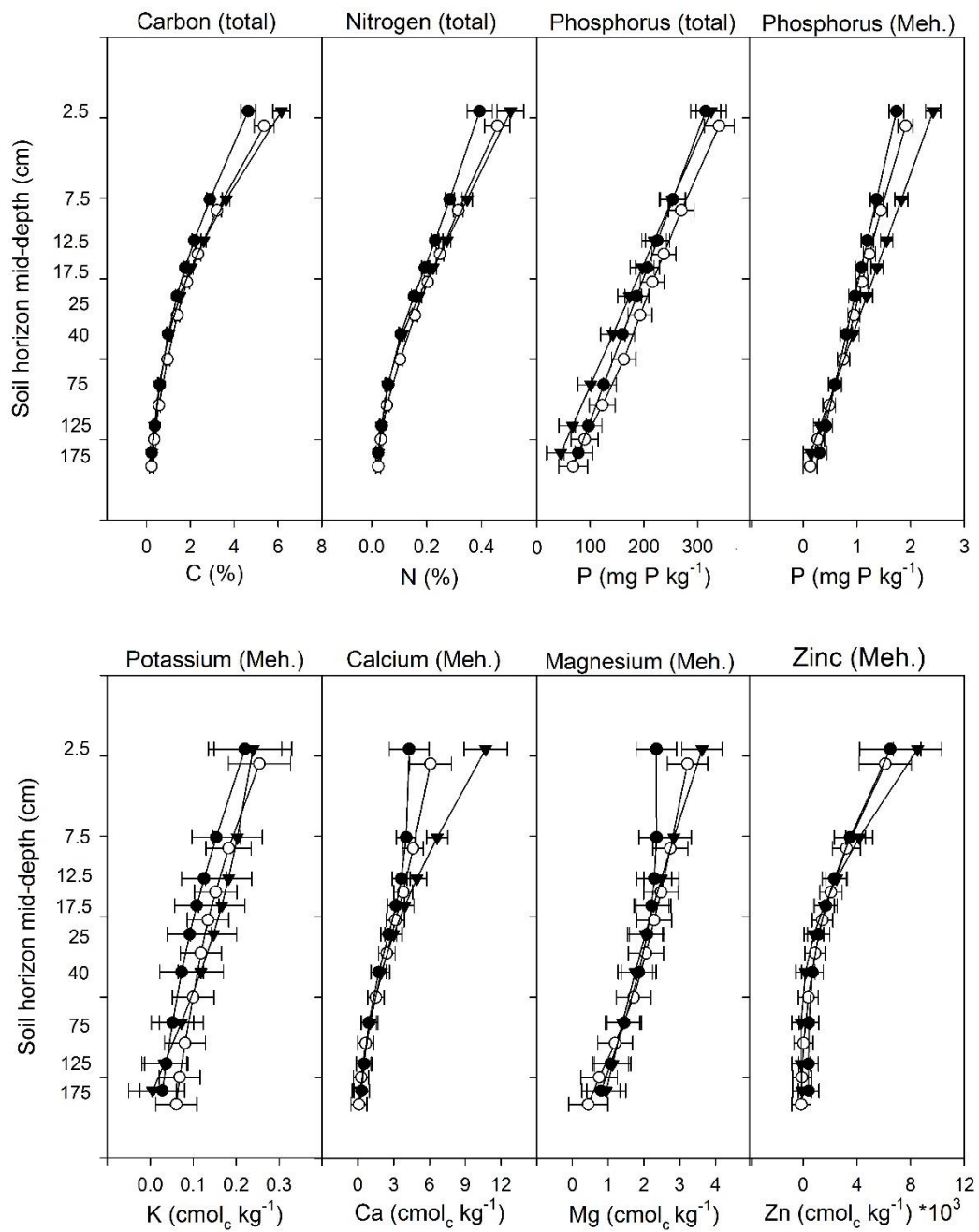
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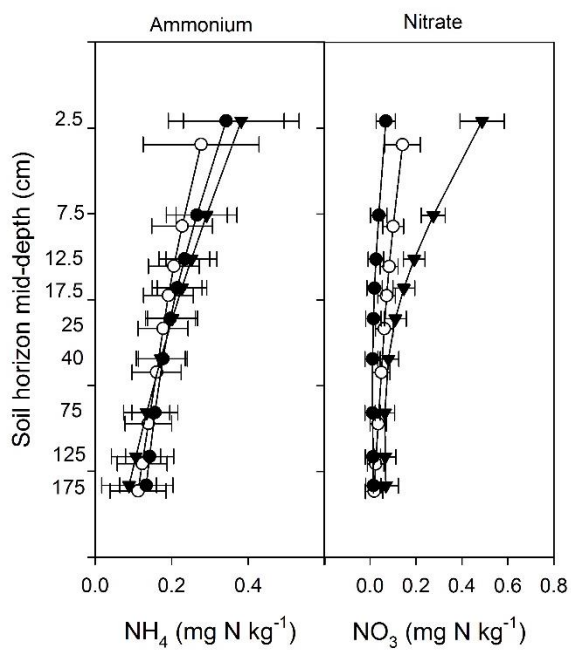


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1506 Fig. 1 Concentrations of soil C, N, P (various fractions) and cations (Mehlich extractions), plotted
 1507 against the mid-point of the soil layers sampled (Zn values should be divided by 1000 to obtain
 1508 actual means), control points are displaced below treatments. Data are fitted values of the mixed
 1509 effects models with 95% confidence intervals (see Methods), in litter removal ●, control ○ and litter
 1510 addition ▼ plots.

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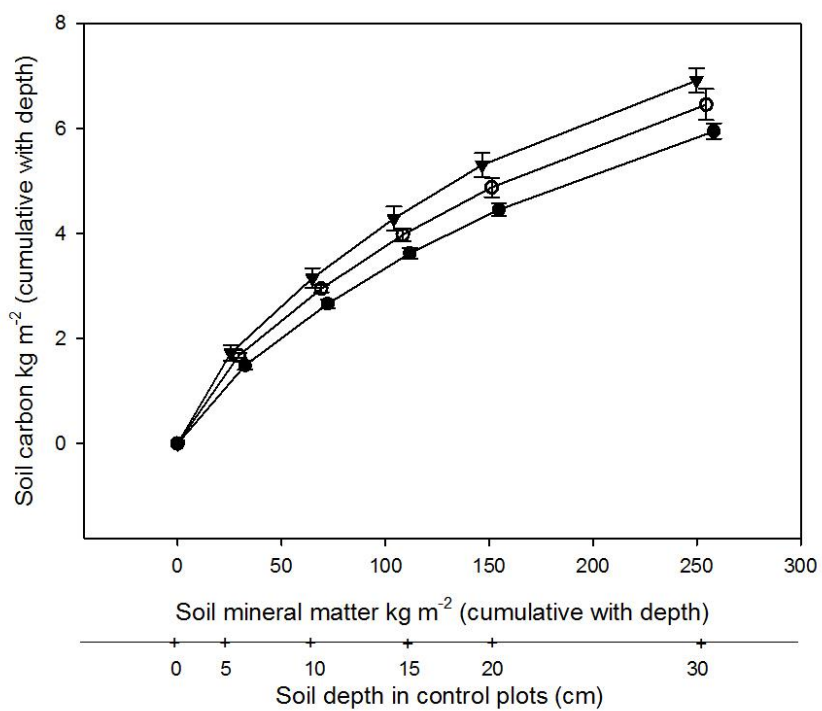
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1514 Fig. 2 Mean concentrations of ammonium and nitrate plotted against the mid-point of the soil layers
1515 sampled, control points are displaced below treatments. Data are fitted values of the mixed effects
1516 models with 95% confidence intervals (see Methods), in litter removal ●, control ○ and litter
1517 addition ▼ plots.

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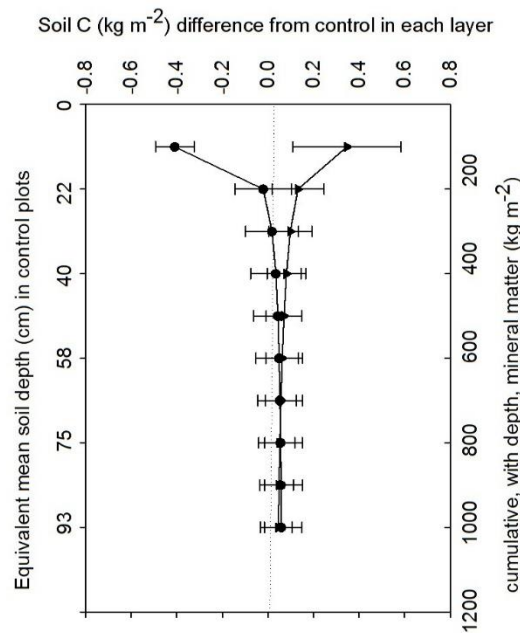
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1522 Fig. 3 Soil carbon content and mineral content in litter addition, control, and litter addition
 1523 expressed as kg C m⁻² cumulatively from 0 to 30 cm soil depth. Values are means for 5 plots per
 1524 treatment +/- SE, litter removal ●, control O₂ and litter addition ▼.

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1528

1529 Fig. 4 Differences in soil carbon content relative to control soils (mean and SE, n = 5), after 6 years of
 1530 litter manipulation, plotted for successive soil layers: 0-100 kg (mineral matter) m⁻², plotted at 100 kg
 1531 m⁻² on right y axis; 100-200 kg m⁻², plotted at 200 kg m⁻²; and so on to 900-1000 kg m⁻², plotted at
 1532 1000 kg m⁻²; in litter removal ● and litter addition ▼ plots. We calculated the soil C in the litter
 1533 removal and litter addition plots at the mineral mass equal to that at various depths in the control
 1534 plots (0-5 cm, 5-10 cm, etc), we then calculated the difference in C between each litter removal (or
 1535 litter addition) and its control plot for the same mineral mass. Approximate depth for cumulative soil
 1536 mineral mass in control plots is shown on left y axis.

1537