Plant-available N:P alters root litter N recycling in a Mediterranean tree–grass ecosystem

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Abstract

Background: Nitrogen deposition can cause an ecosystem-level shift in available N (nitrogen) to P (phosphorus) availability. However, most plant N nutrition is from edaphic sources rather than deposition and in seasonally dry grassland systems, root litter is the predominant nutrient source.
Aims: We were interested how litter turnover and altered nutrient recycling from dead biomass can compensate for these shifts in ecosystem stoichiometry.
Methods: We studied a Mediterranean savanna amended with N or NP treatments three years prior. We measured root and plant-available soil N:P stoichiometry in two micro-habitats: open pasture and beneath oak canopies. ^{15}N-labelled root litter incubated in topsoils without litterbags was used to trace uptake of litter N by herbaceous strata roots.
Results: Since fertilization, NP added sites have become relatively P enriched, resulting in lower N:P ratios in living roots than either when N was added alone or control sites. Total litter-derived ^{15}N uptake by roots was proportional to root ingrowth response but higher in the NP than N treatment, indicating a higher N demand when N and P were added together. We observed more ^{15}N uptake by plants under tree canopies, indicating a tighter nutrient recycling loop in these micro-habitats in contrast to treatment level 'fertility' trends.
Conclusions: Root stoichiometry responded to manipulated soil nutrient availability and N uptake was altered as plants attempted to compensate for nutrient availability imbalances, indicating that these ecosystem perturbations have long term effects on nutrient cycling which can propagate to whole system function. This was also related to functional community-level adaptions between micro-habitats with under canopy communities more able to take advantage of the litter nutrient source.

Key words: ^{15}N tracer / litter turnover / N:P stoichiometry / N:P imbalance / N uptake / nutrient stoichiometry

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Supporting Information available online

1 Introduction

The future biosphere may become more nitrogen (N) limited due to rising CO_2 concentrations (*Luo* et al., 2004) but concurrently, N deposition inputs are also shifting ecosystems from N to phosphorus (P) limitation (*Phoenix* et al., 2003; *Peñuelas* et al., 2012, 2013). Additionally, even in the modern era, most N taken up by plant roots is derived from decomposing plant litter rather than deposition (*Schulze*, 2000; *Högberg*, 2012). Future conditions (*e.g.*, rising CO_2 concentrations, associated warming or changes in precipitation regimes, and altered ecosystem stoichiometry) also cause biological responses such as altered root:shoot ratios, microbial activity and plant investment into recycling of nutrients, which can affect the fate of this N from litter (*Norby* and *Jackson*, 2000). Plant use of this N is important to quantify as commonly applied mineral isotope tracers may not be partitioned between ecosystem pools in the same way as N derived from decomposition (*Nair* et al., 2017). Roots are also commonly the main carbon (C) sink for primary production and hence the main litter source, especially in short-stature systems including savannas, mixed tree-grass ecosystems, and other arid lands (*Puerto*, 1992; *Mokany* et al., 2006; *Peichl* et al., 2012; *Abramoff* and *Finzi*, 2015; *Nair* et al., 2019). Therefore, studying root litter decomposition and turnover in these systems is important both from the point of view of ecosystem nutrition as well as ecosystem C balance.

The western Mediterranean is typified by anthropic savannoid 'ecosystem mimic' (*Joffre* et al., 1999) landscapes where oak woodlands [*Quercus ilex*. Ballota (Desf.) and *Quercus suber* (L.)] have been historically thinned and converted into wood-pastures with scattered (20–40% canopy cover) trees and seasonal pasture (*Moreno* and *Pulido*, 2009). We henceforth

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refer to these ecosystems as the Spanish 'dehesa'. Such 'Mediterranean' seasonally water limited systems have periods of high productivity without water limitations where either N (*Gallardo* et al., 2000) or N and P together (*Ries* and *Shugart*, 2008) limit plant growth in spring (*Gallardo* et al., 2000), so N deposition and associated alterations in ecosystem N:P ratio may impact ecosystem function (*Giorgi* and *Lionello*, 2008; *Kovats* et al., 2014; *Peñuelas* et al., 2018). Arid and grass-dominated ecosystems also tend to have high root:-shoot ratios (*Mokany* et al., 2006) and, indeed in dehesa, an almost complete herbaceous layer senescence in summer and strong intra-annual species turnover (*Moreno*, 2008) result in large amounts of short-lived and fast decomposing fine roots in surface soils (*Casals* et al., 2010). While their geneses are very different, savanna- and savannoid-ecosystems (both natural and anthropogenic) are also found worldwide (*e.g*., Southeast Asia, Central America, Eastern South America, central and coastal West Africa), cover between 450 million ha (*Nair*, 2012) to 1 billion ha (*Zomer* et al., 2014) and feature similar shifts between water limited (in dry season) and nutrient limited (in wet season) dynamics (*Ludwig* et al., 2004; *Moreno Marcos* et al., 2007; *Moreno*, 2008; *Pellegrini*, 2016). Seasonally dry systems are highly important to the intra-annual variability of the global C sink (*Poulter* et al., 2014) and badly quantified in vegetation models (*Beringer* et al., 2011). Process-based understanding of both plant and soil function in these regions and how these are affected by environmental change is essential to predict the future state of such systems.

Several field experiments have used ^{15}N tracers in field-applied litter to quantify plant nutrient recycling from litter turnover (*Zeller* and *Colin-Belgrand*, 2001; *Bimüller* et al., 2013; *Guo* et al., 2013; *Nair* et al., 2017). The resulting isotope composition of new roots and other components in the plant-soil system (*e.g*., leaves, soil, leachate, trace gases, the litter itself) informs how N is partitioned from decomposition. While such field studies have to date used leaf litter, a similar technique can be used with labelled roots, if it is possible to recover and separate root litter from new root growth *in situ* (*Bird* et al., 2008; *Casals* et al., 2010). This is complicated, as the common litterbag technique artificially separates roots from the surrounding soil and may bias results (*Fahey* and *Hughes*, 1994). To our knowledge at the time of submission, there have been no similar tracer studies from litterbag-free root litter in the field, despite the relevance of root litter due to its decomposition *in situ* in the soil and the molecular and isotopic evidence for its importance for plant nutrition (*Kramer* et al., 2010; *Mendez-Millan* et al., 2014). We are also unaware of field studies using labelled root litter in combination with experimental nutrient manipulations.

Additionally, plant communities respond to changing conditions, such as ecosystem-level shifts in N and P availability (*Peñuelas* et al., 2013), by optimizing aspects of individual growth and physiology (*Sardans* et al., 2017) or by community-level species succession (*Elser* et al., 2007). This N and P limitation is often assessed by foliar tissue stoichiometry (*Ostertag* and *DiManno*, 2016), but leaves are not the only plant organs responsive to nutrient availability. Indeed, leaf signals are a result of both resources acquired and plastic whole-plant nutrient budgets (*Caldararu* et al., 2019) which may alter both allometry and stoichiometry both above and belowground. These changes can include less root biomass due to less demand for nutrient acquisition (*Wurzburger* and *Wright*, 2015) or more due to increased productivity and continued limitation by other soil-derived resources (*Nair* et al., 2019). This latter change, observed at the dehesa site of this study during the productive, and non-water limited spring and the following dry-down period, calls into question if biomass changes occur alongside changes in stoichiometry and function, which we will examine more in depth through tissue stoichiometry and uptake of isotope tracers.

The objectives of this study are to examine herbaceous plant N nutrition from ^{15}N-labelled root litter and root elemental concentrations, then interpret both of these properties as responses to N and/or P limitation under ecosystem-level nutrient treatments. We worked within a stoichiometric manipulation experiment (N and NP addition 2–3 years prior) in a Mediterranean tree-grass dehesa. The oaks in such a landscape are very slow growing, with large internal pools of C, N, and P and relatively static stoichiometry, and are thus difficult to study in such an experiment, so we focused on the herbaceous layer, the dynamics of which control most of both interannual and seasonal variability (*Luo* et al., 2020). Prior work from this site shows +N and +NP additions increased root biomass, but root length density (RLD) and rooting depth only increased under +NP treatments, and both effects occurred in the main growing period in spring (*Nair* et al., 2019). It is unclear to what extent root stoichiometry reflects the overall treatments; root tissue stoichiometry is generally less responsive to fertilization than shoots (*Ostertag* and *DiManno*, 2016) and release from nutrient limitation should increase nutrient concentrations, but stoichiometric effects could be buffered by concurrent species or trait changes (*Meunier* et al., 2017). These overall changes in root biomass and morphology should also result in more uptake of N to support greater biomass but nutrient treatments could result in less nutrition from litter sources (*i.e*., a less 'N conservative') system or more nutrition from litter sources (more 'N conservative'). Alternatively, root responses could be due to other limitations, such as water deficits going into the dry summer, which are strongest in the +N treatment due to increased biomass but decreased water use efficiency (*Luo* et al., 2020).

As tree canopy cover affects soil properties in the dehesa with more fertile micro-sites sites under tree canopies (*Gallardo*, 2003; *Howlett* et al., 2011; *Rolo* et al., 2013), we studied distinct under-tree and open pasture micro-sites. There are relatively more graminoids under canopies (*López-Carrasco* et al., 2015) than in open grasslands, although RLD is higher in open pasture areas, and root biomass greater under trees (*Nair* et al., 2019). Mineral ^{15}N tracers suggest that habitat is a much stronger determinant of N partitioning between soil and plant pools than nutrient treatments (*Morris* et al., 2019). Canopy microsites thus have overall higher N availability, and may recover relatively less N from added litter in plant biomass. Alternatively, as this fertility is due to larger litter inputs, these communities could be better adapted to directly recover resources from decomposing litter before it is leached to deeper soil layers. We could also expect that previously

observed greater root length (*Nair* et al., 2019), which can be associated with nutrient acquisition (*Hill* et al., 2006) in open pastures may lead to better uptake of N, although this could also be for uptake of water. Finally, by sampling at two distinct periods of the year, we also expected to see differences in both root stoichiometry and ^{15}N partitioning. Root N and P concentrations would be lower in the more productive period (May) than the less productive period (December) and overall tracer return should be lower due to progressive N losses, but we were unsure if the pattern between treatments would change between different sampling periods.

We thus aimed to answer the following questions:

(1) Are root responses to +N/+NP addition treatments reflected in changing root stoichiometry? Does this reflect the 'balanced' N:P stoichiometry in control and +NP and the 'imbalanced' N:P stoichiometry in +N?
(2) Does root ^{15}N recovery from decomposing root litters decrease with more relative N availability (in +N plots), indicating alleviation of N limitation? Is this change compensated by the addition of P (in +NP plots) as the system returns to a more 'balanced' stoichiometry?
(3) Are observed effects affected by micro-habitat and season? Can the major differences in microsite fertility explain the pattern in results?

2 Material and methods

2.1 Overview of methods

In this experiment, large multi-hectare treatments in a dehesa ecosystem were fertilized with either no fertilizer, +N, or +NP treatments in the growing seasons of 2015/2016. We aimed to study the effects of altered stoichiometry, rather than instantaneous fertilization effects, so ingrowth core mesocosms containing ^{15}N-labelled root litter were installed in December 2016. We recovered these ingrowth cores in May 2017 (at the end of the annual growing season) and December 2017 (one year after installation).

2.2 Study site and nutrient treatments

We worked at Majadas de Tiétar, a typical seasonally dry tree–grass dehesa [about 20 trees ha^{-1} of *Quercus* spp, mostly *Q. Ilex* (L.) and scattered *Q. suber* (L)] in Extremadura, Spain, with a highly spatially and seasonally diverse mix of annual grasses, forbs, and legumes between and under trees (*Moreno*, 2008). Most herbaceous plants at the site, including the locations used for the sampling in this study, are annual and senesce over summer (> 95% species according to unpublished annual site inventories). The ecosystem is grazed by cows during productive seasons at low density (< 0.3 cows ha^{-1}). In this study, cows were absent from June to December 2017. Mean annual temperature is 16°C, mean annual precipitation is ≈ 650 mm, mostly between October and April, with a Mediterranean climate of long, hot, dry summers and mild, wet winters.

Soils at the site are Abruptic Luvisols with a sandy upper layer (0–20 cm ≈ 5% Clay, 20% silt, 75% sand) and a clay layer between 30 and 60 cm. Between microsites, surface soils (0–5 cm) under canopy locations have higher C, N, and Olsen-Extractable P contents (≈ 14 mg g^{-1}, ≈ 1,5 mg g^{-1}, and 5.4 μg g^{-1}, respectively) than grassland locations (≈ 4.9 mg g^{-1}, ≈ 0.9 mg g^{-1}, and 2.3 μg g^{-1}) (*Nair* et al., 2019). As common in grazed open woodlands, the soil surface is mostly free of litter, even beneath tree canopies. At the site, a large-scale nutrient manipulation experiment 'MANIP' added either no fertilizer, additions of N (as Ca-ammonium nitrate fertilizer) or NP fertilizers (ammonium nitrate and triple super-phosphate fertilizer) to three 20-ha areas in the growing seasons of 2015 (100 kg N ha^{-1}, 50 kg P ha^{-1}) and 2016 (20 kg N ha^{-1}, 10 kg P ha^{-1}) as one application per year. Managed as a low-input extensive livestock farm, there are no records of previous site fertilization. The design of these applications was to alter the 'ecosystem stoichiometry' but not simulate real-time N deposition. The site (central location: 39°56′25.12′′N, 5°46′28.70′′W) is equipped with two eddy covariance tower stations per fertilized area (FLUXNET ID: Es-LMa, ES-LM1, ES-LM2). A large number of other studies report aspects of the biological and biophysical characterization and its response to nutrient treatments (*El-Madany* et al., 2018; *Luo* et al., 2018; *Migliavacca* et al., 2017; *Perez-Priego* et al., 2017; *Morris* et al., 2019; *Nair* et al., 2019). In general, seasonally arid Mediterranean systems are co-limited by N and P (*Ries* and *Shugart*, 2008; *Sardans* and *Peñuelas*, 2013; *Sardans* et al., 2017). Our fertilization contained no P-only treatment; in preliminary trials the addition of P alone did not significantly impact vegetation–atmosphere C fluxes (*i.e.*, GPP, NEE, ecosystem respiration), vegetation properties such as LAI or chlorophyll content (*Migliavacca* et al., 2017; *Perez-Priego* et al., 2017) nor stoichiometric properties beyond leaf tissue P and P turnover rate (*Perez-Priego* et al., 2017; *Weiner* et al., 2018). This suggested that any co-limitation followed the 'serial' model of responsiveness to N only, but stronger responses with both N and P added together (*Harpole* et al., 2017). During the period of the experiment in this paper, both nutrient treatments influence K_2SO_4 extractable soil N:P stoichiometry (*Nair* et al., 2019) as shown in Fig. 1.

2.3 Field protocol

Within each of the three distinct nutrient treatment areas (henceforth, 'control': no additions, '+N': nitrogen additions, '+NP': nitrogen and phosphorus additions), we established twelve micro-sites (36 micro-sites in total). Within treatment, these were split between two habitats; open pasture without tree cover, and pasture under tree canopies, hereafter referred to as open pasture and under canopy. Under canopy locations were approximately halfway between the central stem of a particular tree and the edge of its canopy, while open pasture were always at least three times the canopy radius from any stem. Micro-sites were clustered in sets of four (two open pasture and two under canopy) around individual oaks (three per treatment), with at least 5 m between microsites. This site is highly heterogeneous and previously no evidence of spatial correlation in soil properties within clusters has been found (*Nair* et al., 2019), so we treat micro-sites as independent and representative of the larger treatment area.

At each micro-site, we established two 50 × 50 cm square sub-locations, within 1 m of each other but clearly distinct, to

allow separate location of ^{15}N-labelled and unlabelled ingrowth core treatments and limit cross-contamination. These areas were selected based on qualitative similarity of aboveground vegetation within micro-site. We found no evidence of cross-contamination in isotope measurements between labelled and unlabelled samples.

In each of these sub-locations, we installed three root mesocosms in mid-December 2017. Critically, we did not use the common buried mesh bag (*Silver* and *Miya*, 2001) approach for litter introduction, but installed labelled litter in direct contact with the soil. We installed these at the soil surface, due to the high proliferation of fine roots in the shallowest soil for much of the year, with the exception of summer months (*Nair* et al., 2019). Per mesocosm, a soil corer (4.5 cm diameter) was used to remove a 13 cm column of soil, which was gently homogenized, with living roots removed before pre-fragmented (coarsely cut with scissors) root litter was added. A 4 cm diameter, 13 cm aluminium 'ingrowth core' with three large windows to allow colonization by roots from the surrounding soil was placed in each hole left by the corer. The amended soil was replaced, packing tight inside and around the core. We either installed three natural abundance or three ^{15}N-enriched mesocosms per sub-location (so six per micro-site / 216 across the experiment in total), each containing 0.6 g of *Anthroxanthum odoratum* litter. This litter was grown on sand in a growth chamber and was introduced to fully replace litter removed from the soil. ^{15}N-labelled litter was produced with ^{15}N-enriched ammonium nitrate fertilizer, while natural abundance litter was produced identically except for use of a natural abundance fertilizer. The field applications of labelled litter had a δ^{15}N of 4190 ± 131‰ (mean ± s.d.) and average N% of 1.39 although there was some variation in litter δ^{15}N, which we took into account in our calculations. Unlabelled litter had a natural abundance δ^{15}N signature (2.5‰) and a N% of 1.13. This could have slightly affected N availability (root N was ≈ 3% of total soil N in the mesocosms) and hence N concentrations of new roots recovered (Fig. S1). We pooled both labelled and natural abundance mesocosms together per micro-site for all stoichiometric analyses, so this difference, if it exists, does not invalidate comparisons between micro-habitats, dates, or treatments. We expected to solely sample the roots of pasture species as a combination of slow growth rates and vertical partitioning of root activity (*Moreno* et al., 2005); we found < 1% of the ingrowth cores colonized by (visually distinct, dark) tree roots, which were removed from the material used in the analysis .

We recovered two of each three ingrowth cores in May 2017 and the remaining core the following December (so the May 2017 represented the first main 'growing season' and December 2017 a year after installation) As expected by the seasonal cycle, May was drier than December (average volumetric soil moisture content at 10 cm depth in grasslands was 10% in May 2017 and 16% in December 2017). To recover the ingrowth cores we hammered the corer down directly above the mesocosm (often obscured by vegetation growth or slightly buried by soil expansion) to remove the ingrowth core intact. Most cores had herbaceous layer plants rooted within the core, which we did not collect due to sampling bias concerns. We immediately sealed each ingrowth core in a plastic bag and stored these at 4°C until processing. One set from May and one set from December was used for dry soil C, N, and P analysis. The remaining mesocosm from May was used for microbial biomass and extractable N measurements; root stoichiometry and root and soil δ^{15}N measurements were made from all cores. Total P concentration was only measured on roots. Alongside the root ingrowth data, 2 M KCl and 0.5 M $NaHCO_3$ extractable soil N and P content were sampled (although at slightly different dates May and late November 2017), for 0–5 cm soil at locations within 1m to our ingrowth cores. These were not taken directly from the ingrowth cores due to logistical demands across multiple experiments sharing resources and person-hours. These data were not used for the isotope calculations and so should not bias interpretation of the ^{15}N tracer.

2.4 Tissue stoichiometry and ^{15}N measurements

Samples were processed by sieving (2 mm), retrieving all root biomass in the upper sieve. We treated material that repeatedly passed through the sieve as part of the 'soil' fraction. We additionally filtered the root biomass for qualitative criteria indicative of living roots (*i.e.*, intactness, colour, attachment to green biomass) and assigned all remaining material to the soil fraction. The root fraction was washed and dried at 60°C until weight loss ceased, then milled in a ball mill (Retsch mm400) to a fine powder. An identical protocol without washing was followed for soil. Subsamples of the resulting powders were used in the following analyses:

For root tissue and soil total C and N, concentrations were determined on a Vario EL II (Elementar Analysensysteme GmbH, Hanau, Germany). For root total tissue P, concentrations were measured with an ICP OES Optima 3300 (Perkin Elmer, MA, USA). In these measurements only, some root samples (4% of the total) did not include enough material for analysis, and were not measured. For δ^{15}N and total N on both root tissue and total soil pools, samples were run on a DeltaPlus isotope ratio mass spectrometer (Thermo Fisher, Bremen, Germany) coupled *via* a ConFlowIII open-split to an elemental analyser (Carlo Erba 1100 CE analyzer; Thermo Fisher Scientific, Rodano, Italy). Standard deviation of the measured standards was 0.2‰ or better.

2.5 Additional analyses

To supplement our main experiment, we also made measurements of N leaching beneath and extractable K_2SO_4-N from the unlabelled mesocosms in May 2017. The dry summer and logistical limitations prevented also making these measurements the following December. Unfortunately, a combination of an unexpected fast dry-down and a technical mistake in the laboratory meant that most of these resin bags were not suitable for analysis. We were able to measure only from a small subset of bags (12% of the total). We therefore present in the results section only a basic estimate of leaching and present a full method in the supplementary material.

For measurements of soil-extractable K_2SO_4-N from the ingrowth cores we used two cores (one ^{15}N-labelled and one natural abundance) per micro-site from the May 2017 harvest.

Twenty mg of sieved soil at field capacity was weighed into small sample cups along with 45 mL of 0.5 M K_2SO_4. These were shaken at 120 rpm for 2 h and allowed to settle before filtering through Whatman no.1 filter paper. The filtrate was analyzed for total N content (but not ^{15}N content). We also made a paired measurement of K_2SO_4-extractable N after 48h chloroform-fumigation. These were measured for total N content on a TN-100 (A1 Envirotech, Düsseldorf, Germany). This allowed a calculation of microbial biomass N (*Brookes* et al., 1985). Instead of using a conversion factor K_N, which is not determined for our study system, we report microbial N as if $K_N = 1$. As K_N is a constant, our relative microbial N masses are comparable between treatments.

2.6 Statistics and experimental assumptions

Commonly, root litter decomposition is measured with buried mesh bags (see studies in *Silver* and *Miya*, 2001) which introduce artificial separation from the complex microbial rhizosphere (*Fahey* and *Hughes*, 1994) and affect the ingrowth of new roots. In this experiment we added root litter to the soil without the use of litterbags, which allowed us to eliminate these artefacts but also meant it was not possible to measure litter turnover directly. We also used fragmented non-native litter which we assumed had decomposed sufficiently in all treatments to not be returned in our 'root' pool. 'Litterbag-free roots probably decay faster than those within this artificial separation (*Dornbush* et al., 2002) and litterbags at our site have already found high decomposition rates (*Casals* et al., 2010). Indeed, it was theoretically possible to visually distinguish between the introduced roots and native root litter. Our criteria of indicators of 'livingness' rather than 'deadness' in roots aimed to bias any errors towards misclassification of living roots as litter, rather than the inverse. We did not identify any litter in either of the two samplings so we assumed that initially added labelled root litter was not found in recovery root ingrowth at either date (*i.e.*, that added root litter was fragmented beyond the 2 mm size threshold of the sieve).

We calculated recovery of the ^{15}N isotope by calculating the amount of label in (A) the initial root litter application, and the amount in (B) the final recoveries in May 2017 and December 2017, using $\delta^{15}N$, N% and root masses, and total soil mass recovered from the cores, then calculated the absolute difference (A – B) / A.

For ^{15}N recoveries, unlabelled roots were used to provide natural abundance $\delta^{15}N$, which may change throughout the year and/or differ between treatment areas or micro-sites. As previously mentioned, for elemental stoichiometry we pooled both isotope treatments together. This doubled sample sizes and improved detection of treatment effects.

For statistics presented in the results section, uncertainties are expressed as ± standard deviation unless otherwise stated. We tested the effects of micro-habitat × nutrient treatment × sampling date (if measured in both dates) for all variables of interest using analysis of variance (ANOVA) linear models unless otherwise stated. Data were transformed if appropriate using log transformation or selection using Tukey's ladder of powers to maximize the Shapiro–Wilks statistic for a normal distribution of residuals. We treated recovery date as an independent variable as each core from a different spatial location in a highly heterogeneous system and two dates is too few to fit a time series structure. We treated micro-sites as independent; building a mixed effect structure using clusters as a random effect would lead to over-fitting of the sparse point data. We have previously discussed the rationale and limitations of this point measurements approach within a technically pseudoreplicated multi-hectare fertilization experiment (*Nair* et al., 2019). The site is very heterogeneous, even at micro-scales: variation in root ingrowth within soil cores recovered from the same micro-site at the same time was much larger than average differences between micro-sites (Fig. S2) so we judged this compromise acceptable. We selected the most parsimonious models using Aikake's Information Criterion (AIC). We performed all statistical analyses in R version 3.5.0 (*R Core Team*, 2018).

3 Results

For the 13 cm of topsoil sampled, root ingrowth was 7.670 ± 50 (S.E.) kg ha^{-1} under canopies and 5.670 ± 40 kg ha^{-1} in open pastures in May, and 2670 ± 40 kg ha^{-1} under canopies and 1670 ± 30 kg ha^{-1} in open pastures in December (Fig. 1A, B). For the two dates in

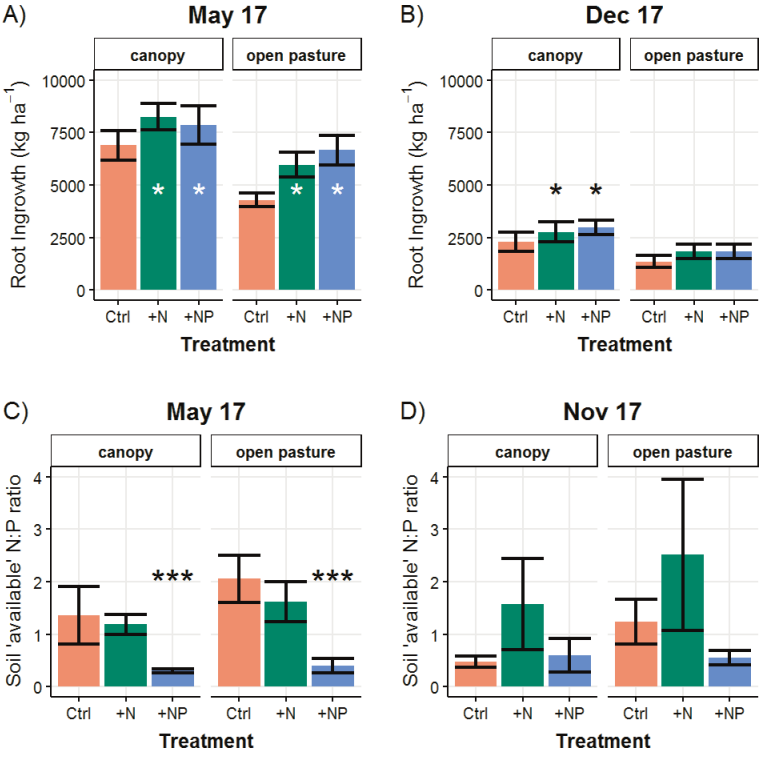

Figure 1: Absolute ingrowth root production in 0–13 cm soil and extractable soil N:P ratio in 0–5 cm soil. For soil available N:P, the 'Nov 17' date is 2 weeks before root sampling and the 'May 17' date is concurrent with our sampling. Stars indicate significant differences (*$p < 0.05$, ***$p < 0.001$) compared to other treatments at the same date/habitat combination.

this study (Fig. 1) we found: (1) more root mass in May than December ($p < 0.001$), (2) more root mass under canopies than in open pastures ($p < 0.001$), and (3) both nutrient treatments increased root ingrowth (+N *vs*. control: $p < 0.05$, +NP *vs*. control: $p < 0.01$, +N *vs*. +NP: non-significant). There were no significant interactions between treatment, sampling date, or micro-habitat in terms of root mass. In soil, the plant-available N:P ratio was strongly affected by nutrient treatment ($p < 0.001$) in the most parsimonious model and no other significant effects. This difference was due to a low N:P in +NP in May, although high N:P was also observed in +N in November and data are very variable between cores (Fig. 1C, D).

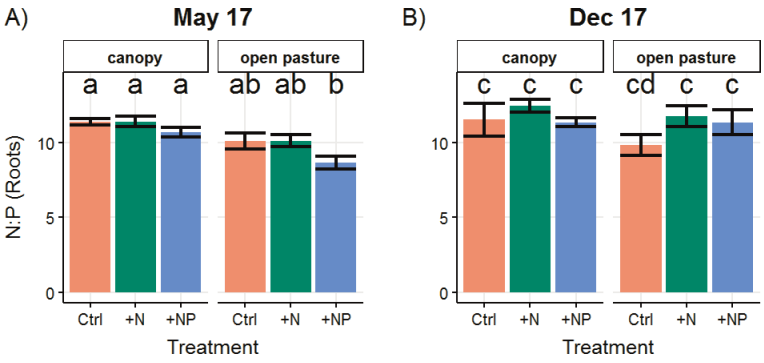

Figure 2: Root N and P stoichiometric ratio (N:P). Absolute amounts of N and P were highly variable within treatments but affected by micro-habitat and sampling date. N:P ratio was affected by treatment ($p < 0.05$), driven by the differences between the two nutrient addition treatments. Letters show Tukey HSD groupings per sampling date. This model is examined in more detail in Tab. 1 and absolute concentrations of N and P are shown in supplementary material S3.

3.1 Root stoichiometry

N concentration of roots (Fig. S3A, B) was higher under canopies (mean: 11.5 ± 0.3 g kg^{-1}) than in open pastures (mean: 9.12 ± 0.26 g kg^{-1}, $p < 0.001$), and in December (mean: 11.8 ± 0.31 g kg^{-1}) than May (mean: 9.6 ± 0.2 kg^{-1}, $p < 0.001$). Due to the strong effect of sampling date and the high variability between micro-sites there was no overall treatment effect, although an interaction between treatment and sampling date remained in the most parsimonious model alongside the main effects. Root total P (Fig. S3C, D) was also more strongly affected by habitat ($p < 0.01$) and sampling date ($p < 0.001$) than by the nutrient treatment, although treatment had a significant ($p < 0.05$) effect in the most parsimonious model, driven by a higher P concentration in +NP in May. Total P concentration was slightly higher in December (May mean 0.9 ± 0.2 g kg^{-1}, December mean: 1.06 ± 0.3 g kg^{-1}, $p < 0.001$). Similar to N, roots were more P enriched under canopies ($p < 0.01$) than in open pastures (1.02 ± 0.0 *vs*. 0.92 ± 0.0 g kg^{-1}).

N:P ratios of roots were more variable than either N or P concentrations (Fig. 2). In May, this ratio was 11:1 for under canopies and 10:1 for open pastures, with minor differences between nutrient addition treatments due to a lower ratio in +NP open pastures. In December, this ratio was higher (12:1 under canopies, 11:1 in open pasture). A weak treatment difference was again visible in open pastures, but due to higher ratios in the two treated areas compared to the control. At this sampling date there was also much more variation in the data (and a smaller sample size). The most parsimonious model explaining root N:P ratios (Tab. 1) included a significant ($p < 0.001$) effect of micro-site and a significant effect of treatment ($p < 0.05$) and sampling date ($p < 0.01$) as well as the interaction between treatment and sampling date ($p < 0.05$); in general, N:P was high in +N ($p < 0.05$), and in May, low in +NP ($p < 0.05$).

Table 1: Significant terms from post-hoc analysis of the root N:P ratio model. Meaningless interactions (without a treatment or date in common) are excluded and other two-way interactions (treatment:micro-habitat and micro-habitat:date) removed during model selection. In general, the direction of N and NP effects are opposite, while < and > indicate direction of contrast.

Term	Contrast	*p*-value
treatment	+N–Control	n.s.
treatment	+NP < +N	$p < 0.01$
treatment	+NP–Control	n.s.
micro-habitat	open pasture < canopy	$p < 0.001$
date	May < Dec	$p < 0.01$
treatment:date	Control:May–Control:Dec	n.s.
treatment:date	+N:May–+N:Dec	n.s.
treatment:date	+NP:May < +NP:Dec	$p < 0.05$

3.2 ^{15}N Recovery

In both root and soil pools, recovery of the tracer was very variable. More of the initial tracer was recovered in May in these two pools (Fig. 3A; all treatment mean: 45.2 ± 20%) than December (Fig. 3B; 23.9 ± 11%, $p < 0.001$) and in canopy locations (41.6 ± 21%) than open pasture locations (28.7 ± 15%, $p < 0.001$) with no interaction terms in the most parsimonious model. In the soil pool, mean recovery of the ^{15}N label was quite stable (with high error), as 13.0 ± 8.1% of the label was recovered in May and 9.3 ± 5.0% recovered in December. This sampling date difference was the main driver of differences in recovery ($p < 0.01$) as there was no difference between micro-habitats or treatments.

Notably, the root pool contained more of this recovered ^{15}N than soil (Tab. 2). A three-way interaction term remained in the initial model ($p = 0.07$) driven by high root recovery in +N in open pastures in May ($p < 0.02$). If this three-way interaction was disallowed, the model resolved to having significant effects for treatment ($p < 0.05$) and habitat ($p < 0.05$) with the same patterns as found in total recovery. These two factors resulted in a model with an adj. R^2 of 0.44. Root ingrowth was highly correlated (root mass: $p < 0.001$, adj. $R^2 = 0.52$, root N mass: $p < 0.001$, adj. $R^2 = 0.76$; Fig. 4) with percentage root

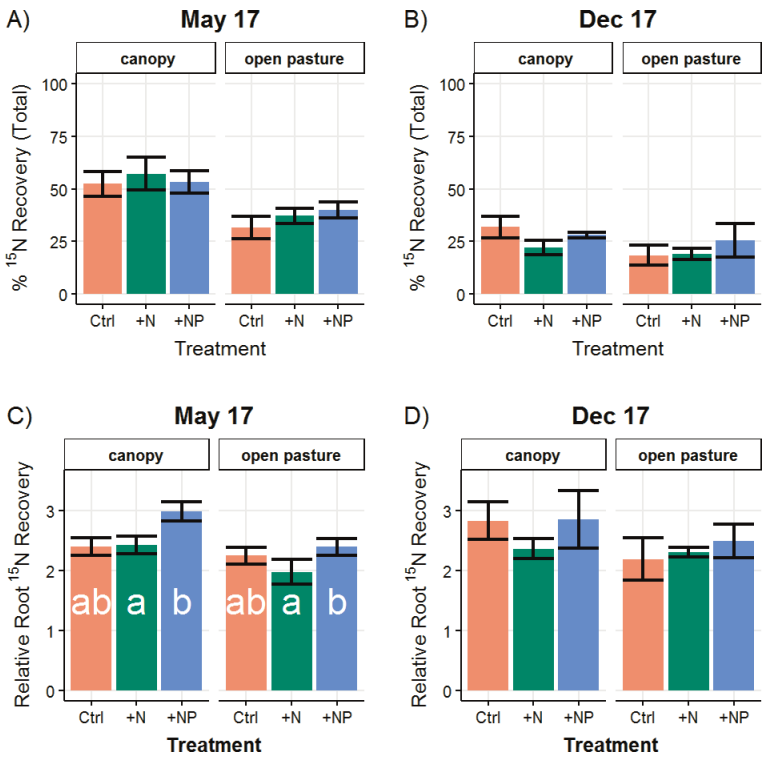

Figure 3: Results of the ^{15}N isotope trace. Total ^{15}N recovery (in measured soil and root pools, shown in more detail in Tab. 2) was not affected by treatment but was by micro-habitat ($p < 0.01$). Root recovery is shown adjusted for root mass due to the relationship shown in Fig. 4. Letters for root ^{15}N recovery (panel C) show Tukey HSD differences between treatments in the most parsimonious model, which did not have an interaction with habitat. In total recovery, but not mass-controlled recovery, there was a difference between the two sampling dates ($p < 0.001$).

^{15}N recovery. We therefore adjusted the ^{15}N recovery found in roots by dividing the recovery per root ingrowth (Fig. 3C, D). This relative ^{15}N recovery in roots differed between treatments (overall $p < 0.05$) and micro-habitat ($p < 0.01$) but not between dates (Fig. 3C, D). The December sampling was much more variable than May, and when we split these data between dates, the significant effects of both treatment and micro-habitat were confined to May. At this time, proportionally, more of the labelled N was retained in the new root pool under canopies compared to open pasture areas ($p < 0.01$). More of the mass-corrected ^{15}N was recovered in +NP roots ($p < 0.05$) than the other treatments. Tukey HSD post-hoc tests revealed a significant difference between +N and +NP ($p < 0.01$) but no difference between control and the two treatments; hence the nutrient stoichiometry treatments increased mass-corrected root ^{15}N recovery in new roots in +NP, and reduced it in +N. Nutrient treatment and micro-habitat were not the major drivers of this recovery; the best model (for May only) had an adjusted R^2 of 0.20.

3.3 Supplementary analyses

Mean N leaching below the cores (*i.e.*, N captured in the resin bags located beneath the cores) from initiation to recovery in May (165 d during the main growing season) was 0.013 ± 0.01 kg N ha^{-1}. Per core, this was equivalent to about 20% of the N added in litter. K_2SO_4-Extractable N was around 5–10 mg g^{-1}, and differed significantly between both treatment ($p < 0.05$) and micro-habitat ($p < 0.01$). This was primarily driven by low extractable N in + N under canopies. Microbial N was higher under canopies than in open pasture areas ($p < 0.01$; Fig. 5). While treatment alone did not have a significant effect on the microbial N concentration, the interaction between treatment and micro-habitat ($p < 0.01$) did, driven by differences in +N ($p < 0.05$), which had a lower average microbial N than +NP treatments under canopies.

4 Discussion

Our research questions concerned (1) root stoichiometry, (2) root uptake of the ^{15}N tracer, and (3) how responses to this were mediated by micro-habitat and the highly seasonal dehesa environment. In general, the stoichiometric ratios of both roots (Fig. 2) and leaves (Fig. S7) at our site are in the range of N or P co-limitation in dry grasslands (*Güsewell*, 2004). Hence, coupled with nutrient limitation at the site (see methods section), we expected ^{15}N recovery to be mainly driven by an excess of N in in the +N treatment and an associated stoichiometric imbalance not found in +NP which would reduce N requirements from litter recycling. However, when corrected for biomass differences, we found an increased recovery of ^{15}N in roots in the +NP treatment, as well as a higher recovery under canopies and an interaction with the two seasonal sampling dates. We can relate these observations to differential

Table 2: Summary of the isotope tracer recovery in the three treatments. All values are percentage recovery ± standard error. Root ingrowth is very variable (Fig. 1), which contributes to this high standard error.

	Control			+N			+NP		
	Root	Soil	Total	Root	Soil	Total	Root	Soil	Total
Open Pasture: May 2017	19 ± 6	13 ± 4	32 ± 7	24 ± 7	14 ± 4	37 ± 8	26 ± 7	12 ± 4	39 ± 8
Open Pasture: December 2017	9 ± 4	9 ± 4	18 ± 5	14 ± 6	5 ± 2	19 ± 6	14 ± 6	11 ± 5	25 ± 7
Under Canopy: May 2017	33 ± 10	16 ± 5	49 ± 11	40 ± 11	10 ± 3	50 ± 12	37 ± 11	13 ± 4	51 ± 11
Under Canopy: December 2017	26 ± 11	6 ± 2	32 ± 11	12 ± 5	11 ± 5	23 ± 7	16 ± 6	13 ± 5	29 ± 8

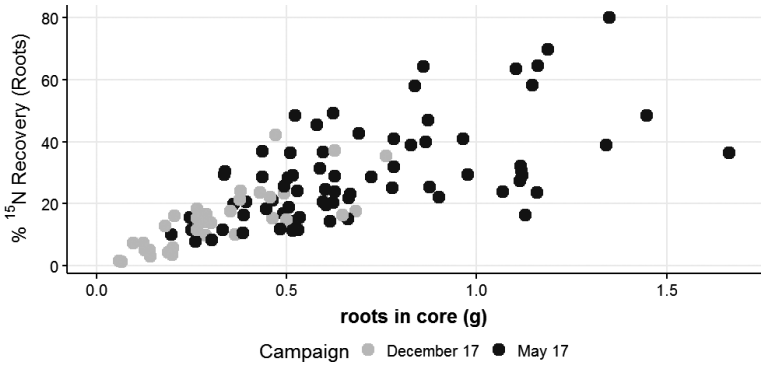

Figure 4: ^{15}N recovery in roots was heavily influenced by root ingrowth [more ^{15}N is recovered per root mass ($p < 0.005$, adj. $R^2 = 0.52$)].

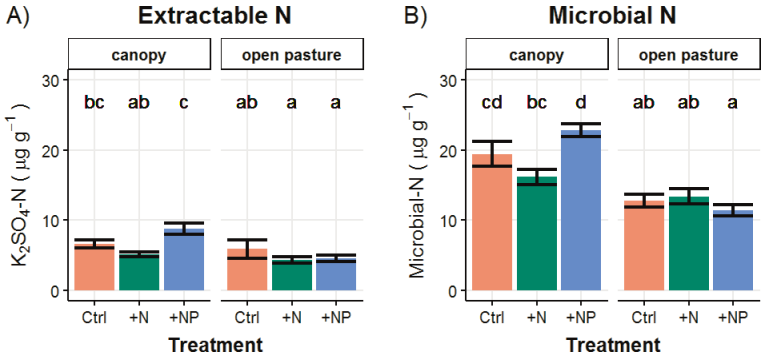

Figure 5: 0.5 M K_2SO_4 Extractable and Microbial N from ingrowth core soil in May 2017. +NP has a higher N availability under canopies and lower in open pasture, which is reflected in N concentration. Letters show Tukey HSD groupings.

losses in N and P over time following the 2015/2016 fertilization, resulting in a different stoichiometric response to fertilizer additions.

4.1 Root and soil stoichiometric response to fertilizer addition

We expected to see that root N:P ratios increase in +N (N:P imbalanced) and remain similar in +NP (N:P balanced). Instead, the root N:P ratio relative to the control was slightly increased in +N but decreased in +NP (Tab. 1, Fig. 2). The main explanation for this difference was the observed soil N:P ratios (Fig. 1) and the differential loss of N and P from soils. As surface soil N contents (Fig. S4) were relatively similar between treatments, N additions did not have an effect on available N by the time of this study (2–3 years after fertilization). In contrast the +NP treatment still had a strong effect on soil N:P ratio (Fig. 1C), which was reflected in roots (Fig. 2A). While P is commonly understood to be readily immobilized in non-bioavailable forms (*Harrison*, 1987), N leaching is also very common in Mediterranean ecosystems during winter, when low vegetation activity coincides with high concentrations of water soluble nitrate ions and wet or saturated soil conditions (*Bernal* et al., 2005). Indeed, the stoichiometric ratios of the initial fertilizations applied over a year prior was most likely offset by N losses over time (*Nair* et al., 2019). Furthermore, the highest soil extractable N:P ratios were measured in the +N treatment in November, in agreement with the potentially slightly increased root N:P at that treatment (Fig. 1; not statistically significant due to high variability). Soil extractable N:P ratios were, however, probably due to the turnover of N from biomass pools (with dissimilar N:P ratios between treatments) in a flush of microbial activity after the moisture-limited summer rather than a year-round higher N-availability (*Morris* et al., 2019). Hence, we can explain the root stoichiometric response with the available soil N:P ratios, which indicated that +N was slightly P deficient, and +NP was P enriched, compared to the control treatment.

4.2 Root ^{15}N Uptake

We used a novel method of ^{15}N tracer delivery, introducing our label as litter inserted *in situ* without litterbags. Litterbags provide a physical (but permeable) barrier between introduced litter and soil and so may introduce artefacts to decomposition rate and accessibility by plants and mycorrhizal fungi. However, this methodology relied on our ability to distinguish between the added litter and new roots. At our site we expected turnover to be fast (*Casals* et al., 2010), in contrast to expectations from litterbag-calibrated fine root decomposition in other ecosystems (*e.g.*, *Li* et al., 2015). We combined this expectation with criteria for positive indication of vitality in material we classed as roots and so did not expect to miss-classify 'initiation' material as 'living roots', rather than the inverse. In fact, we did not identify root matter originating from our additions in the cores in May at all, and could account for ≈ 50% of the N added in the two pools measured (notably excluding above-ground biomass and leaching), so assumed decomposition had been rapid before the first sampling, and that our ^{15}N recovery in newly grown roots was not contaminated by remaining labelled material identified as roots. If we misclassified substantial amounts of this litter as new roots (a classification direction error we tried to minimise as previously mentioned), we may have biased recovery, for this to affect treatment differences a systematic difference in *total* losses from these pool (rather than rates) would need to have occurred, which we consider unlikely due to the aforementioned typically high decomposition rates.

As total ^{15}N recovery in roots was driven by root ingrowth at the level of individual cores, this recovery was hence influenced by absolute productivity. Nonetheless, when we controlled for biomass, we still found differences between treatments in May. At this time, roots had obtained less N from the litter in +N, and more in +NP (Fig. 3C), indicating +NP had led to a more 'N conservative' system better adapted to recovering N from litter decomposition. +N had the inverse effect, reducing recovery (although only in the pasture micro-sites). This was probably due to the previously discussed P surplus relative to N in the +NP treatment (but not the control treatment), and increases in both above and below-ground bio-

mass (*Nair* et al., 2019) requiring more N uptake from the decomposing litter. However, the dissimilar N:P ratios of the +NP treatment found in soil extracts (Fig. 1), grassland roots in May (Fig. 2) and leaf tissue in May 2016 and 2017 (Fig. S7) suggest that this extra N uptake does not fully satisfy N demand. This tightly coupled co-limitation has been found in P limited systems, including N saturated Mediterranean forests, as P additions may directly increase N uptake (*Blanes* et al., 2012; *Mori* et al., 2014) , and here we can demonstrate that in our study system this includes additional utilization of N directly from recent biomass turnover.

4.3 Temporal effects on results

We did not find a similar effect in December, when total below-ground recoveries were lower (around 25% of added ^{15}N, compared to 30–55%; Fig. 1) and no treatment difference in relative ^{15}N recovery was found. This was probably because of a longer time since application, which contained both the spring growing season, summer drought, and wet autumn growing season. Due to the incorporation into biomass in May and implicit high turnover, most of the ^{15}N found in biomass in December had probably passed through this 2017 season litter, resulting in a progressive dilution of the isotope signal. Indeed, the biomass decrease between May and December implied a large turnover of roots between these dates (consequently becoming part of the soil pool). Time since initiation would not have had the same effect on root stoichiometry, but we did expect this to change between sampling dates. Plant N and P concentrations tend to decrease in periods of drought stress as nutrient uptake is hampered more than C assimilation (*He* and *Dijkstra*, 2014) and indeed we observed a slightly lower average N and P content in our roots in May than December.

Mediterranean vegetative N:P ratio decreases throughout the spring as resources are gradually shifted towards reproduction (*Corona* et al., 1998) and we found a higher root N:P ratio in December than May in +N and +NP (but not Control; Tab. 1). This is because of demand for above-ground reproductive tissues in May, and relatively high P concentration of seeds compared to vegetative tissues (*Güsewell*, 2004), meaning that more nutrients likely were in vegetative organs such as roots in December (*Figueroa* and *Davy*, 1991; *Peco* et al., 2005). In seasonal systems, resource limitations shift throughout the year, and plants can adapt to accommodate these by altering biomass ratios and allometry (*Poorter* and *Nagel*, 2000) such as the changes in root:shoot ratio and root length density (RLD) differences at the site (*Nair* et al., 2019). This previous study showed a higher RLD throughout springtime which could contribute to lower root N:P. Root length is both adaptive for nutrient (*Bardgett* et al., 2014) and water acquisition (*Comas* et al., 2013) as more root length means both greater volume and depth of soil can be accessed, which is particularly relevant in infrequent spring re-wetting events (*Mikha* et al., 2005). Other site-level conclusions suggest the +N treatment was increasingly water stressed (*Luo* et al., 2020) to the extent of accelerating dry-down. This water stress may induce root adaptions for water harvesting rather than nutrient uptake. As the main difference in per biomass organic-source ^{15}N recovery was in +NP in May (Fig. 3) corresponding high RLD within this treatment (*Nair* et al., 2019), this RLD may have been related to N demand. However, higher resolution sampling and/or usage of stable isotopes of oxygen in water would be necessary to tease apart the functional effects of changes in belowground plant biomass.

4.4 Habitat effects on results

We expected habitat effects due to differing fertility between microsites. From tissue stoichiometry, we only found differences in N:P of roots between nutrient treatments in open pasture microsites (Fig. 2) despite differences in extractable N:P (Fig. 1) at both locations in May and high N at some +N microsites in December. This may relate to higher total nutrient availability (Fig. S4), microbial biomass and extractable N (Fig. 5); under canopy locations in dehesa have higher overall nutrient availabilities and more organic matter than pasture micro-sites (*Gallardo*, 2003; *Howlett* et al., 2011; *Rolo* et al., 2013). We expected root recovery of ^{15}N added in litter to dilute against this background of higher N abundance, but instead, higher nutrient availability under canopies was accompanied by more litter N uptake by roots per biomass (Fig. 3). This is contrary to ecosystem gradient studies (*e.g.*, *Averill* and *Finzi*, 2011), which tend to find organic N uptake is more important under N-limiting conditions. The observed higher recovery may be explained by differences in the biological community between microsites. Indeed, our most parsimonious model (using nutrient treatment and micro-habitat as predictors) only had a R^2 of 0.2, suggesting that there were other factors within-treatment × habitat combination driving this recovery, such as plant and microbial communities, or organic matter content. As well as higher microbial biomass, (which may include mycorrhizal fungi facilitating plant N uptake), there tend to be more grasses and less legumes in the more fertile locations under trees (*López-Carrasco* et al., 2015), at our site, increasing N 'fertility' with +N had completely suppressed legumes in these locations in spring (Fig. S7). While speculation at the level of individual species traits is beyond the scope of this study, this difference potentially occurs because the community in under canopy micro-sites are more adapted to directly compete for litter N in a much more litter rich environment. This could include either direct organic uptake or increased mycorrhizal symbiotic associations (*Weigelt* et al., 2003; *Zeller* and *Colin-Belgrand*, 2001; *Fay* et al., 2015; *Vadeboncoeur* et al., 2015; *Nair* et al., 2019), although further work is necessary to discern the precise mechanism.

Additionally it was within open pasture areas where the largest RLD differences were previously found (*Nair* et al., 2019) but this for the habitat comparison (unlike the treatment comparison), this did not appear to result in more successful per biomass N uptake from litter sources (Fig. 3). In this savannoid system, these open pasture micro-sites experience more runoff and drainage but also higher temperatures in spring (*Joffre* and *Rambal*, 1993). Thus, the uppermost layer of uncanopied soils dries quicker than canopied soil, while the opposite occurs in deeper layers (*Moreno*, 2008; *Moreno* and *Cubera*, 2008) because of the distinct rooting profiles in the two micro-habitats (*Moreno* et al., 2005). This may result in overall deeper herbaceous root development in open pasture areas, to access water. Hence, while in terms of the treatment

difference, RLD increases may correlate with uptake of litter N, this explanation does not hold across the habitat comparison as these habitat effects confound the nutrient response. The site has relatively low tree cover (and hence, proportionately less 'under canopy' soil) compared to most dehesas (*Moreno* and *Pulido*, 2009) and scaling any response must take such factors into account in these heterogeneous systems.

4.5 Comparison with mineral tracers and wider implications

Turnover of dead biomass is the major source of both N and P in unfertilized ecosystems, and usually a far larger N source than either deposition or biological N fixation. Litter as a N source is very different to typical experimental fertilizations as N release is chronic and usually biologically mediated, and by-products persist in soils in a variety of intermediate organic polymer forms (*Schulten* and *Schnitzer*, 1997). Here, we showed that N:P imbalances (applied initially as mineral fertilizer, but persisting in both biomass pools and soil available N:P ratios) altered the acquisition of this litter-derived N.

In total, as we only measured recovery in root and soil, we can account for around 25% of added ^{15}N after one year and cannot perform a full mass balance due to the lack of measurements in other major pools. However, this recovery is notably very different than a similar study within the same system using ^{15}N labelled mineral fertilizer (*Morris* et al., 2019). This mineral ^{15}N amendment found an even ratio of recovery of ^{15}N between above- and below ground plant components on comparable time scales. If our organic tracer was partitioned similarly within plants, the mineral tracer had a much lower total ^{15}N recovery within the herbaceous layer. Additionally, the mineral tracer had higher recovery in pasture than under canopy micro-sites and a much higher total recovery in soil compared to plant biomass. Microbial and mineral sinks usually dominate mineral N competition at the expense of plants (*Templer* et al., 2012), and such mineral traces may not be representative of 'internal' N recycling when directly compared (*Nair* et al., 2017). In general, knowledge gained from mineral tracer partitioning, as commonly informs N cycling processes, should be applied cautiously if used to also predict plant N nutrition derived from turnover of dead biomass.

While we did not measure litter turnover directly, nor C fluxes, the nutrient treatments altered the per-biomass incorporation of litter turnover ^{15}N in the P-enriched +NP treatment and may have altered both these fluxes through direct belowground C partitioning. In a multi-resource limited system such as our study site, belowground responses to the nutrient treatment are highly complex and likely related to plant assignment to fulfil a time-variable demand for N and P or other nutrients, as well as water. In the absence of a stable isotope for P, understanding P foraging responses is much more difficult. It is not clear how well linked N and P release from decomposing litter are, how this relates to plant demand for these nutrients, and how this could be altered by plant demand in future, N-saturated conditions. In more arid grassland systems, N deposition drives additional P absorption by plants (*Long* et al., 2016). However as such knowledge is gained from fertilization experiments, future work should focus on validating that such conclusions also apply to litter turnover products as well as fertilizer additions.

5 Conclusions

In this study, we demonstrate that altered ecosystem stoichiometry affected both root tissue stoichiometry and root nutrient foraging at our dehesa site. Plants compensated for relative P or N enrichment by acquiring more root litter derived N in the P enriched +NP treatment, and less in the relatively N-rich +N treatment. As such systems become more N enriched due to N deposition, the litter loop may loosen, potentially slowing rates of mineralization as well as increasing leaching losses. However, this also depends on how plants forage for other resources. In our seasonally arid ecosystem, root N:P stoichiometry and uptake of litter-derived ^{15}N is responsive to manipulated ecosystem-level nutrient stoichiometry, suggesting that these nutrient imbalances are fundamentally altering the plant-soil feedbacks of such systems in addition to any productivity changes.

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References

Abramoff, R. Z., *Finzi, A. C.* (2015): Are above- and below-ground phenology in sync? *New Phytol.* 205, 1054–1061.

Averill, C., *Finzi, A.* (2011): Increasing plant use of organic nitrogen with elevation is reflected in nitrogen uptake rates and ecosystem δ^{15}N. *Ecology* 92, 883–891.

Bardgett, R. D., *Mommer, L.*, *De Vries, F. T.* (2014): Going underground: root traits as drivers of ecosystem processes. *Trends Ecol. Evol.* 29, 692–699.

Beringer, J., *Hutley, L. B.*, *Hacker, J. M.*, *Neininger, B.*, *Paw U, K. T.* (2011): Patterns and processes of carbon, water and energy cycles across northern Australian landscapes: From point to region. *Agric. Forest Meteorol.* 151, 1409–1416.

Bernal, S., *Butturini, A.*, *Sabater, F.* (2005): Seasonal variations of dissolved nitrogen and DOC : DON ratios in an intermittent Mediterranean stream. *Biogeochemistry* 75, 351–372.

Bimüller, C., *Naumann, P. S.*, *Buegger, F.*, *Dannenmann, M.*, *Zeller, B.*, *von Lützow, M.*, *Kögel-Knabner, I.* (2013): Rapid transfer of ^{15}N from labeled beech leaf litter to functional soil organic matter fractions in a Rendzic Leptosol. *Soil Biol. Biochem.* 58, 323–331.

Bird, J. A., *Kleber, M.*, *Torn, M. S.* (2008): ^{13}C and ^{15}N stabilization dynamics in soil organic matter fractions during needle and fine root decomposition. *Org. Geochem.* 39, 465–477.

Blanes, M. C., *Emmett, B. A.*, *Viñegla, B.*, *Carreira, J. A.* (2012): Alleviation of P limitation makes tree roots competitive for N against microbes in a N-saturated conifer forest: A test through P fertilization and ^{15}N labelling. *Soil Biol. Biochem.* 48, 51–59.

Brookes, P. C., *Kragt, J. F.*, *Powlson, D. S.*, *Jenkinson, D. S.* (1985): Chloroform fumigation and the release of soil nitrogen: the effects of fumigation time and temperature. *Soil Biol. Biochem.* 17, 831–835.

Caldararu, S., *Thum, T.*, *Yu, L.*, *Zaehle, S.* (2019): Whole-plant optimality predicts changes in leaf nitrogen under variable CO_2 and nutrient availability. *New Phytol.* 225, 2331–2346.

Casals, P., *Garcia-Pausas, J.*, *Montané, F.*, *Romanyà, J.*, *Rovira, P.* (2010): Root decomposition in grazed and abandoned dry Mediterranean dehesa and mesic mountain grasslands estimated by standard labelled roots. *Agric. Ecosyst. Environ.* 139, 759–765.

Comas, L. H., *Becker, S. R.*, *Cruz, V. M. V.*, *Byrne, P. F.*, *a Dierig, D.* (2013): Root traits contributing to plant productivity under drought. *Front. Plant Sci.* 4. DOI: https://doi.org/10.3389/fpls.2013.00442.

Corona, M. E. P., *de Aldana, B. R. V.*, *Garci, B.*, *Garci, A.* (1998): Variations in nutritional quality and biomass production of semiarid grasslands. *Rangeland Ecol. Manag. / J. Range Manag. Arch.* 51, 570–576.

Dornbush, M. E., *Isenhart, T. M.*, *Raich, J. W.* (2002): Quantifying fine-root decomposition: An alternative to buried litterbags. *Ecology* 83, 2985–2990.

El-Madany, T. S., *Reichstein, M.*, *Perez-Priego, O.*, *Carrara, A.*, *Moreno, G.*, *Pilar Martín, M.*, *Pacheco-Labrador, J.*, *Wohlfahrt, G.*, *Nieto, H.*, *Weber, U.*, *Kolle, O.*, *Luo, Y. P.*, *Carvalhais, N.*, *Migliavacca, M.* (2018): Drivers of spatio-temporal variability of carbon dioxide and energy fluxes in a Mediterranean savanna ecosystem. *Agric. Forest Meteorol.* 262, 258–278.

Elser, J. J., *Bracken, M. E. S. S.*, *Cleland, E. E.*, *Gruner, D. S.*, *Harpole, W. S.*, *Hillebrand, H.*, *Ngai, J. T.*, *Seabloom, E. W.*, *Shurin, J. B.*, *Smith, J. E.* (2007): Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecol. Lett.* 10, 1135–1142.

Fahey, T. J., *Hughes, J. W.* (1994): Fine root dynamics in a northern hardwood forest ecosystem, Hubbard Brook Experimental Forest, NH. *J. Ecol.* 82, 533–548.

Fay, P. A., *Prober, S. M.*, *Harpole, W. S.*, *Knops, J. M. H.*, *Bakker, J. D.*, *Borer, E. T.*, *Lind, E. M.*, *MacDougall, A. S.*, *Seabloom, E. W.*, *Wragg, P. D.*, *Adler, P. B.*, *Blumenthal, D. M.*, *Buckley, Y. M.*, *Chu, C.*, *Cleland, E. E.*, *Collins, S. L.*, *Davies, K. F.*, *Du, G.*, *Feng, X.*, *Firn, J.*, *Gruner, D. S.*, *Hagenah, N.*, *Hautier, Y.*, *Heckman, R. W.*, *Jin, V. L.*, *Kirkman, K. P.*, *Klein, J.*, *Ladwig, L. M.*, *Li, Q.*, *McCulley, R. L.*, *Melbourne, B. A.*, *Mitchell, C. E.*, *Moore, J. L.*, *Morgan, J. W.*, *Risch, A. C.*, *Schütz, M.*, *Stevens, C. J.*, *Wedin, D. A.*, *Yang, L. H.* (2015): Grassland productivity limited by multiple nutrients. *Nat. Plants* 1. DOI: https://doi.org/10.1038/nplants.2015.80.

Figueroa, M. E., *Davy, A. J.* (1991): Response of Mediterranean grassland species to changing rainfall. *J. Ecol.* 79, 925–941.

Gallardo, A. (2003): Effect of tree canopy on the spatial distribution of soil nutrients in a Mediterranean Dehesa. *Pedobiologia* 47, 117–125.

Gallardo, A., *Rodríguez-Saucedo, J. J.*, *Covelo, F.*, *Fernández-Alés, R.* (2000): Soil nitrogen heterogeneity in a Dehesa ecosystem. *Plant Soil* 222, 71–82.

Giorgi, F., *Lionello, P.* (2008): Climate change projections for the Mediterranean region. *Global Planet. Change* 63, 90–104.

Guo, C., *Dannenmann, M.*, *Gasche, R.*, *Zeller, B.*, *Papen, H.*, *Polle, A.*, *Rennenberg, H.*, *Simon, J.* (2013): Preferential use of root litter compared to leaf litter by beech seedlings and soil microorganisms. *Plant Soil* 368, 519–534.

Güsewell, S. (2004): N : P ratios in terrestrial plants: variation and functional significance. *New Phytol.* 164, 243–266.

Harpole, W. S., *Sullivan, L. L.*, *Lind, E. M.*, *Firn, J.*, *Adler, P. B.*, *Borer, E. T.*, *Chase, J.*, *Fay, P. A.*, *Hautier, Y.*, *Hillebrand, H.*, *MacDougall, A. S.*, *Seabloom, E. W.*, *Bakker, J. D.*, *Cadotte, M. W.*, *Chaneton, E. J.*, *Chu, C.*, *Hagenah, N.*, *Kirkman, K.*, *La Pierre, K. J.*, *Moore, J. L.*, *Morgan, J. W.*, *Prober, S. M.*, *Risch, A. C.*, *Schuetz, M.*, *Stevens, C. J.* (2017): Out of the shadows: multiple nutrient limitations drive relationships among biomass, light and plant diversity. *Funct. Ecol.* 31, 1839–1846.

Harrison, A. F. (1987): Soil Organic Phosphorus: A Review of World Literature. CABI, Wallingford, UK.

He, M., *Dijkstra, F. A.* (2014): Drought effect on plant nitrogen and phosphorus: a meta-analysis. *New Phytol.* 204, 924–931.

Hill, J. O., *Simpson, R. J.*, *Moore, A. D.*, *Chapman, D. F.* (2006): Morphology and response of roots of pasture species to phosphorus and nitrogen nutrition. *Plant Soil* 286. DOI: https://doi.org/10.1007/s11104-006-0014-3.

Högberg, P. (2012): What is the quantitative relation between nitrogen deposition and forest carbon sequestration? *Global Change Biol.* 18, 1–2.

Howlett, D. S., *Moreno, G.*, *Mosquera Losada, M. R.*, *Nair, P. K. R.*, *Nair, V. D.* (2011): Soil carbon storage as influenced by tree cover in the Dehesa cork oak silvopasture of central-western Spain. *J. Environ. Monit.* 13, 1897–1904.

Joffre, R., *Rambal, S.* (1993): How tree cover influences the water balance of Mediterranean rangelands. *Ecology* 74, 570–582.

Joffre, R., *Rambal, S.*, *Ratte, J. P.* (1999): The dehesa system of southern Spain and Portugal as a natural ecosystem mimic. *Agroforest. Syst.* 45, 57–79.

Kovats, R. S., *Valentini, R.*, *Bouwer, L. M.*, *Georgopoulou, E.*, *Jacob, D.*, *Martin, E.*, *Rounsevell, M.*, *Soussana, J.-F.* (2014): Europe, in Barros, V. R., Field, C. B., Dokken, D. J., Mastrandrea, M. D., Mach, K. J., Bilir, T. E., Chatterjee, M., Ebi, K. L., Estrada, Y. O., Genova, R. C., Girma, B., Kissel, E. S., Levy, A. N., MacCracken, S., Mastrandrea, P. R., White, L. L. (eds.): Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK, pp. 1267–1326.

Kramer, C., *Trumbore, S.*, *Fröberg, M.*, *Cisneros Dozal, L. M.*, *Zhang, D.*, *Xu, X.*, *Santos, G. M.*, *Hanson, P. J.* (2010): Recent (< 4 year old) leaf litter is not a major source of microbial carbon in a temperate forest mineral soil. *Soil Biol. Biochem.* 42, 1028–1037.

Li, A., *Fahey, T. J.*, *Pawlowska, T. E.*, *Fisk, M. C.*, *Burtis, J.* (2015): Fine root decomposition, nutrient mobilization and fungal communities in a pine forest ecosystem. *Soil Biol. Biochem.* 83, 76–83.

Long, M., *Wu, H.-H.*, *Smith, M. D.*, *La Pierre, K. J.*, *Lü, X.-T.*, *Zhang, H.-Y.*, *Han, X.-G.*, *Yu, Q.* (2016): Nitrogen deposition promotes phosphorus uptake of plants in a semi-arid temperate grassland. *Plant Soil* 408, 475–484.

López-Carrasco, C., *López-Sánchez, A.*, *San Miguel, A.*, *Roig, S.* (2015): The effect of tree cover on the biomass and diversity of the herbaceous layer in a Mediterranean dehesa. *Grass Forage Sci.* 70, 639–650.

Ludwig, F., *de Kroon, H.*, *Berendse, F.*, *Prins, H. H. T.* (2004): The influence of savanna trees on nutrient, water and light availability and the understorey vegetation. *Plant Ecol.* 170, 93–105.

Luo, Y., *El-Madany, T.*, *Ma, X.*, *Nair, R.*, *Jung, M.*, *Weber, U.*, *Filippa, G.*, *Bucher, S. F.*, *Moreno, G.*, *Cremonese, E.*, *Carrara, A.*, *Gonzalez-Cascon, R.*, *Cáceres Escudero, Y.*, *Galvagno, M.*, *Pacheco-Labrador, J.*, *Martín, M. P.*, *Perez-Priego, O.*, *Reichstein, M.*, *Richardson, A. D.*, *Menzel, A.*, *Römermann, C.*, *Migliavacca, M.* (2020): Nutrients and water availability constrain the seasonality of vegetation activity in a Mediterranean ecosystem. *Global Change Biol.* 2020. DOI: https://doi.org/10.1111/gcb.15138.

Luo, Y., *El-Madany, T. S.*, *Filippa, G.*, *Ma, X.*, *Ahrens, B.*, *Carrara, A.*, *Gonzalez-Cascon, R.*, *Cremonese, E.*, *Galvagno, M.*, *Tiana, W.* (2018): Using near-infrared-enabled digital repeat photography to track structural and physiological phenology in Mediterranean tree–grass ecosystems. *Remote Sens.* 10. DOI: https://doi.org/10.3390/rs10081293.

Luo, Y., *Su, B.*, *Currie, W. S.*, *Dukes, J. S.*, *Finzi, A.*, *Hartwig, U.*, *Hungate, B.*, *McMurtrie, R. E.*, *Oren, R.*, *Parton, W. J.*, *Pataki, D. E.*, *Shaw, R. M.*, *Zak, D. R.*, *Field, C. B.* (2004): Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *BioScience* 54, 731–739.

Mendez-Millan, M., *Nguyen Tu, T. T.*, *Balesdent, J.*, *Derenne, S.*, *Derrien, D.*, *Egasse, C.*, *Thongo M'Bou, a.*, *Zeller, B.*, *Hatté, C.* (2014): Compound-specific ^{13}C and ^{14}C measurements improve the understanding of soil organic matter dynamics. *Biogeochemistry* 118, 205–223.

Meunier, C. L., *Boersma, M.*, *El-Sabaawi, R.*, *Halvorson, H. M.*, *Herstoff, E. M.*, *Van de Waal, D. B.*, *Vogt, R. J.*, *Litchman, E.* (2017): From elements to function: toward unifying ecological stoichiometry and trait-based ecology. *Front. Environ. Sci.* 5. DOI: https://doi.org/10.3389/fenvs.2017.00018.

Migliavacca, M., *Perez-Priego, O.*, *Rossini, M.*, *El-Madany, T. S.*, *Moreno, G.*, *van der Tol, C.*, *Rascher, U.*, *Berninger, A.*, *Bessenbacher, V.*, *Burkart, A.*, *Carrara, A.*, *Fava, F.*, *Guan, J. H.*, *Hammer, T. W.*, *Henkel, K.*, *Juarez-Alcalde, E.*, *Julitta, T.*, *Kolle, O.*, *Martín, M. P.*, *Musavi, T.*, *Pacheco-Labrador, J.*, *Pérez-Burgueño, A.*, *Wutzler, T.*, *Zaehle, S.*, *Reichstein, M.* (2017): Plant functional traits and canopy structure control the relationship between photosynthetic CO_2 uptake and far-red sun-induced fluorescence in a Mediterranean grassland under different nutrient availability. *New Phytol.* 214, 1078–1091.

Mikha, M. M., *Rice, C. W.*, *Milliken, G. A.* (2005): Carbon and nitrogen mineralization as affected by drying and wetting cycles. *Soil Biol. Biochem.* 37, 339–347.

Mokany, K., *Raison, R. J.*, *Prokushkin, A. S.* (2006): Critical analysis of root: shoot ratios in terrestrial biomes. *Global Change Biol.* 12, 84–96.

Moreno, G. (2008): Response of understorey forage to multiple tree effects in Iberian dehesas. *Agric. Ecosyst. Environ.* 123, 239–244.

Moreno, G., *Cubera, E.* (2008): Impact of stand density on water status and leaf gas exchange in *Quercus ilex*. *Forest Ecol. Manag.* 254, 74–84.

Moreno, G., *Obrador, J. J.*, *Cubera, E.*, *Dupraz, C.* (2005): Fine root distribution in dehesas of central-western Spain. *Plant Soil* 277, 153–162.

Moreno, G.., *Pulido, F. J. J.* (2009): The Functioning, Management and Persistence of Dehesas, in Rigueiro-Rodríguez, A., McAdam, J., Mosquera-Losada, M. R. (eds.): Agroforestry in Europe. Springer, Dordrecht, The Netherlands, pp. 127–160.

Moreno Marcos, G., *Obrador, J. J.*, *García, E.*, *Cubera, E.*, *Montero, M. J.*, *Pulido, F.*, *Dupraz, C.* (2007): Driving competitive and facilitative interactions in oak dehesas through management practices. *Agroforest. Syst.* 70, 25–40.

Mori, T., *Ohta, S.*, *Ishizuka, S.*, *Konda, R.*, *Wicaksono, A.*, *Heriyanto, J.* (2014): Phosphorus application reduces N_2O emissions from tropical leguminous plantation soil when phosphorus uptake is occurring. *Biol. Fertil. Soils* 50, 45–51.

Morris, K. A., *Nair, R. K. F.*, *Moreno, G.*, *Schrumpf, M.*, *Migliavacca, M.* (2019): Fate of N additions in a multiple resource-limited Mediterranean oak savanna. *Ecosphere* 10. DOI: https://doi.org/10.1002/ecs2.2921.

Nair, P. K. R. (2012): Climate Change Mitigation: A Low-Hanging Fruit of Agroforestry, in Nair, P. K. R., Garrity, D. (eds.): Agroforestry—The Future of Global Land Use. Springer Dordrecht, The Netherlands, pp. 31–67.

Nair, R. K. F., *Morris, K. A.*, *Hertel, M.*, *Luo, Y.*, *Moreno, G.*, *Reichstein, M.*, *Schrumpf, M.*, *Migliavacca, M.* (2019): N:P stoichiometry and habitat effects on Mediterranean savanna seasonal root dynamics. *Biogeosciences* 16, 1883–1901.

Nair, R. K. F., *Perks, M. P.*, *Mencuccini, M.* (2017): Decomposition nitrogen is better retained than simulated deposition from mineral amendments in a temperate forest. *Global Change Biol.* 23, 1711–1724.

Norby, R. J., *Jackson, R. B.* (2000): Root dynamics and global change: seeking an ecosystem perspective. *New Phytol.* 147, 3–12.

Ostertag, R., *DiManno, N. M.* (2016): Detecting terrestrial nutrient limitation: a global meta-analysis of foliar nutrient concentrations after fertilization. *Front. Earth Sci.* 4. DOI: https://doi.org/10.3389/feart.2016.00023.

Peco, B., *de Pablos, I.*, *Traba, J.*, *Levassor, C.* (2005): The effect of grazing abandonment on species composition and functional traits: the case of dehesa grasslands. *Basic Appl. Ecol.* 6, 175–183.

Peichl, M., *Leava, N. A.*, *Kiely, G.* (2012): Above- and belowground ecosystem biomass, carbon and nitrogen allocation in recently afforested grassland and adjacent intensively managed grassland. *Plant Soil* 350, 281–296.

Pellegrini, A. F. A. (2016): Nutrient limitation in tropical savannas across multiple scales and mechanisms. *Ecology* 97, 313–324.

Peñuelas, J., *Poulter, B.*, *Sardans, J.*, *Ciais, P.*, *van der Velde, M.*, *Bopp, L.*, *Boucher, O.*, *Godderis, Y.*, *Hinsinger, P.*, *Llusia, J.*, *Nardin, E.*, *Vicca, S.*, *Obersteiner, M.*, *Janssens, I. A.* (2013): Human-induced nitrogen–phosphorus imbalances alter natural and managed ecosystems across the globe. *Nat. Commun.* 4. DOI: https://doi.org/10.1038/ncomms3934.

Peñuelas, J., *Sardans, J.*, *Filella, I.*, *Estiarte, M.*, *Llusià, J.*, *Ogaya, R.*, *Carnicer, J.*, *Bartrons, M.*, *Rivas-Ubach, A.*, *Grau, O.* (2018): Assessment of the impacts of climate change on Mediterranean terrestrial ecosystems based on data from field experiments and long-term monitored field gradients in Catalonia. *Environ. Exp. Bot.* 152, 49–59.

Peñuelas, J., *Sardans, J.*, *Rivas-Ubach, A.*, *Janssens, Ivan. A.* (2012): The human-induced imbalance between C, N and P in Earth's life system. *Global Change Biol.* 18, 3–6.

Perez-Priego, O., *El-Madany, T. S.*, *Migliavaca, M.*, *Kowalski, A. S.*, *Jung, M.*, *Carrara, A.*, *Kolle, O.*, *Martín, M. P.*, *Pacheco-Labrador, J.*, *Moreno, G.*, *Reichstein, M.* (2017): Evaluation of eddy covariance latent heat fluxes with independent lysimeter and sapflow estimates in a Mediterranean savannah ecosystem. *Agric. Forest Meteorol.* 236, 87–99.

Phoenix, G. K., *Booth, R. E.*, *Leake, J. R.*, *Read, D. J.*, *Grime, J. P.*, *Lee, J. A.* (2003): Effects of enhanced nitrogen deposition and phosphorus limitation on nitrogen budgets of semi-natural grasslands. *Global Change Biol.* 9, 1309–1321.

Poorter, H., *Nagel, O.* (2000): The role of biomass allocation in the growth response of plants to different levels of light, CO_2, nutrients and water: a quantitative review. *Funct. Plant Biol.* 27, 1191–1191.

Poulter, B., *Frank, D.*, *Ciais, P.*, *Myneni, R. B.*, *Andela, N.*, *Bi, J.*, *Broquet, G.*, *Canadell, J. G.*, *Chevallier, F.*, *Liu, Y. Y.*, *Running, S. W.*, *Sitch, S.*, *van der Werf, G. R.* (2014): Contribution of semi-arid ecosystems to interannual variability of the global carbon cycle. *Nature* 509, 600–603.

Puerto, A. (1992): Fitomasa subterránea y aérea en pastos de dehesa. *Pastos* 22, 3–19.

R Core Team (2018): R: A language and environment for statistical computing. R Foundation, Vienna, Austria.

Ries, L. P., *Shugart, H. H.* (2008): Nutrient limitations on understory grass productivity and carbon assimilation in an African woodland savanna. *J. Arid Environ.* 72, 1423–1430.

Rolo, V., *Plieninger, T.*, *Moreno, G.* (2013): Facilitation of holm oak recruitment through two contrasted shrubs species in Mediterranean grazed woodlands. *J. Veget. Sci.* 24, 344–355.

Sardans, J., *Grau, O.*, *Chen, H. Y. H.*, *Janssens, I. A.*, *Ciais, P.*, *Piao, S.*, *Peñuelas, J.* (2017): Changes in nutrient concentrations of leaves and roots in response to global change factors. *Global Change Biol.* 23, 3849–3856.

Sardans, J., *Peñuelas, J.* (2013): Plant–soil interactions in Mediterranean forest and shrublands: impacts of climatic change. *Plant Soil* 365, 1–33.

Schulten, H. R., *Schnitzer, M.* (1997): The chemistry of soil organic nitrogen: a review. *Biol. Fertil. Soils* 26, 1–15.

Schulze, E. D. (2000): The Carbon and Nitrogen Cycle of Forest Ecosystems, in: Carbon and Nitrogen Cycling in European Forest Ecosystems. Springer, Berlin, Germany.

Silver, W. L., *Miya, R.* (2001): Global patterns in root decomposition: comparisons of climate and litter quality effects. *Oecologia* 129, 407–419.

Templer, P. H., *Mack, M. C.*, *Chapin III, F. S.*, *Christenson, L. M.*, *Compton, J. E.*, *Crook, H. D.*, *Currie, W. S.*, *Curtis, C. J.*, *Dail, D. B.*, *D'Antonio, C. M.*, *a Emmett, B.*, *Epstein, H. E.*, *Goodale, C. L.*, *Gundersen, P.*, *Hobbie, S. E.*, *Holland, K.*, *Hooper, D. U.*, *Hungate, B. A.*, *Lamontagne, S.*, *Nadelhoffer, K. J.*, *Osenberg, C. W.*, *Perakis, S. S.*, *Schleppi, P.*, *Schimel, J.*, *Schmidt, I. K.*, *Sommerkorn, M.*, *Spoelstra, J.*, *Tietema, A.*, *Wessel, W. W.*, *Zak, D. R.* (2012): Sinks for nitrogen inputs in terrestrial ecosystems: a meta-analysis of ^{15}N tracer field studies. *Ecology* 93, 1816–29.

Vadeboncoeur, M. A., *Ouimette, A. P.*, *Hobbie, E. A.* (2015): Mycorrhizal roots in a temperate forest take up organic nitrogen from ^{13}C- and ^{15}N-labeled organic matter. *Plant Soil* 397, 303–315.

Weigelt, A., *King, R.*, *Bol, R.*, *Bardgett, R. D.* (2003): Inter-specific variability in organic nitrogen uptake of three temperate grassland species. *J. Plant Nutr. Soil Sci.* 166, 606–611.

Weiner, T., *Gross, A.*, *Moreno, G.*, *Migliavacca, M.*, *Schrumpf, M.*, *Reichstein, M.*, *Hillman, B.*, *Carrara, A.*, *Angert, A.* (2018): Following the turnover of soil bioavailable phosphate in Mediterranean Savanna by oxygen stable isotopes. *J. Geophys. Res. Biogeosci.* 123, 1850–1862.

Wurzburger, N., *Wright, S. J.* (2015): Fine-root responses to fertilization reveal multiple nutrient limitation in a lowland tropical forest. *Ecology* 96, 2137–2146.

Zeller, B., *Colin-Belgrand, M.* (2001): Fate of nitrogen released from ^{15}N-labeled litter in European beech forests. *Tree Physiol.* 21, 153–162.

Zomer, R. J., *Trabucco, A.*, *Coe, R.*, *Place, F.*, *van Noordwijk, M.*, *Xu, J. C.* (2014): Trees on Farms: An Update and Reanalysis of Agroforestry's Global Extent and Socio-Ecological Characteristics. Working Paper 179. World Agroforestry Center, Bogor, Indonesia.