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Root functional parameters along a land-use gradient: evidence of a community-level economics spectrum

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Summary

1. There is a fundamental trade-off between leaf traits associated with either resource acquisition or resource conservation. This gradient of trait variation, called the *economics spectrum*, also applies to fine roots, but whether it is consistent for coarse roots or at the plant community level remains untested.

2. We measured a set of morphological and chemical root traits at a community level (functional parameters; FP) in 20 plant communities located along land-use intensity gradients and across three climatic zones (tropical, mediterranean and montane). We hypothesized (i) the existence of a *root economics spectrum* in plant communities consistent within root types (fine, < 2 mm; coarse, 2–5 mm), (ii) that variations in root FP occur with soil depths (top 20 cm of soil and 100–150 cm deep) and (iii) along land-use gradients.

3. Root FP covaried, in line with the resource acquisition–conservation trade-off, from communities with root FP associated with resource acquisition (e.g. high specific root length, SRL; thin diameters and low root dry matter contents, RDMC) to root FP associated with resource conservation (e.g. low SRL, thick diameters and high RDMC). This pattern was consistent for both fine and coarse roots indicating a strong consistency of a trade-off between resource acquisition and conservation for plant roots.

4. Roots had different suites of traits at different depths, suggesting a disparity in root function and exploitation capacities. Shallow, fine roots were thinner, richer in nitrogen and with lower lignin concentrations associated with greater exploitation capacities compared to deep, fine roots. Shallow, coarse roots were richer in nitrogen, carbon and soluble concentrations than deep, coarse roots.

5. Fine root parameters of highly disturbed, herbaceous-dominated plant communities in poorer soils were associated with foraging strategies, that is greater SRL and lower RDMC and lignin concentration than those from less disturbed communities. Coarse roots, however, were less sensitive to the land-use gradient.

6. *Synthesis.* This study demonstrates the existence of a general trade-off in root construction at a community level, which operates within all root types, suggesting that all plant tissues are controlled by the trade-off between resource acquisition and conservation.

Key-words: coarse roots, deep roots, fine roots, functional traits, plant–soil (below-ground) interactions, root economics spectrum, shallow roots, trade-off

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Introduction

Plant roots play a critical role in ecosystem functioning as they supply nutrients and water to above-ground plant tissues and represent one of the main pathways for carbon transfer to the soil (Rasse, Peresta & Drake 2005; Clemmensen *et al.* 2013). Plant productivity and biogeochemical cycles are thus strongly influenced by the root traits of the co-occurring species in a plant community (Fornara, Tilman & Hobbie 2009; Orwin *et al.* 2010). Despite this evidence, only few *in situ* studies have considered root traits at a community level (FP; functional parameters *sensu* Violle *et al.* 2007) (Holdaway *et al.* 2011; Pérez-Ramos *et al.* 2012; Valverde-Barrantes *et al.* 2013). Therefore, it is yet uncertain how root FPs vary among and within plant communities and whether they are subjected to trade-offs between resource acquisition and conservation as found above-ground (Wright *et al.* 2005). At the species level, a suite of correlated leaf traits, known as the leaf economics spectrum (Wright *et al.* 2004), has been found world-wide describing the existence of a fundamental trade-off between acquisition and conservation of resources in plant species (Grime *et al.* 1997; Wright *et al.* 2004; Freschet *et al.* 2010). Fast-growing species produce short-lived leaves with high nutrient concentrations, specific leaf areas and photosynthetic rates, whereas slow-growing species have opposite traits (Wright *et al.* 2004). Similar trade-offs have been found for stems (Chave *et al.* 2009), while our knowledge of below-ground traits and their *economics* remains limited (Reich 2014) and inconsistent (Tjoelker *et al.* 2005; Freschet *et al.* 2010; Chen *et al.* 2013). The extent to which trade-offs can be generalized at the community level remains largely untested, limiting our understanding of how root FPs may impact ecosystem functioning (De Deyn, Cornelissen & Bardgett 2008; Holdaway *et al.* 2011; Lavorel & Grigulis 2012).

Most of the studies on root trait covariation below-ground have focused on fine roots (Craine, Lee & Bond 2005; Tjoelker *et al.* 2005; Freschet *et al.* 2010; McCormack *et al.* 2012; Chen *et al.* 2013), generally defined as those < 2 mm in diameter (Vogt *et al.* 1996) because of their fundamental role in water and nutrient uptake and in root turnover (Eissenstat *et al.* 2000). There is now some evidence that fine root traits covary and are indeed linked to root economics (Reich 2014), but such evidence is lacking in the literature for coarse roots (2–5 mm). Fine and coarse roots have contrasted roles in plant functioning; fine roots play a fundamental role in water and nutrient uptake, exudation and root turnover (Eissenstat *et al.* 2000), while coarse roots perform more specialized functions such as water transport, water and nutrient storage and plant anchorage. On one hand, this suggests that trait syndromes might be different between coarse and fine roots, but on the other hand, because similar trade-offs have been described for leaves, stems and more recently for fine roots (Wright *et al.* 2004; Chave *et al.* 2009; Freschet *et al.* 2010; Reich 2014), all performing different functions within the plant, we would then expect that coarse roots exhibit similar trade-offs. To the best of our knowledge, no data are yet available to test this hypothesis.

Despite the importance of deep roots for plant anchorage, water acquisition and C sequestration (Maeght, Rewald & Pierret 2013), very few studies have dealt with root trait variation in relation to soil depth (Vanguelova *et al.* 2005; Zhou & Shangguan 2006; Borken, Kossmann & Matzner 2007; Makita *et al.* 2010). Gaining knowledge on deep root systems and testing whether root functional traits are similar for shallow and deep roots globally would help us understand in detail how these changes may impact ecosystem functioning. There are theoretical reasons for contrasted sets of traits between shallow and deep roots (Schenk 2008). In soil surface layers, many factors, including high concentrations of N, P and K (Jobbagy & Jackson 2001; Arndt *et al.* 2004), low soil strength and high water availability during small precipitation events, may favour proliferation of roots with a more acquisitive strategy. Opposite, in deep soil layers where water is generally more abundant (Laclau *et al.* 2013), roots should ensure water transport and anchorage and be adapted to high soil compaction (Taylor & Ratliff 1969), oxygen deficiency and less fluctuating soil temperatures (Pregitzer *et al.* 2000); their traits are thus expected to be associated with persistence and conservation. These differences in abiotic conditions between shallow and deep soil layers may lead to contrasting suites of traits with depth since root traits are highly plastic and respond to heterogeneous resource distributions (Hodge 2004; Zhou & Shangguan 2006; Ostonen *et al.* 2007). Thus, we hypothesize that roots in shallow, less compact and nutrient-rich soils have a suite of FP attributes associated with nutrient acquisition strategies [i.e. high specific root length (SRL) and N concentrations], and that roots in deeper, more compact and nutrient-poor soils display resource conservation strategies, that is high root diameters or lignin concentrations.

Although global patterns of fine root trait coordination are likely to exist (Reich 2014), the increase in anthropogenic impacts, especially land uses that induce changes in plant community composition and soil fertility (Garnier *et al.* 2007; Bakker, Carreño-Rocabado & Poorter 2011), may lead to changes in root traits among plant communities. Changes in above-ground traits along land-use changes have often been reported; species from frequently disturbed sites (e.g. agricultural fields) have leaf traits consistent with a resource acquisition strategy and fast growth rates, whereas abandonment of agricultural fields led to an increase in slow-growing species with a resource conservation strategy (Bazzaz 1996; Garnier *et al.* 2004; Pakeman 2004; Reich 2014). Such leaf trait variations along disturbance gradients are likely to be reflected below-ground if leaf and root traits covary across species (Kerkhoff *et al.* 2006; Liu *et al.* 2010; Reich 2014). However, empirical evidence of leaf–root correlations is inconsistent whether for individual species (Craine, Lee & Bond 2005; Tjoelker *et al.* 2005; Geng *et al.* 2014) or plant communities (Kembel & Cahill 2011; Pérez-Ramos *et al.* 2012) and differential responses to soil nutrient availability have been observed in leaves and roots (Wright & Westoby 1999), which may lead to contrasted responses between these organs along disturbance gradients. There is therefore a need to understand general patterns of root trait responses to human-induced land-use change gradients (Holdaway *et al.* 2011).

In this study, our aim was to characterize and establish the consistency in root trait relationships at the community level, that is to test the existence of a *community-root economics spectrum*. In order to span a large range of root traits, we selected contrasting plant communities established along land-use gradients (e.g. from agricultural to natural forest communities) in a large range of climate and soil conditions. We collected shallow and deep roots from different plant communities and measured average root FPs in composite samples that comprised roots of the whole community rather than sorting individual roots per species. We focused on root FPs representative of the conservation–acquisition trade-off defined at the species level (Freschet *et al.* 2010; Reich 2014): three morphological FPs [root diameter (D_m), root dry matter content (RDMC), SRL] and five root chemical FPs [nitrogen (N), carbon (C), water-soluble compounds (soluble), cellulose and lignin concentrations].

We aimed to respond to three outstanding questions. First, we asked whether the trade-off found at the species level for fine roots applies to whole plant communities and whether it is consistent within coarse roots. Secondly, we asked whether root morphology and chemistry varied with soil depth, and thirdly, we questioned whether root FP attributes changed along land-use gradients as previously reported for leaf traits (Navas *et al.* 2010; Bakker, Carreño-Rocabado & Poorter 2011) or leaf FP (Garnier *et al.* 2004, 2007; Fortunel *et al.* 2009). We hypothesized that (i) fine roots present a FP covariation along a continuum from resource acquisition to resource conservation at the community level and that coarse roots present a similar trade-off; (ii) roots from shallow soils present suites of FP attributes associated with greater resource acquisition capacities [e.g. greater SRL and root N concentrations (RNC), and lower root carbon, cellulose and lignin concentrations] than roots from deep soils; and that (iii) root FP attributes associated with a fast-growing foraging strategy are more common in disturbed agricultural communities with faster growing annual species, while communities dominated by slower-growing species (trees) are associated with a resource conservation strategy.

Materials and methods

STUDY SITES AND EXPERIMENTAL DESIGN

Studies were carried out in either agricultural, agro-ecosystems or forestry systems in three different climates. A total of seven sites were selected (Table 1), of which three were situated in a tropical climate, three were in a montane climate and one was in a subhumid mediterranean climate. Two tropical sites were located in the Central Valley of Costa Rica; the Aquiares site was located in the Reventazón river watershed on the slope of the Turrialba volcano and the Llano Bonito site in the Pirris river watershed. Both areas have a rainfall season from May to October and a dry season from December to March. The third tropical climate site was located in northern Laos, 10 km south of Luang Prabang, in the Houay Pano catchment. Most precipitation (90%) falls within the rainy season from mid-May to October (Pierret *et al.* 2007). For the montane climate, three sites were

Table 1. Summary of the main geographical and climatic characteristics of the studied sites

Country	Site (abbreviation)	Coordinates	Altitude (m)	Climate	MAT (°C)	MAP (mm)	Soil type	Max. soil depth (m)	Land-use types	References
Costa Rica	Aquiares (AQ)	9°56′ N, 9°56′ W	1020–1280	Tropical	20.8	3014	Andosols	4.5	3	
Costa Rica	Llano Bonito (LB)	9°16′ N, 8°33′ W	1200	Tropical	21	2500	Andosols	4.5	3	Harmand *et al.* (2007)
Laos	Houay Pano (HP)	19°50′ N; 102°10′ E	400–800	Tropical	25.7	1300	Entisols	> 3.0	4	Pierret *et al.* (2007)
France	Premol (PR)	45°06′ N; 5°53′ E	1400	Montane	5	1530	Cambisols	1.0	2	Mao *et al.* (2012)
France	Bachat-Boulod (BB)	45°06′ N; 5°53′ E	1700	Montane	3.5	1710	Cambisols	0.8	2	Mao *et al.* (in press)
France	Achard (AC)	45°07′ N; 5°54′ E	2000	Montane	1.8	1900	Umbrisols	0.5	2	Mao *et al.* (in press)
France	Restinclières (RE)	43°42′ N; 3°51′E	100	Mediterranean	14.5	950	Fluvisols	8.0	4	Dufour *et al.* (2013)

MAT, mean annual temperature; MAP, mean annual precipitation; Max. soil depth, maximum soil depth at the site; Nb. Land-use types, number of land-use types per site.

selected in the French Alps within the Belledonne mountain range at three altitudes: 1400 (Premol), 1700 (Bachat-Boulod) and 2000 m a.s.l. (Achard; Mao *et al.* 2012). The precipitation regime is homogenous all year round with slightly more precipitation during the winter period. The subhumid mediterranean climate site (Restinclières) is located in southern France, at the Departmental property of Restinclières 15 km north of Montpellier (Mulia & Dupraz 2006) close to the river Le Lez. Precipitation is highly seasonal and takes place mainly in autumn (Daget 1977).

Within each site except the montane sites, we selected three to five contrasting land-use types along a gradient of disturbance from monocultures to secondary forests. The five land-use types chosen comprised (Table S1 in Supporting Information) the following: agricultural fields with one species cultivated alone (CA); agroforestry sites with a tree and the cultivated species (TC); agroforestry sites with a tree and the natural/regenerated vegetation, mostly herbaceous species (TV); fallows, that is regeneration phase after culture (FA); and secondary forests (FO). When there were no agricultural practices in a site (i.e. montane sites), only two land uses were selected: clusters of secondary forest (FO) and fallow areas created after tree thinning with mostly herbs and small shrubs (FA). These contrasted land-use types were characterized by six variables (reported in Table S1): the percentage of herbaceous species, the time to last disturbance (ploughing in agricultural and agroforestry sites or tree thinning in montane sites), the level of fertilization (fertilized or not), total soil nitrogen (N, mg g^{-1}), available phosphorus (P, mg kg^{-1} using the Olsen method) and soil organic carbon (SOC, mg g^{-1}) concentrations.

In 2012, in each type of land use and site, a 3.0 × 2.0 m trench was dug to a depth of 1.6 m. At the three montane sites and in the forest site at Restinclières, the soil was rocky and the maximum depth attained before encountering the bedrock was 60–80 cm at Premol, Bachat-Boulod and Restinclières and 20 cm at Achard. The percentage foliar cover for tree, shrub and herbaceous species was recorded in a 6.0 × 6.0 m area around the trench. Species composition and abundance of herbaceous species were determined more precisely on four quadrats (1.0 × 1.0 m), each adjacent to the four sides of the trench. The foliar cover of species was recorded for each quadrat using the following scale, 0: < 1%; 1: 1–5%; 2: 5–10%; 3: 10–25%; 4: 25–50%; 5: 50–75%; 6: > 75%, and then averaged for each trench. Within each trench, a mixture of roots (<5 mm diameter) belonging to all species present in the neighbourhood of the trench was collected in the excavated shallow (top 20 cm) and deep soil horizons. Deep soil horizons were those within the 100–150 cm or within the last third of the total soil depth when soils were shallower (60–80 cm, Table 1). At Achard, roots were only extracted from the top 20 cm. During collection, fine (< 2 mm) and coarse (2–5 mm) roots were sorted by hand, taken to the laboratory and immediately washed to eliminate adhered soil particles. A finer separation between fine and coarse roots was carried out in the laboratory with a precision calliper (accuracy of 0.01 mm). We rejected roots that did not fit into these two diameter classes.

For each site, land-use type, root depth and diameter class, seven root subsamples were prepared: three subsamples were conserved in distilled water and frozen until further root morphological measurements, and four subsamples were oven-dried at 40 °C for 72 h before chemical analyses were performed.

ROOT FUNCTIONAL PARAMETERS

Root traits were measured on a composite sample that represented a mixture of roots from the different species present in the community and referred to hereafter as the root FP *sensu* Violle *et al.* (2007).

Determination of root morphological FP was conducted on three subsamples per trench, depth and root diameter class [mean ± standard error (SE), 2.48 ± 0.12 g, fresh weight]. Prior to scanning, roots were sponged carefully to remove all excess water and weighed to determine their saturated mass (SM), and they were then stained by a 2-min immersion in methyl violet solution (0.5 g L^{-1}) to increase contrast. Immediately after immersion, roots were rinsed, spread out in distilled water onto a mesh tray and finally transferred on a transparent acetate sheet and scanned at 400 dpi (Hummel *et al.* 2007). The resulting image was processed with image analysis software (Winrhizo, version 2009; Regent Instrument, Quebec, QC, Canada) to determine total root length (L) and mean root diameter (D_m). After scanning, roots were oven-dried at 60 °C for 72 h and then weighed to determine their dry mass (DM). Root dry matter content (mg g^{-1}) was calculated as the ratio between DM and SM, and SRL (m g^{-1}) was calculated as the ratio between L and DM.

Determination of root chemical FP was conducted on four subsamples per trench, depth and root type (2.0–4.0 g fresh weight). Roots were ground in a cyclone mill (Cyclotec Sample Mill 1093; Tecator, Hogänäs, Sweden) with a filter mesh of 1.0 mm aperture diameter. The concentrations of water-soluble compounds (named soluble hereafter), cellulose and lignin concentrations (mg g^{-1}) were obtained by the Van Soest method (Van Soest 1963) with a Fibersac 24 fiber analyzer (Ankom, Macedon, NJ, USA). For determining carbon (C) and nitrogen (N), the roots were ground finely in a ball mill and C and N concentrations [root carbon concentration (RCC) and RNC, respectively; mg g^{-1}] were measured by dry combustion using an elemental analyzer (Thermo-Finnigan EA1112, Milan, Italy).

STATISTICAL ANALYSIS

Principle component analyses (PCAs) and correlation analyses were performed using the means of each FP per trench, depth and site. To search patterns in root FP data, we performed two PCAs (FP-PCAs) for fine and coarse roots separately with eight FP (SRL, D_m, RDMC, RNC, RCC, soluble, cellulose and lignin concentrations). The two first PCA axes were rotated with the Varimax procedure in order to strengthen the contrasts between axes (Craine & Lee 2003). To test for the consistency of the FP syndrome between fine and coarse roots, we performed a Spearman's rank correlation between the axis 1 loadings of the fine FP-PCA and those of the coarse root FP-PCA. Within each FP-PCA (fine or coarse), we tested the effects of *depth* on the axis 1 scores using one-way ANOVA analysis. Bivariate correlations between FP were evaluated using Pearson's correlation coefficient (r).

To test for individual FP differences between shallow and deep roots and between land-use types, we used nested general linear models (GLMs) with *depth* and *climate* as fixed factors, and *land use* nested within *site* and *climate* and mean annual temperature (MAT) and mean annual precipitation (MAP) as covariates. With these covariates, we controlled for potential climatic differences between study sites. We performed separate tests for fine and coarse roots. For the GLMs, we used all individual subsamples from each trench and each depth ($n = 3$ for morphological and $n = 4$ for chemical FP). Since subsamples from each trench and depth were not independent from each other, we accounted for this correlation incorporating a symmetrical compound covariance matrix that partitions the total variance into a within-subject variation (subsamples from the same trench and depth) and a between-subject variation (factors) in the model. For GLMs, residuals were assessed for normality (Shapiro–Wilk's test at $P > 0.05$) and data log-transformed when necessary.

To characterize the land-use gradients across sites, a *land-use* PCA was performed based on six variables, percentage of herbaceous species, time to last disturbance, level of fertilization (fertilized or not) and soil N, P and SOC concentrations of each land-use type at the different sites (Fig. S1 and Table S2). The first axis (axis 1) of the *land-use* PCA (48.0% of the total variation) was positively correlated with the percentage of herbaceous species (loading = 0.67) and negatively with soil N, P and SOC concentrations, three variables related to soil fertility. Projection of sites ($F_{6,13} = 5.62$, $P < 0.01$) and land-use types on the *land-use* PCA showed that the axis 1 discriminated highly disturbed plant communities dominated by herbaceous species (CA) and located on nutrient-poor soils from undisturbed nutrient-rich plots dominated by woody species (FO). Axis 1 scores were thus used in subsequent analyses to represent the land-use gradient (axis $1_{\text{Land-use PCA}}$). The level of fertilization (Fert) was strongly correlated with the second axis (loading = −0.96). Axis 2 discriminated the fertilized cultures (CA, TC) and TV at Restinclières from the rest of the land uses (see Fig. S1 and Table S2). To assess the FP variation along land-use gradients across all sites, we performed general linear mixed models (GLMMs) with each FP (or the FP *scores*, i.e. the axis 1 scores of the FP-PCAs) as the dependent variables, the first axis scores in the *land-use* PCA (*land-use scores)* as a continuous fixed factor and *site* as the random factor. The significance of the fixed factor was tested with type-II analysis of variance and chi-square Wald tests (χ^2).

All calculations and statistical analyses were performed with the R software (v. 2.15.3) using the packages ADE4, VEGAN, CAR, EFFECTS, HMISC, LME4 and NLM (R Development Core Team 2013). Data shown throughout the text are mean ± standard error (SE).

Results

ROOT FUNCTIONAL PARAMETER COVARIATION

Associations between FPs were analysed using FP-PCA. The first two axes of the FP-PCA analysis based on three morphological and five chemical FP explained a total of 60.9% and 63.1% of the variance for fine (Fig. 1a) and coarse (Fig. 1b) roots, respectively. The first FP-PCA axis (axis 1) alone accounted for 39.7% or 45.0% of the variation for fine and coarse roots, respectively. Within the fine and coarse FP-PCAs, RDMC, D_m, SRL, RCC and lignin concentrations contributed substantially to axis 1 as observed by the high-squared FP individual loadings (> 0.40) on this axis (Table 2). Communities with high SRL values (associated with a resource acquisition strategy) have positive scores within the axis 1, whereas communities with high RDMC, D_m, RCC and lignin concentrations (representative of a resource conservation strategy) had negative scores within this axis of variation (Fig. 1a,b; Table 2). Two root chemical FPs (soluble and cellulose) were highly correlated to the second axis of the FP-PCA (axis 2, Table 2) explaining 21.2% and 18.1% of the variation for fine and coarse roots, respectively. Ordination of these FP within the axis 2 opposed cellulose and soluble concentrations in both FP-PCAs. RNC was negatively and strongly correlated to axis 3 (Fig. 1a, b; Table 2). The positive relationship between the loadings of the FP along the FP-PCA axis 1 for fine and for coarse roots ($\rho = 0.76$; $S = 20$, $P < 0.05$; Fig. 2) indicated that the FP ordination along this axis was conserved whether it was for fine or coarse roots. We observed no influence of root depth within the first axis of variation (axis 1) nor for fine nor for coarse roots indicating a similar covariation of FP regardless of deep or shallow roots ($F_{1,38} = 0.57$, $P = 0.45$ for fine and $F_{1,34} = 0.18$, $P = 0.68$ for coarse roots).

Root FPs were highly correlated with each other (Table 3). Within the fine root component (Fig. 3), roots with high SRL had smaller root diameters and lower RDMC, RCC and lignin concentrations. Soluble concentrations were negatively correlated with RCC and lignin concentrations. Lignin was also positively correlated with D_m and RDMC. Variations in RNC were not explained by the FP measured except for a negative relationship with RDMC.

For the coarse root fraction (Fig. 3), SRL was negatively correlated with D_m, RDMC, RCC and lignin and positively correlated with soluble concentration. Roots with greater lignin concentrations had greater root D_m, RDMC and RCC, but lower SRL, RNC and soluble concentrations. Again, RNC was not correlated with other FP except for a negative correlation with lignin. The main differences between correlation

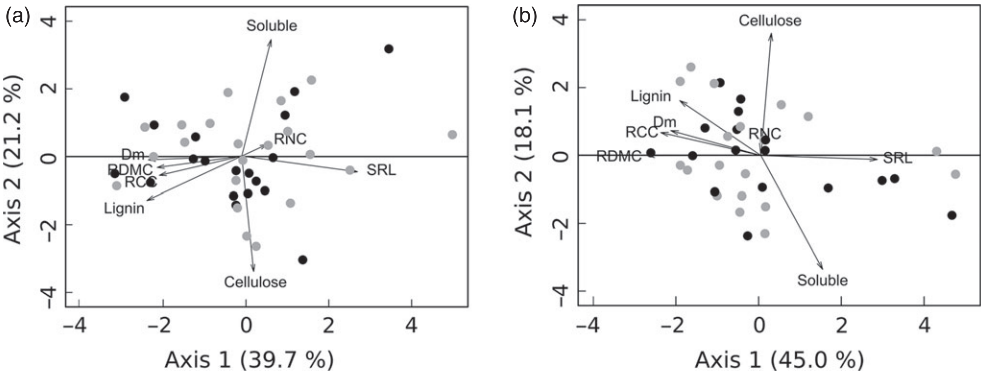

Fig. 1. Principal component analyses (PCA) of root morphological and chemical functional parameters (FP) for (a) fine roots (< 2 mm) and (b) coarse roots (2–5 mm). Arrows show projections of the functional parameters within the PCA. Grey symbols represent roots from shallow soil layers and black symbols represent roots from deep soil layers Abbreviations for FP are as follows: D_m, mean root diameter (mm); RDMC, root dry matter content (mg g^{-1}); SRL, specific root length (m g^{-1}); RCC, root carbon concentration (mg g^{-1}); RNC, root nitrogen concentration (mg g^{-1}); Soluble, water-soluble compounds concentration (mg g^{-1}); Cellulose, cellulose concentration (mg g^{-1}); and Lignin, lignin concentration (mg g^{-1}).

Table 2. Functional parameter loadings on the three first axes of the principal components analyses (FP-PCA) for fine and coarse roots

	Fine roots (n = 40) PCA axis			Coarse roots (n = 36) PCA axis		
Root functional parameter	1	2	3	1	2	3
Mean root diameter	**−0.74**	−0.03	0.04	**−0.66**	0.20	0.11
Root dry matter content	**−0.67**	−0.09	0.23	**−0.85**	−0.01	0.09
Specific root length	**0.92**	−0.13	−0.04	**0.88**	−0.03	−0.09
Root nitrogen concentration	0.20	0.09	**−0.88**	−0.03	0.10	**−0.97**
Root carbon concentration	**−0.66**	−0.15	−0.63	**−0.75**	0.17	−0.20
Soluble concentration	0.23	**0.93**	0.08	0.46	**−0.85**	−0.14
Cellulose concentration	0.09	**−0.92**	0.13	0.07	**0.92**	−0.14
Lignin concentration	**−0.76**	−0.35	−0.25	−0.59	0.40	0.54

Loadings in bold have squared loadings > 0.40 and indicate the significance of the functional parameter in the PCA, according to Richman (1988).

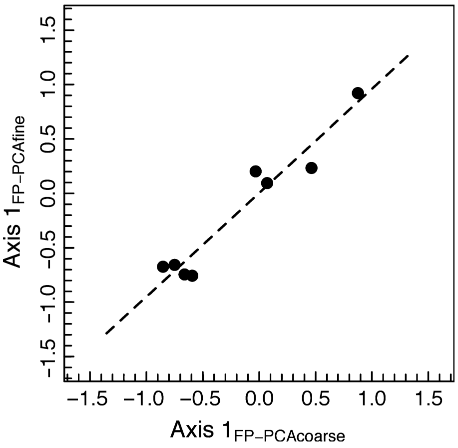

Fig. 2. Relationship between loadings of fine and coarse root functional parameters (FP) on the first axis of FP-PCA. Each point represents one of the eight FP measured on fine and coarse roots. See Table 2 and Fig. 1 for more details. Results from a Spearman's rank correlation test are: $\rho = 0.76$; $S = 20$, $P < 0.05$. Displayed are the model-predicted relationship between $\text{Axis1}_{\text{FP-PCAfine}}$ and $\text{Axis1}_{\text{FP-PCAcoarse}}$ (Pearson's correlation, $r = 0.97$, $P < 0.001$). PCA, principal component analyses.

patterns in fine and coarse roots concerned the soluble concentrations. In coarse roots, soluble concentrations were correlated with morphological FP (D_m, RDMC and SRL), but this was not the case for fine roots.

SHALLOW AND DEEP ROOTS

Some functional parameters differed between shallow and deep roots (Tables 4 and S3,S4 for detailed statistical analysis). Shallow fine roots were significantly thinner and had higher RNC and lower lignin concentrations compared to deeper roots. In coarse roots, we observed no differences in morphological FP between soil depths, but with regard to chemical FP, shallow coarse roots had greater RNC and RCC but lower cellulose concentrations than deep roots. Absolute differences between FP were nonetheless small for most of the traits measured (e.g. shallow fine roots were approximately 0.1 mm thicker or had 5.0 mg g^{-1} lower lignin concentrations than deeper roots). These differences were more pronounced for RNC, with shallow roots having approximately 2.0 and 1.0 mg g^{-1} more N than deep roots for fine and coarse roots, respectively.

LAND-USE GRADIENT AND FP

Five of the eight FP measured on fine roots varied significantly along the land-use gradient (axis $1_{\text{Land-use PCA}}$) (Fig. 4). Fine roots decreased in diameter, RDMC, RCC and lignin concentrations (Fig. 4a,b,e,h, respectively) and increased in SRL (Fig. 4c) along the land-use gradient from negative (undisturbed forest communities on fertile soils) to positive values of the land-use scores (e.g. disturbed communities on less fertile soils and with a higher percentage of herbaceous species), As a consequence, land-use scores were positively correlated with axis 1 in the FP-PCA representing the root FP syndrome (axis $1_{\text{FP-PCAfine}}$, Fig. 4i). Sites with undisturbed fertile soils and a lower percentage of herbaceous species had roots associated with a conservation strategy (negative scores in the axis $1_{\text{FP-PCAfine}}$), whereas fine roots from disturbed less fertile communities with a greater percentage of herbaceous species displayed an acquisitive strategy (positive scores in the axis $1_{\text{FP-PCAfine}}$).

The FP of coarse roots only varied slightly along the land-use gradient with only lignin concentrations showing a significant response to land use (Fig. 5). Coarse roots had greater lignin concentrations in fertile communities with a lower percentage of herbaceous species (Fig. 5h). There was no general effect on the coarse root FP syndrome (scores in the FP-PCA, axis $1_{\text{FP-PCAcoarse}}$, $P > 0.30$, Fig. 5i).

Discussion

RELATIONSHIPS BETWEEN ROOT FUNCTIONAL PARAMETERS

We demonstrated that at the community level, root morphological and chemical FPs covaried and identified a root FP

Table 3. Correlation matrix showing Pearson's correlation coefficients (*r*) for root morphological and chemical functional parameters of fine (diameter < 2 mm) and coarse roots (diameter between 2 and 5 mm)

	Specific root length (SRL)	Root dry matter content (RDMC)	Root nitrogen concentration (RNC)	Root carbon concentration (RCC)	Soluble concentration	Cellulose concentration	Lignin concentration
Fine roots (n = 36–40)							
Mean root diameter (D_m)	−0.86**	0.16	−0.03	0.42*	−0.22	0.06	0.44**
Specific root length		−0.53*	0.20	−0.48**	0.10	0.12	−0.55**
Root dry matter content			−0.39*	0.34*	−0.23	0.04	0.53**
Root nitrogen concentration				0.19	0.20	−0.24	−0.09
Root carbon concentration					−0.35*	−0.06	0.75**
Soluble						−0.75*	−0.49**
Cellulose							0.13
Coarse roots (n = 30–36)							
D_m	−0.80**	0.49**	−0.13	0.31	−0.48**	0.17	0.46*
Specific root length		−0.73**	0.08	−0.55**	0.54**	−0.10	−0.49**
Root dry matter content			−0.11	0.73**	−0.48**	0.03	0.56**
Root nitrogen concentration				0.22	0.02	0.18	−0.40**
Root carbon concentration					−0.52**	0.00	0.57**
Soluble						−0.66**	−0.74**
Cellulose							0.09

**$P < 0.01$; *$P < 0.05$.

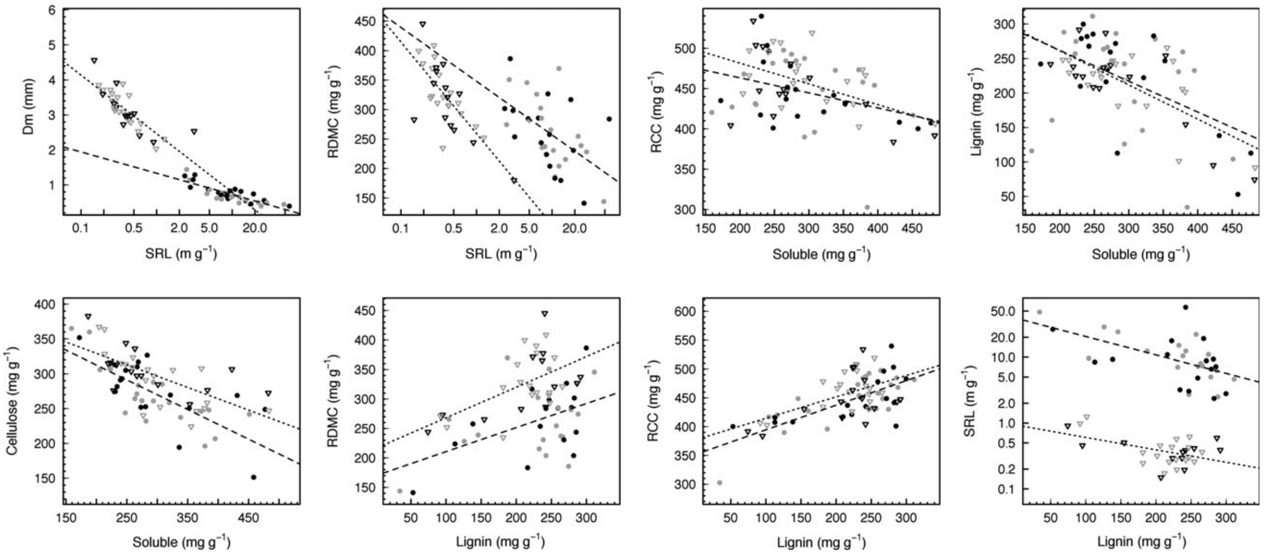

Fig. 3. Relationships between root functional parameters (FP) measured in fine (circles) and coarse (triangles) roots. Grey symbols represent roots from shallow soil layers and black symbols represent roots from deep soil layers. Displayed are the model-predicted significant relationships for fine (dashed line) and coarse (dotted line) roots. See Table 3 for the complete set of Pearson's correlation coefficients (*r*) and significances (*P*-values). Abbreviations for FP are given in Fig. 1. Note the natural log scale for specific root length.

syndrome highlighting the existence of a below-ground trade-off between resource acquisition and conservation. This syndrome was consistent within each of the root types, suggesting similar constraints on root construction and a continuum between these different root compartments. Changes in the values of root FPs among communities may result from changes in species composition, from changes in trait values within species (e.g. in response to environmental conditions) or a combination of the two. Despite these multiple sources of variation, our results clearly demonstrate that at the community level, the patterns and trade-offs of FPs are similar to those observed at the species level for fine roots (Freschet *et al.* 2010; Birouste *et al.* 2012; Chen *et al.* 2013) and for different plant tissues, including leaves and stems (Wright *et al.* 2004; Chave *et al.* 2009; Freschet *et al.* 2010; Reich 2014). This suggests that similar constraints operate at both levels of organization and that species coexisting in communities exhibit similarities in their morphology and physiology to better adjust to environmental constraints (Grime 2006).

Regardless of the root type (fine or coarse), we identified a root trade-off at the community level opposing communities that produced roots with high SRL to communities that produced thick roots with high RDMC, RCC and lignin concentrations. Thinner roots with high SRL are often related to better

Table 4. Root functional parameter (FP) values (mean ± SE, n = 106 for fine morphological, n = 154 for fine chemical FP and n = 87 for coarse morphological and n = 120 for coarse chemical FP) for fine and coarse roots at two soil depths (shallow and deep)

	Mean root diameter (D_m) (mm)	Root dry matter content (RDMC) (mg g^{-1})	Specific root length (SRL) (m g^{-1})	Root nitrogen concentration (mg g^{-1})	Root carbon concentration (mg g^{-1})	Soluble concentration (mg g^{-1})	Cellulose concentration (mg g^{-1})	Lignin concentration (mg g^{-1})
Fine roots								
Shallow	$\underline{0.70 \pm 0.03^{a}}$	261.89 ± 8.23	12.90 ± 1.54	$\underline{11.29 \pm 0.50^{a}}$	446.00 ± 4.99	292.21 ± 8.40	270.0 ± 4.82	$\underline{216.67 \pm 8.07^{a}}$
Deep	$\underline{0.78 \pm 0.03^{b}}$	259.15 ± 9.77	12.74 ± 1.90	$\underline{9.71 \pm 0.48^{b}}$	445.40 ± 4.72	297.50 ± 10.94	275.77 ± 6.02	$\underline{221.69 \pm 8.67^{b}}$
Coarse roots								
Shallow	3.15 ± 0.09	326.99 ± 7.04	0.43 ± 0.04	$\underline{8.84 \pm 0.44^{a}}$	$\underline{463.34 \pm 4.15^{a}}$	302.19 ± 8.71	292.00 ± 4.95^{a}	213.48 ± 5.71
Deep	3.08 ± 0.16	315.78 ± 10.27	0.60 ± 0.11	$\underline{7.98 \pm 0.39^{b}}$	$\underline{448.33 \pm 5.61^{b}}$	289.43 ± 12.41	305.15 ± 5.04^{b}	213.46 ± 8.26

Different letters within columns indicate differences between deep and shallow roots at $P < 0.05$ (underlined). When not underlined, $P < 0.10$. Probabilities shown are from a general linear model with a symmetrical compound covariance matrix to account for within-subject variation (See Tables S3 and S4 and Material and methods section for model details).

exploitation capacities (Hodge 2004) and higher growth rates and nutrient uptake (Reich *et al.* 1998). Conversely, thicker roots display thicker cortex and more cortical cell layers (Gu *et al.* 2014; Kong *et al.* 2014) and thus require more investment of carbon and lignin in cell walls, have greater tissue density and are associated with longer root life spans and greater resource conservation (Eissenstat *et al.* 2000; Withington & Reich 2006; McCormack *et al.* 2012). Therefore, the trait syndrome identified in this study suggests the existence, at the root community level, of a resource acquisition–conservation *economics spectrum* analogous to the leaf economics spectrum (Wright *et al.* 2004), except for RNC. Indeed, RNC was not correlated with either morphological or other chemical FPs in fine or coarse roots (except for a negative correlation with RDMC in fine roots and with lignin concentration in coarse roots). Recent studies also reported this lack of correlation between RNC and root morphology (Chen *et al.* 2013; Geng *et al.* 2014), in contrast to the general correlation found between specific leaf area (SLA) and leaf N concentration, suggesting a different N economy in these organs. In leaves, high N concentration is linked to high Rubisco concentrations and high SLA, both aimed at maximizing photosynthetic rates (Reich, Ellsworth & Walters 1999). In roots, the decoupling between RNC and resource acquisition strategy might reflect that N in roots is not associated with a particular enzyme involved in nutrient acquisition as Rubisco is in leaves, but may also indicate that nutrient uptake is achieved through high SRL but also through association with mycorrhizal fungi or N_2-fixing bacteria leading to diverse strategies of resource acquisition. Therefore, we suggest that RNC is not linked to root morphology in the same way as N concentration is linked to leaf morphology and that the root economics spectrum would be linked to a set of traits related to construction trade-offs, notably SRL or root diameter (McCormack *et al.* 2012).

FUNCTIONAL DIFFERENCES BETWEEN DEEP AND SHALLOW ROOTS

In support of our second hypothesis, we found that shallow fine roots have a more acquisitive strategy than deep fine roots as shown by their smaller D_m, higher RNC and lower lignin concentrations. These traits are indicative of enhanced soil exploitation capacities and in turn greater nutrient and water uptake capacities (Eissenstat 1992; Hodge 2004; Roumet *et al.* 2006; Zarebanadkouki, Kim & Carminati 2013) and higher respiration and growth rates (Andersen 2003). Our results are in line with previous observations at the species level (Burton *et al.* 2002; Makita *et al.* 2009). In deeper soil layers, FPs were more consistent with a resource conservation strategy as roots were thicker (greater D_m) and lignin concentrations were greater, probably in response to lower nutrient availabilities (Hodge 2004; Zhou & Shangguan 2006; Ostonen *et al.* 2007) or higher soil compaction (Taylor & Ratliff 1969). The FPs observed in deep roots may also be related to their water transport capacity, which would maximize water uptake and transport from deep layers where water has accumulated (Hernández *et al.* 2010). We observed less variability between depths in coarse root

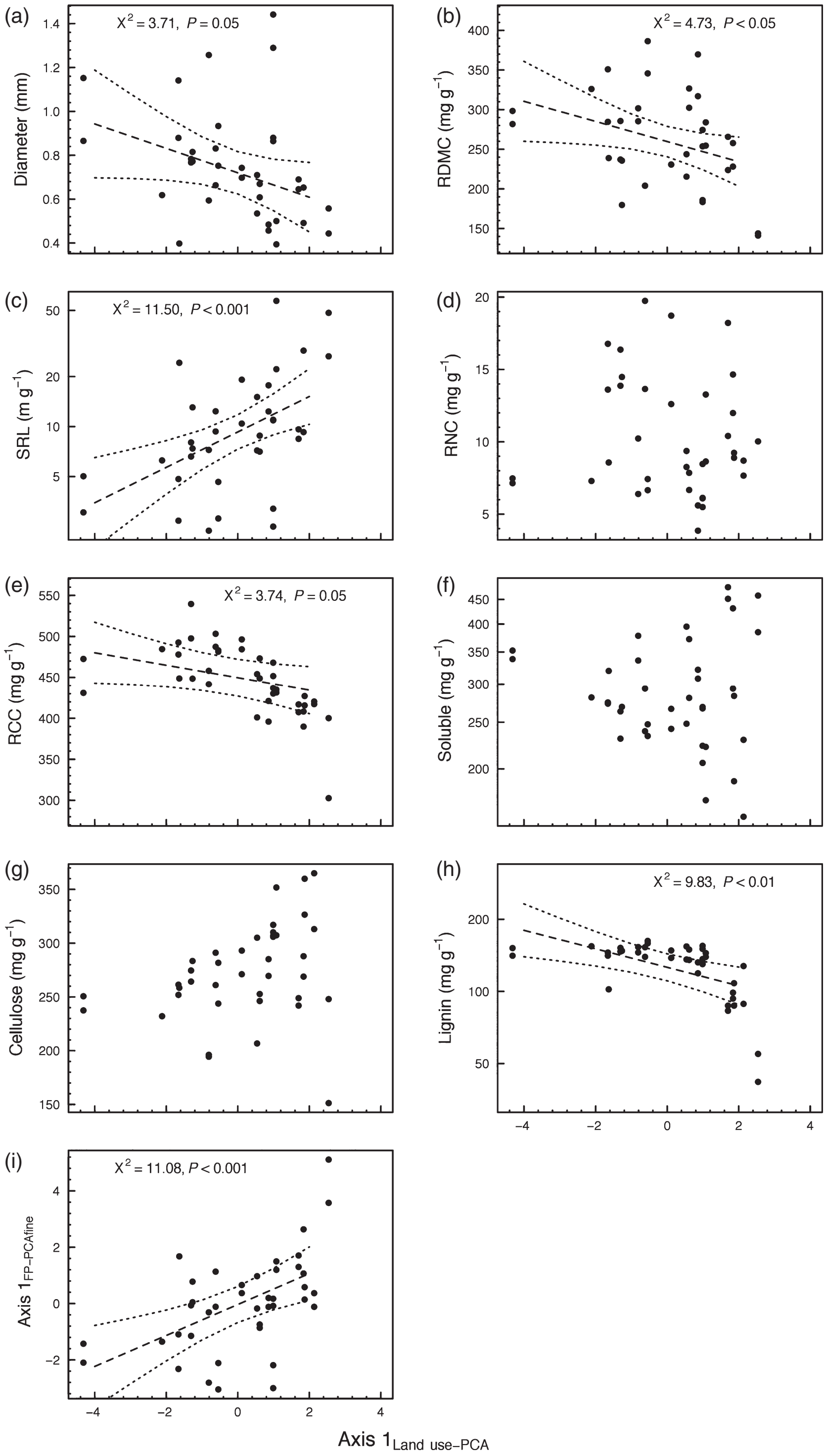

Fig. 4. Variation in fine root functional parameters (FP) along the land-use gradient (Axis $1_{\text{Land-use PCA}}$). Positive values represent the disturbed and less fertile sites with a greater percentage of herbs (i.e. annual crops) and negative values indicate less disturbed and more fertile sites with a greater percentage of woody species (i.e. forests). In panel i), axis $1_{\text{FP-PCAfine}}$ represents the root syndrome, that is the scores of fine roots on the FP-PCA represented in Fig. 1a. Displayed are the model-predicted relationships (dashed lines) with 95% confidence intervals (dotted lines) and the measured values (circles). Statistical models are general linear mixed models with the corresponding FP as the dependent variable, the first axis scores in the land-use PCA (Axis $1_{\text{Land-use PCA}}$) as a continuous fixed factor and *site* as a random factor. Model χ^2 and *P*-values are shown only when significant. Root FP abbreviations are given in Fig. 1. Note the natural log scale for SRL and soluble and lignin concentrations. PCA, principal component analyses.

morphological traits, but we did observe differences in root chemistry. This could reflect a similarity in coarse root functions at different depths, namely water transport and anchorage (Danjon, Stokes & Bakker 2013). Coarse roots accumulated more C and soluble compounds and had lower cellulose concentrations at shallow depths, which may imply a storage function of carbohydrates that could later be mobilized when needed by the above-ground plant parts.

Since we collected roots from contrasting plant communities in different climates with a variety of environmental and soil conditions, our data can be interpreted as a general trend in plant communities to produce finer, smaller roots with high nutrient acquisition capacity in surface soils associated with greater foraging capacities and likely shorter life spans (McCormack *et al.* 2012). Changes in community FPs with soil depth may result from a response of roots to soil conditions (e.g. oxygen, bulk density, water and nutrient availability) or from different inherent root architectures between species comprising the different plant communities. Although our data provide some insights into how root traits vary with root

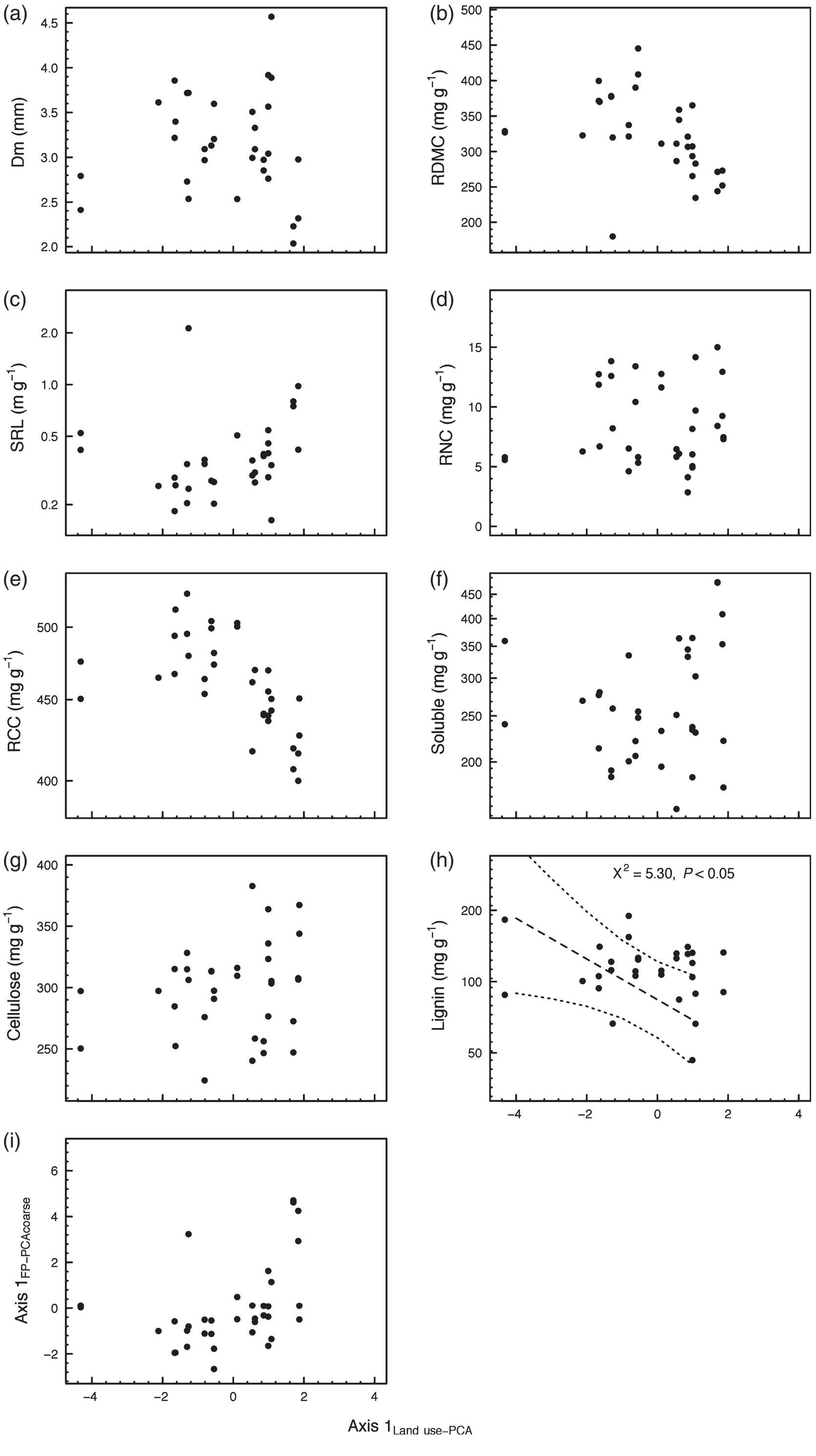

Fig. 5. Variation in coarse root functional parameters (FP) along the land-use gradient (Axis $1_{\text{Land-use PCA}}$). Positive values represent the disturbed and less fertile sites with a greater percentage of herbs (i.e. annual crops), and negative values indicate less disturbed and more fertile sites with a greater percentage of woody species (i.e. forests). In panel i), axis $1_{\text{FP-PCAcoarse}}$ represents the root syndrome, that is the scores of coarse roots on the FP-PCA represented in Fig. 1b. Displayed are the model-predicted relationships (dashed lines) with 95% confidence intervals (dotted lines) and the measured values (as dots). Statistical models are general linear mixed models with the corresponding FP as the dependent variable, the first axis in the land-use PCA (Axis $1_{\text{Land-use PCA}}$) as a continuous fixed factor and *site* as a random factor. Model χ^2 and *P*-values are shown only when significant. Root FP abbreviations are given in Fig. 1. Note the natural log scale for SRL, RCC and soluble and lignin concentrations. PCA, principal component analyses.

depth, a more precise analysis of FP variation and root biomass distributions along the soil profile would be necessary to fully understand the potential implications at an ecosystem level.

RESPONSE OF ROOT FP TO LAND-USE GRADIENT

Our study demonstrated that roots changed in a coordinated way along the land-use gradient. Roots possessed higher SRL and lower RDMC, carbon and lignin concentrations in communities experiencing high disturbance (e.g. monocultures of annual species such as rice and wheat), while the opposite was observed in older, less disturbed communities. The same pattern has been observed in plant communities along a successional gradient in Brazil for SRL, diameter and tissue density (Zangaro *et al.* 2008). These results are in line with leaf trait studies, which found that in highly disturbed sites, or during early stages of succession, fast-growing species with leaf traits associated with a rapid resource acquisition are dominant (Garnier *et al.* 2004; Navas *et al.* 2010). But this result was not shown along a long-term chronosequence in temperate rain forests where patterns of SLA and SRL were inversed along the succession (Holdaway *et al.* 2011). The shift in root FP attributes along land-use gradients may reflect changes in both species composition and soil fertility. In our study, roots with higher SRL were found in disturbed but also less fertile communities. This result could be explained by the dominance of herbaceous species, especially crops (rice or wheat), which are fast-growing species with, in general, thinner roots than slow-growing species such as shrubs and trees (Roumet *et al.* 2008; Danjon, Stokes & Bakker 2013). High SRL values could also reflect a response of these species to less fertile conditions with SRL increasing in response to nutrient limitations, a pattern observed both at the species (Tjoelker *et al.* 2005; Ryser 2006; Poorter *et al.* 2012) and at the community level (Zangaro *et al.* 2008; Holdaway *et al.* 2011). In this study, we are unable to disentangle the individual effect of soil fertility, species identity or disturbance on root FPs attributes. However, the reported variation of root FPs along land-use gradients, whether caused by an individual factor or all factors together, may have strong implications on ecosystem functioning. Our results suggest that, for example, root FP attributes in older forest communities (high diameter, RDMC, carbon and lignin concentrations) may lead to slower decomposition (Freschet, Aerts & Cornelissen 2012), lower rates of nitrification of soil bacterial communities and thus lower N cycling (Legay *et al.* 2014) and a stronger accumulation of organic matter in the soil.

Surprisingly, we did not detect significant changes in coarse root FP variation associated with land-use changes, suggesting that coarse root traits are less affected by disturbance or nutrient availability. The abundance of coarse roots in soil samples was largely due to the presence of woody species in the plots, and coarse roots are usually less plastic than fine roots in terms of the response of their traits to environmental variables (Eissenstat 1991). Therefore, associated root functions and processes will be more variable across land-use gradients or disturbances for fine-rooted plant communities than for coarse-rooted ones.

Conclusions and perspectives

Our finding of a general trade-off between a suite of morphological and chemical root functional parameters indicates the existence of a trade-off of root construction at a community level. Functional parameter relationships were consistent within root types and depths, clearly indicating the existence of a general FP syndrome defining a global *spectrum of root economics* at a community level. A necessary step after identifying the FP syndrome for plant communities below-ground would be to identify its effect on root functioning, for example root respiration, root decomposability and/or root turnover that would ultimately affect ecosystem services such as C cycling (De Deyn, Cornelissen & Bardgett 2008; Kell 2012). Identifying these links would be a major advance in ecology (Mommer & Weemstra 2012) since it will allow us to better understand plant community functioning and to easily identify plant ecosystem services related to the below-ground component. Although we spanned large gradients of land-use types and climates and obtained a high variability in the root FPs measured, we still lack information on the most extreme ends of the variability (e.g. plant communities from the most arid or hyper humid ends of the climate gradient) and hence, these hypotheses should be further extended to other ecosystems and climates. The existence of such consistent trade-offs in below-ground plant organs, if widely applicable, would imply a significant increase in our knowledge on the hidden half of plants (Eshel & Beeckman 2013).

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Data accessibility

Data available from the Dryad Digital Repository (Prieto *et al.* 2014).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Description of the different land-use types and species composition and abundance at the different sites.

Table S2. Loadings of the variables from a principal component analysis (*land-use* PCA) characterizing land uses.

Table S3. Statistical results for the nested general linear models (GLMs) for fine root functional parameters (FP).

Table S4. Statistical results for the nested general linear models (GLMs) for coarse root functional parameters (FP).

Fig. S1. Principal component analysis (*land-use* PCA) characterizing the land uses.