CHAPTER TWO

Connecting the Green and Brown Worlds: Allometric and Stoichiometric Predictability of Above- and Below-Ground Networks

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Abstract

We examine the potential of trait-based parameters of taxa for linking above- and below-ground ecological networks (hereafter 'green' and 'brown' worlds) to understand and predict community dynamics. This synthesis considers carbon, nitrogen and phosphorus-related traits, the abundance of component species and their size distribution across trophic levels under different forms of management. We have analysed existing and novel databases on plants, microbes and invertebrates that combine physico-chemical and biological information from (agro)ecosystems spanning the globe. We found (1) evidence that traits from above- and below-ground systems may be integrated in the same model and (2) a much greater than expected stoichiometric plasticity of plants and microbes which has implications for the entire food-web mass–abundance scaling. Nitrogen and phosphorus are primary basal resources (hence, drivers) and more retranslocation of P than of N from leaves will lead to higher N:P in the litter and soil organic matter. Thus, under

nutrient-rich conditions, higher foliar concentrations of N and P are reflected by lower N:P in the brown litter, suggesting less P retranslocated than N. This apparent stoichiometric dichotomy between green and brown could result in shifts in threshold elemental ratios critical for ecosystem functioning. It has important implications for a general food-web model, given that resource C:N:P ratios are generally assumed to reflect environmental C:N:P ratios. We also provide the first evidence for large-scale allometric changes according to the stoichiometry of agroecosystems. Finally, we discuss insights that can be gained from integrating carbon and nitrogen isotope data into trait-based approaches, and address the origin of changes in Δ^{13}C and Δ^{15}N fractionation values in relation to consumer–resource body-mass ratios.

ABBREVIATIONS

$\mathbf{\Delta^{13}C}$ δ^{13}C consumer–δ^{13}C resource
$\mathbf{\Delta^{15}N}$ δ^{15}N consumer–δ^{15}N resource
AM arbuscular mycorrhizal fungi
ECM ectomycorrhizal fungi
$\boldsymbol{M}$ estimated body mass at population level
$\boldsymbol{N}$ numerical abundance observed at population level
SOM soil organic matter
TAC C_{tot} accumulated in above–ground plant tissues
TAN N_{tot} accumulated in above–ground plant tissues
TAP P_{tot} accumulated in above–ground plant tissues
WoS Web of Science

A full understanding of the causes and consequences of biological diversity, in all its richness, probably cannot be had until the contribution made by decomposers to the structure and functioning of ecosystems is fully understood.

Lord May of Oxford (1997)

1. INTRODUCTION

Ecological functioning in natural and managed ecosystems provides us with enormous material benefits, yet quantifying the capacity to provide these services is challenging because of the complexity of the underlying processes involved (e.g. Costanza et al., 1997; De Vries et al., 2013; Raffaelli and White, 2013; Sutherland et al., 2006). Organisms are interconnected within complex interacting networks which influence the resulting ecological processes and ecosystem services, and their responses to disturbance and environmental change (e.g. Chapin et al., 2000; Hagen et al., 2012; Lavorel and Garnier, 2002; Ledger et al., 2012, 2013; Naeem et al., 2000; Vandermeer et al., 2008). For instance, regulating processes associated with nutrient cycling

depend on the nature of elemental resources that are returned to the soil via the biota. Furthermore, evaluations of the ecological processes that support ecosystem service provision need to consider appropriate temporal and spatial scales of the assessment (O'Gorman et al., 2011; Raffaelli and White, 2013). A wide range of observational scales is often necessary not only because many aspects of biodiversity differ in their importance but also because social actors influence perceptions of the benefits received (Díaz et al., 2011; Raffaelli and White, 2013). Most farmers will probably regard 'organic matter decomposition' in their managed agroecosystems as synonymous with the ecosystem service of 'soil formation and retention, and sustained fertility', whereas ecologists perceive decomposition more as an ecological process involved in 'nutrient cycling' (Díaz et al., 2006; Faber et al., 2013; Hooper et al., 2005).

Across much of the Earth, land is used intensively, changes in management are common, and dramatic changes are foreseen in the coming decades, with important consequences for planetary life-support systems and the services they provide to mankind. Although croplands cover more than 2 million km^2 of continental Europe (e.g. Ellis and Ramankutty, 2008) and 21.8% of land area has already been converted globally to human-dominated uses (Hoekstra et al., 2005), research published in the 10 target ecological journals taken into account by Martin et al. (2012) shows a disproportionate number of studies in protected or undisturbed areas. Conversion from forests to croplands and agricultural intensification as well as the converse restoration from agriculture to nature, and transitions from conventional farming to either organic or extensive agriculture are examples of some of the main predicted changes (Ellis et al., 2010), but there are uncertainities embedded in the models currently used for agroecosystems due to the forced use of data from pristine ecosystems. One way to estimate the capacity of nature to deliver and support ecosystem services is to construct general models based on principles of elemental fluxes within and across trophic levels in above- and below-ground systems. We propose a novel way to assess the delivery of ecosystem services based on a general framework that combines allometric and stoichiometric relationships, with validation on small-scale level observations *a posteriori*.

Such a goal may seem both overly simplistic and ambitious, not least because living organisms strongly differ in their sensitivities to climate (e.g. Voigt et al., 2003) and to chemical drivers (Sterner and Elser, 2002). Nonetheless, we present a comprehensive trait-driven framework applicable to general concepts of macro and applied ecology, with a primary focus on the many linkages between above- and below-ground food webs by

Figure 2.1 Some examples of biotic interactions from the brown world (plates 1–3) and the green world (plates 4–7) at different observational scales: (1) The springtail *Folsomia candida* (mesofauna) plays often a beneficial role in the establishment of plant–fungal symbioses (Klironomos and Moutoglis, 1999); (2) the soil-dwelling *Enchytraeus albidus* (mesofauna) is a key decomposer for generating, aerating and maintaining the fertility of soil; (3) hyphae of the nematophagous fungus *Drechslerella* (microflora) 'preying' on the microbivore *Caenorhabditis elegans* (microfauna); (4) A leaf skeletonised by insect herbivores in the rainforest of Belize, leaving only the major veins intact; (5) pupae of a parasitoid fly (Tachinidae) and of its host, the butterfly *Aglais urticae* (macrofauna); (6) Larvae of a saturniid moth (macrofauna) feeding on foliage of *Dialium guianense* tree; (7) Adults of the butterfly *Plebejus argus* (macrofauna) resting on a stem of *Molinia caerulea* grass. *Photo credits: Michael Bonkowski (1), Tamás Salánki (2), Joost Riksen (3), Owen Lewis (4–6) and Gert Gelmers (7).*

modelling plant–arthropod, soil–bacteria and detritus–invertebrate interactions (some examples are shown in Fig. 2.1). Although we will mainly address above- and below-ground food webs, this framework should also be relevant to more general concepts in macroecology and applied ecology.

According to Sutherland et al. (2006), three research themes that would help us understand which ecosystem components are essential for providing human societies with services are:

I. the role of biodiversity in maintaining biogeochemical cycles (functional and taxonomic diversity as driving forces for nutrient supply and resource quality);

II. the role of soil biodiversity in resource recovery (for instance how faunal biomass distribution changes when N is released/sequestered by bacteria and fungi); and

III. the way soil biodiversity both influences and responds to above-ground biodiversity (bottom-up regulation controls nutrient availability and faunal biomass while top-down regulation reflects land-use history, with consequences on energy fluxes in the soil compartment).

Responses of soil biota are caused by (the top-down view) or reflected in (the bottom-up view) variations across ecosystems that arise from elemental factors like soil pH, soil C, N and P contents, priming effects of soil organic matter (SOM) (increased decomposition rate after fresh organic matter input *sensu* Fontaine et al., 2003), litter quality and quantity, and competition for nutrients (Chapin and Eviner, 2003; Fontaine et al., 2004; Pugnaire, 2010; Wardle, 2002). While theme number I has received much attention (Cardinale et al., 2006; Hooper et al., 2005; Maestre et al., 2012; Reich et al., 2012), a comprehensive and coherent analysis of themes II and III is missing. Here, we aim to synthesise the advances made by linking below- and above-ground biodiversity and to highlight the potential to connect ecological networks by using trait-based perspectives to forecast functional properties of ecological communities. To achieve this goal, we consider both existing studies as well as novel analyses of recently collated databases that address the incidence of traits and the abundance and biomass distribution of component species on the corresponding C, N and P cycles. Drawing on empirical examples from a wide range of terrestrial ecosystems we finally discuss the new insights that can be gleaned from trait-based modelling, including novel ways to measure the impacts of altered environmental conditions.

2. AIMS AND RATIONALE

Vascular plants are excellent bioindicators and their responses and adaptations to the environment (nutrient and water availability, light, temperature, fire and grazing) have been major topics in geobotany for over a century (e.g. Braun-Blanquet, 1951; Raunkiær, 1910; Walter, 1951;

Walter, 1964). Recognition of adaptive strategies of plants, including those of N use and C metabolism to prevailing climatic and environmental conditions (as in Bailey and Sinnott, 1916; Du Rietz, 1931; Hanson, 1917; Raunkiær, 1934; Schimper, 1898; Warming, 1909, and many more) has led to considerable advances in the mechanistical understanding of plant biogeographies and species distributions (Borhidi, 1995; Box, 1981; Ellenberg et al., 1992; Pyankov et al., 1998; Schulze, 1982; Schulze and Chapin, 1987; Solbrig, 1993; Soó, 1980).

Plants display a multitude of chemical as well as physical adaptations to defend themselves from herbivory, such as the production of tannins and toxic compounds like phenolics, and the uptake of metals from the soil to reduce leaf palatability. For instance, hundreds of plant species have adapted the strategy of transferring heavy metals from the soil to their living tissues (Baker and Brooks, 1989), often in extraordinarily high concentrations (Jaffré et al., 1976). This hyperaccumulation of metals in plants has been widely investigated (Boyd, 2004; Van Genderen et al., 1997), mostly with a focus on rare elements (Hanson et al., 2003, 2004) and on the consequences of consuming plant tissues with elevated metal concentrations by herbivores that share those habitats (Jhee et al., 1999; Van Genderen et al., 1997). Other studies have focused on chemotaxonomy and plant–insect coevolution (cf. Ehrlich and Raven, 1964; Jones and Firn, 1991; Van Genderen et al., 1997; Wilf and Labandeira, 1999), confirming that even the loss of non-target insect species (i.e. non-pathogenic species) may disrupt ecosystem services.

Less attention has been paid to the importance of P in plants in terrestrial ecosystems as drivers of energy and nutrient cycling processes, with most dynamic models continuing to focus only on C or N gains and water availability and uptake (for C: Edwards and Walker, 1983; Ehleringer et al., 1997; Mulder and Ellis, 2000; for N: Field and Mooney, 1986; Reich et al., 2009, 2012; Wright et al., 2004, 2005; for drought: Ellis, 1990; Sardans et al., 2008). This is despite growing empirical evidence for wide P limitation on productivity of autotrophs (Elser et al., 2007, 2010; Xu et al., 2013) and on related grazers (Hall, 2009; Hunt and Wall, 2002; Sterner and Elser, 2002), and the variation of C:N ratios in mass units at the basal level of food webs [9.5–56 for living leaves (Willis et al., 2010), 15–115 for leaf litter (Díaz et al., 2004) and 16–161 for fine roots (White et al., 2000), with C:N averages of 25.7, 37.7 and 76.0, respectively].

Although a large number of studies have assessed both N and P contents in plant tissues (Aerts and Chapin, 2000; Güsewell and Bollens, 2003;

Han et al., 2005; Kerkhoff et al., 2006; Niklas et al., 2005; Niklas, 2006; Reich and Oleksyn, 2004; Reich et al., 2010; Yuan and Chen, 2009), little is known about all the physiological mechanisms involved in the regulation of the nutrient to C balance, despite the growing recognition of an imbalance between C, N and P (Elser, 2011; Elser and Bennett, 2011; Peñuelas et al., 2012). Elemental factors are essential to quantify the energy flows among trophic levels and for connecting species and processes in the phyllosphere (all microbiota associated with plant leaves and herbaceous stems) and related above-ground food webs with the rhizosphere (all microbiota associated with plant roots) and related below-ground food webs. In this chapter, we will present examples of how these indicators encapsulate ecological structures (e.g. networks and food webs) and processes (carbon and nutrient cycling), with a particular focus on the interrelationships between the above- and below-ground biological systems (hereafter, the 'green' and 'brown' worlds, respectively, *sensu* Allison, 2006).

McGill et al. (2006) suggested that community ecology could be revitalised by emphasising the themes of functional traits, environmental gradients and interaction. To explore how trait variation affects performance of individuals or species, a common currency that is comparable across species and environmental gradients is needed (McGill et al., 2006). Biological properties such as traits of organisms, biological and ecological stoichiometry and allometric and metabolic scaling are increasingly recognised as being robust indicators of ecosystem functioning, and predictors of the capacity for supporting service provision, such as forecasting the effects of the loss of key species from ecological networks (Garibaldi et al., 2011; Kearns et al., 1998; Kremen et al., 2007; Losey and Vaughan, 2006).

Traits have been classified as being 'soft' or 'hard' by Hodgson et al. (1999), the former easy to measure if continuous or to assess if categorical, the latter are more difficult to measure directly and have to be derived. As an example, the buccal morphology of soil nematodes would be a *categorical soft trait* (Yeates et al., 1993), like the colour of a flower; the measured length of a nematode a *continuous soft trait* (Mulder and Vonk, 2011), like the shape of a corolla; and the calculated weight (i.e. the allometric estimate of body mass based on empirical measurements of length) of the same nematode a *continuous hard trait* (Andrássy, 1956), like the amount of nectar produced or pollen distributed. The kind of trait might influence the results of our analyses. For instance, Taper and Marquet (1996) assessed the amount of statistical error in body mass and its consequences for mass–abundance allometry and investigated alternative ways and consequences for scaling error propagation.
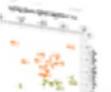
Further, many continuous and categorical traits (*sensu* Eklöf et al., 2013) also need to match with each other for occurring interspecific interactions (cf. Brose et al., 2008; Loeuille and Loreau, 2005; Mulder et al., 2009; Yodzis and Innes, 1992). Multitrophic interactions are generally simplified into what are essentially syndromes, using suites of traits such as feeding guilds (e.g. Coleman, 1985; Hunt et al., 1987) or body size or body mass (e.g. Brown and Gillooly, 2003; Mulder, 2006). Two main expectations will be central to our review:

2.1. Expectation I—Biological properties determine ecological processes that support ecosystem services that connect the green and brown worlds

The direct comparison of soft and hard traits at different organisational levels (from species to ecosystems) is known as allometric (and in particular cases, isometric) scaling. Allometry derives from the Greek άλλος (other) and μέτρον (measure) and refers to the disproportionate changes of dimensions of organisms and to their development as relative proportions of webs. In contrast, isometry derives from ισος (equal) and μέτρον (measure) and refers to the equivalent changes of dimensions of organisms and to their variation in relative proportions during development. Mulder et al. (2011a: their fig. 2.1) suggest that allometric (and not necessarily metabolic) scaling can be regarded as a powerful tool also for assessing autecology (e.g. eco-physiological responses to environmental constraints as specific allometric co-variation between traits at species level) and synecology (e.g. size-based consumer–resource interactions as multiple population responses centred on allometric food-web relationship at community level) and to connect the general allometric co-variation in the green and the brown worlds (Table 2.1).

Merging allometric scaling relationships with the stoichiometry of basal chemical elements has potential to improve food web theory. Soil organisms of a certain size, for instance, those belonging to the mesofauna, are important drivers of litter decomposition rates (Wall et al., 2008). In a global decomposition experiment, Wall et al. (2008) used two thousand glass-fibre bags filled with sterilised and air-dried *Agropyron* litter to show that arthropods in this size range enhanced decomposition rates in certain areas, relative to site-specific climate and carbon content of native litter (Fig. 2.2A, in red). These authors clearly demonstrated that above- and below-ground processes supporting decomposition varied geographically in relation to climate, although they did not address elemental variations. In contrast, Makkonen et al. (2012) showed that litter type (and, hence, the effect of plant species' elemental

Table 2.1 Schematic representation of the multiple forms of scaling, ordered according to increasing complexity, from simple trait correlations between parts of individuals, scaling populations and assemblages, up to metabolic theory and ecological stoichiometry

Function	Domain	Allometry/isometry	Dominant range	Selected references
Trait correlation	If significant, can be positive (direct correlation) or negative (inverse correlation); traits can be split according to a trophic operational level into 'effect' and 'response' traits	Both isometry as allometry are possible	No	Craine et al. (2009), Díaz et al. (2004), Lavorel et al. (2012), Poorter et al. (2009, 2013), Reich et al. (2009), Sardans and Peñuelas (2012), Wright et al. (2004, 2005)
Soft versus hard traits	Mostly positive (dominant direct correlations), but negative values can occur	Both isometry as allometry are possible	Usually >0	Abrahamsen (1973), Andrássy, (1956), Hodgson et al. (1999), Kattge et al. (2011a), Lavorel and Garnier (2002), Mulder et al. (2011b), Mulder and Vonk (2011)
Mass-Abundance Scaling	Strictly *negative* (like in aquatic ecosystems, always an inverse correlation between mass and abundance in both above- and below-ground food webs)	Both isometry as allometry are possible	-1.5 to -0.2 in a *continuum* whose median in terrestrial ecosystems approaches -0.66	Cohen et al. (2003, 2009), Jonsson et al. (2005), Hildrew (2009), Mulder et al. (2005a, 2011a), Pawar et al. (2012), Reuman et al. (2008, 2009), Woodward et al. (2005)

Biomass Body Size Spectrum	Mostly positive, but in exploited ecosystems can be slightly negative	Allometry, being isometry possible but unreported yet	−0.5 to +0.8 in a *continuum* due to derivation from the mass–abundance scaling (Box 2.1)	Jennings et al. (2002), Jennings and Mackinson (2003), Kerr and Dickie (2001), Mulder (2006), Mulder et al. (2008, 2009), Mulder and Elser (2009), Sheldon et al. (1972), Siemann et al. (1996)
Metabolic Scaling	Almost always *positive*, but for protozoans it is difficult to get it due to different morphologies within a species	Allometry	+0.25 to +1.5, with two distinct peaks at +0.66 and +0.75	Brown et al. (2004), Dodds et al. (2001), Hoste-Danyłow et al. (2013), Makarieva et al. (2008), Meehan (2006a,b), Reich et al. (2006, 2010), West et al. (1997, 1999)
Ecological Stoichio-metry	If homeostasis is strict, no trend at all; otherways trends according to the degrees of C: N:P regulation	If on a log–log plane, mostly allometry (any isometry is rare)	No	Elser et al. (2000a,b, 2007), Fagan and Denno (2004), Fagan et al. (2002), Mulder and Elser (2009), Persson et al. (2010), Sistla and Schimel (2012), Sterner and Elser (2002)
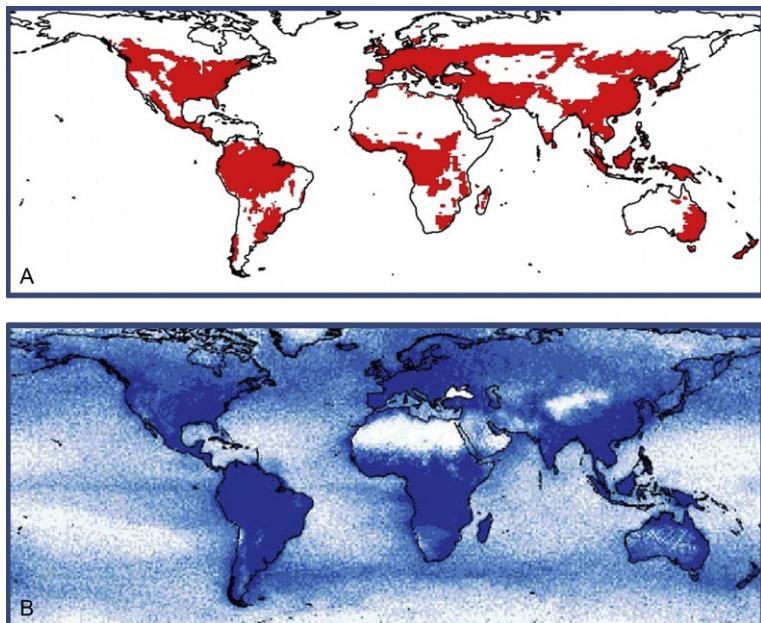
Figure 2.2 Connectedness between the brown and the green world is a driver in ecosystem processes such as decomposition (A) and biomass productivity (B). In an empirical study on data from the Global Litter Invertebrate Decomposition Experiment (Wall et al., 2008), the soil and litter mesofauna enhances the decomposition in different temperate and tropical regions (redrawn figure (A), red areas), despite circumneutral effects in other regions across the globe (Wall et al., 2008). Most temperate and tropical regions are characterised by higher ecosystem productivity (figure b from Purves et al., 2013, showing the total biomass derived from empirical data on the carbon flows), with the exception of boreal areas. *Map (A) projected and redrawn with permission from the first author and map (B) reprinted with permission from Macmillan Publishers Ltd., respectively.*

composition) affected decomposition rates consistently across biomes, explaining 34% of the total variation (although soil decomposers were estimated only indirectly, by varying the accessibility of the microcosms). In a previous experiment with a comparable design for macrofauna, Hättenschwiler and Gasser (2005) reported that the interface between litter and faunal decomposers is relevant for nutrient supply rates and forest productivity and, in turn, likely to influence the fate of carbon during decomposition. However, none of these investigations addressed whether body size of decomposers varies as a function of environmental conditions (such as litter input and/or litter quality).

For many organisms, allometric 'rules of existence' have been determined mathematically, making the building of 'general ecosystem models' possible (Purves et al., 2013). The Madingley model, running on data of C flows (Purves et al., 2013), shows that, on average, areas with faunal-enhanced decomposition (Fig. 2.2A, in red) are also areas with large biomass productivity (Fig. 2.2B, dark blue). Purves et al. (2013) show that the individual properties and basic processes of metabolism, reproduction and feeding behaviour (all three related to body size; see among others Hendriks and Mulder, 2008, 2012 and literature therein) can be used to determine abundance and mass of organisms and hence, to estimate the total biomass. Moreover, such a general ecosystem model enables us to relate total biomass to mean trait values according to the so-called 'mass ratio hypothesis' (Grime, 1998). Although focusing only on plant communities, the 'mass ratio hypothesis' predicts that ecosystem functioning is determined by the trait values of the organisms in proportion to their mass relative to the entire community. This makes the mass ratio useful for predicting rules of existence.

2.2. Expectation II—Allometric scaling is less universal than commonly assumed and reflects variation in environmental conditions
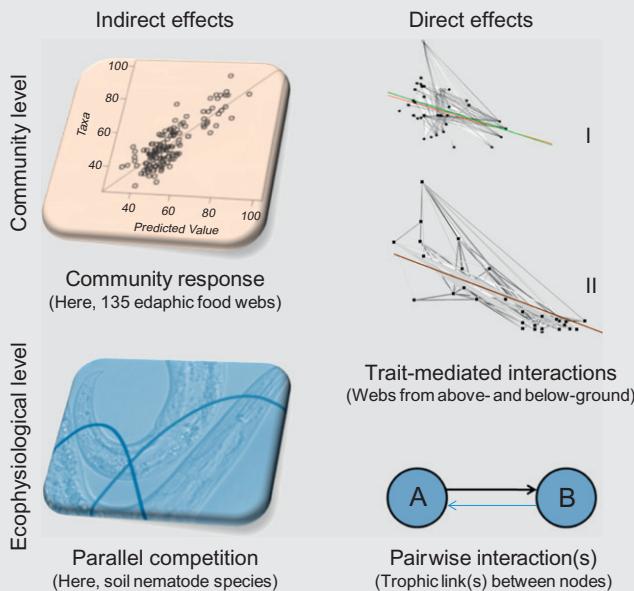
Ecosystem functioning can be quantified as elemental flows across trophic levels, which are dependent on soft and hard traits of organisms like numerical abundance and body mass, respectively. Such flows can be described by allometric slopes of linear relationships between abundance, mass and biomass (all of them at the population level), or by metabolic scaling (Box 2.1). In general, all forms of allometry can be thought of as characteristic attributes of organisms that allow coarse but statistically powerful descriptions of community patterns (Brose et al., 2006; Cohen et al., 2003; Hendriks and Mulder, 2008, 2012; Hudson et al., 2013; Jonsson et al., 2005; Mulder et al., 2005a; Reuman et al., 2009; White et al., 2007; Woodward et al., 2005). Brown et al. (2004) stated in metabolic allometry there are fundamental rules of chemistry, physics and biology that provide the means to link individual organisms and their populations to entire ecosystems and their underlying ecological processes. Although the use of log–log scales is still disputed (compare Heusner, 1982; Warton et al., 2006, with Kerkhoff and Enquist, 2009 and Lloyd et al., 2013 with their 'Lulu Effect' for outliers), log axes perform better than geometrical axes for detecting the existence and the degree of homeostatic

BOX 2.1 Scaling size-based entities

Most dynamic food-web models run on biomass estimates, explaining why the biomass–size spectrum slopes are so popular (Table 2.1), in contrast to habitat–response relationships which forecast the occurrence of taxa at a community level (taxonomic diversity) or detect ecological optima at multiple species level. However, faunal body mass is determinant for spatially scaled predatory activity, for resulting interaction strengths between predator and prey and for the final link structure in any food web (Cohen et al., 2003; Woodward et al., 2005). To a certain extent, relevance of the 'body mass' hard trait explains why density regressions like mass–abundance scaling vary much more than (eco) physiological regressions like those from metabolic scaling (Blackburn and Gaston, 1996, 1997; Brown et al., 2004; West and Brown, 2004). The trait 'body-mass average', in fact, is too often hard to define (Yvon-Durocher et al., 2011), as it can be computed in many ways (e.g. arithmetic- or geometric-mean, median or modal), even using values from the literature (Hendriks and Mulder, 2008; Makarieva et al., 2008; Peters, 1983), taking into account different life-stages or not (e.g. larvae, immature stages and adults) and lumping at species or genus level. Most important, it must always be stated if the body-mass trait is either dry weight (preferred method) or wet weight (demands some care). For instance, due to inhomogenous and highly variable structure of angiosperm wood, empirical models running on the wet weight of plant tissues (supporting the classical metabolic scaling) like the extensive survey of Mori et al. (2010) are likely to deviate significantly from the ¾ law if the measured plant respiration would have been plotted *versus* the dry weight (cf. Peuke et al., 2006). Theory shows that $\log(N)$, $\log(M)$ and $\log(B)$ are strictly correlated (Table 2.1), but recent allometric findings suggest that ecosystem processes seem to be driven more by the numerical abundances N of organisms than by their body-mass average M or by their total biomass $B(N \times M)$. Merging the classic $\log(N) = a \times \log(M) + b$ with $\log(B) = \log(M) + \log(N)$, we obtain the formula $\log(B) = \log(M) + a \times \log(M) + b = (1 + a) \times \log(M) + b$. This explains the correlation between these two main scalings on a double logarithmical scale, as their slopes differ $+1$. But it is splitting biomass in numerical abundance and body-mass average that the resulting structure of a food web can be visualised (Cohen et al., 2003, 2009). Given that the soft trait N is directly observed, despite different sampling protocols for organisms like bacteria, protozoans and the invertebrates belonging to the microfauna, mesofauna and macrofauna (Mulder et al., 2011b), it seems reasonable to predict M by N as well. Since the introduction of this graphical method to visualise entire food webs (Cohen et al., 2003), allometric scaling have been used extensively to visualise both aquatic webs (e.g. Woodward et al., 2005) as terrestrial webs (e.g. Hechinger et al., 2011) with either $\log(N)$ or $\log(M)$ as independent predictors. This method enables the computation of linear regressions for entire community webs, for single compartments of any food web (for instance, the bacterial pathway, linking all bacterial cells through bacteria-grazing invertebrates and/or protists up to their predators),

BOX 2.1 Scaling size-based entities—cont'd
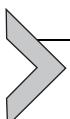
but even for pairwise (trophic) interactions and (multitrophic) ecological pyramids (Trebilco et al., 2013). An isometric slope of -1 means obviously that consumer $N_c \times M_c$ equals resource $N_r \times M_r$ (Cohen and Carpenter, 2005), hence isometry can occur only if biomass remains constant across trophic levels (for a community web, $B_1 = B_2 = B_3$; for a pairwise interaction like one chain $B_c = B_r$). The inverse correlation between N and M remains comparable in terrestrial networks, as appears from the scatter of all above-ground invertebrates occurring in a beet field under conventional farming (Bohan et al., 2005, 2011) and the analogue scatter for all below-ground invertebrates occurring in a grassland under organic farming (Mulder et al., 2005a) shown, respectively, in (I) and (II).

Indirect effects   Direct effects

Community response
(Here, 135 edaphic food webs)

Trait-mediated interactions
(Webs from above- and below-ground)

Parallel competition
(Here, soil nematode species)

Pairwise interaction(s)
(Trophic link(s) between nodes)

Community level

Ecophysiological level

Despite remarkably high differences in taxonomic resolution, sampling protocol and data mining, agroecosystems show similar patterns in their green and brown worlds. For instance, in both cases the long trophic links deviated more in their slope from the diagonal than the short links and in both cases larger organisms do not occupy higher trophic positions. Longer links can enhance the complexity of ecological networks and could, among others, contribute to a natural pest regulation, although different functional groups above-ground were found to clump together less than below-ground. Networks seem to be structured in such a way that the linear regression slope of mass as function of abundance of the above-ground food web (the green line, including carabid larvae, the red line, excluding them: I) is much shallower than in the below-ground food web (the brown line, including microbes: II), sharing all three linear regressions $p < 0.001$.

regulations (Sterner and Elser, 2002, pp. 19–22), like in the case of the N content of wood-consuming fungi (Levi and Cowling, 1969).

Brown and Gillooly (2003) clearly showed that separate taxocenes (clusters of closely related species) derived from smaller datasets exhibit mass–abundance scaling relationships that are divergent from the scaling for all sets together. However, is their universal power law of −¾ really relevant across trophic levels? Applying the allometric co-variation to entire food webs fostered the adoption of a pragmatic interpretation. Species within a given area co-exist in communities and compete for resources (or facilitate one another). There are different ways of describing assemblages within boundaries, and these implicitly reflect the fundamental constraints of stoichiometric niches. This has supported, among others, the prediction of higher P allocation in fast-developing organisms lacking P storage capacity (Elser et al., 1996; Sterner and Elser, 2002), as outlined in the growth rate hypothesis (GRH), given that the rate of change in biomass is associated with higher P concentration and lower C:P and N:P ratios (Ågren, 2008; Mulder and Elser, 2009; Yu et al., 2012). In contrast to the GRH, autotrophs may depart from the model of Sterner and Elser (2002) because they can adjust their elemental ratios while maintaining a constant level of performance (Sistla and Schimel, 2012): their ability to store N and P supplied in excess of optimal ratios is better known as stoichiometric plasticity (Ågren, 2004, 2008; Hall, 2009; Sistla and Schimel, 2012).

3. CAN A STOICHIOMETRICALLY EXPLICIT FIRST TROPHIC LEVEL BE PARAMETERISED?

Terrestrial ecological networks can be subdivided into two broad types: mutualistic networks (e.g. Bascompte and Jordano, 2007) and antagonistic networks (e.g. Ings et al., 2009), although the distinction is not always straightforward (see Loeuille et al., 2013), as certain species may operate in both forms within the same habitat (Frere et al., 2007; Hagen et al., 2012). However, regardless of the network type, the quality and quantity of resources have to be defined. The first trophic level contains all possible resources from both the green and the brown worlds, making a fine-tuned stoichiometrical parameterisation of this basal level of critical importance for a high-resolution general food-web model. We evaluated the *status quo* of literature-compiled databases such as TRY (Kattge et al., 2011a) and compared the C:N:P resource stoichiometry derived from trait assessments of autotrophic and heterotrophic organisms.

3.1. Traits and prejudice

It is incorrect to see traits as a novel item in ecology, despite the exponential increase of the occurrence of the term 'trait' in ecological and evolutionary research published since 1990 (Naeem and Bunker, 2009), because traits have always been used to group individuals into species, and taxonomists used suites of single traits such as the structure, colour and smell of the flower to assign species names. Traits are discrete features (categorical traits) or quantifiable measurement (continuous traits) of an organism (individual-level traits), one population (species-average traits) or an entire assemblage (community-average traits). The recent development of allometric co-variation and trait-based food-web scaling (e.g. Gilljam et al., 2011) implies a shift away from the traditional focus on botanical taxonomy and binomial nomenclature to the broader ecology (Raffaelli, 2007). Besides the historical focus on traits for taxonomical purposes, in recent decades they have caught the attention of ecologists aiming to describe species diversification, trophic complexity and community processes. Shan et al. (2012) explored correlations among traits and how they might vary jointly (Baraloto et al., 2010; Lambers and Poorter, 1992; Reich et al., 2006; Wright et al., 2004). Plant traits often co-vary because of constraints and trade-offs (Reich et al., 2008, 2009; Wright et al., 2001, 2004, 2006).

For instance, on the one hand, tiny, short-lived plants generally have no large leaves (physical constraint: leaves with large area tend to have higher mass), and when internal recycling becomes important (as under nutrient-poor conditions) plants with thinner leaves tend to have higher foliar N and P concentrations. This represents a physiological constraint as both elements are needed for a specific role: N for proteins involved in growth, and P for genes and energy distribution within cells under turgor. On the other hand, big plants (which must maintain a larger total leaf area than small plants) allocate N and P either to lots of small leaves or fewer, but larger, leaves. Such N and P concentrations co-vary because photosynthesis requires N-rich proteins (RUBISCO) and these are synthesised by (P-rich) ribosomes (Ågren, 2004) in response to environmental drivers, such as rainfall, temperature and soil fertility. These constraints and trade-offs have implications for plant physiology, multitrophic interactions, ecosystem functioning and ecological processes supporting ecosystem services.

Chemical constraints and trade-offs also reflect the individual and/or the species-specific potential of plants to adjust their performance to changing environmental conditions. Therefore, it is useful to explore the correlation among traits and to understand underlying mechanisms when developing

Table 2.2 Examples of global changes in the N:P ratios of foliar tissues among four datasets accessed in TRY 1 December 2012

Foliar N:P ratio	Minimum	Average	Maximum	Observations
Wright et al. (2004, 2006)	4.6	19.8	89.0	543
Craine et al. (2009)	5.8	23.5	89.3	1030
Reich et al. (2009)	1.6	13.9	123.9	9902
Peñuelas et al. (2010)	4.2	14.7	160.3	1302
Overall (this study)	1.6	15.0	160.3	12,777

The significant difference between the averages points to the log-normal distribution of N:P ratios known to occur in large datasets (Kattge et al., 2011a).

models to forecast macroecological patterns (Kikuzawa et al., 2013; Verheijen et al., 2012). The release of databases like *Fauna Europaea*, 'FishBase' for fish traits and body size, the 'European Register of Marine Species', and the landmark TRY have enabled discovery of additional macroecological patterns and correlations between species, traits and their environments (cf. Bhagwat and Willis, 2008; Mancinelli et al., 2013; Pawar et al., 2012). However, although the TRY database is huge (Kattge et al., 2011a), individual data are heterogeneous (cf. Table 2.2), have relatively low standardisation (Kattge et al., 2011b), and can be biased. In particular, below-ground traits are under-represented due to the challenges of retrieving roots in the field (Pérez-Harguindeguy et al., 2013; Robinson, 2004; Ryser, 1996; Schenk and Jackson, 2005).

Although some native plant traits (like root exoenzymes) and the cultivated plant traits are not yet entered in TRY, a clear shift between measurements from the brown and from the green world is more than evident in Fig. 2.3: in the entire trait distribution (largest pie, almost 2.5 million observations) and in the morphology group (second largest pie, more than one million observations), brown world observations are under-represented, in contrast to elemental factors (upper smaller pie: root and litter N, root (hemi)cellulose and lignin, root C, N, P content, root alcohol dehydrogenase activity, etc.) and to flux (lower smaller pie: N_2–fixation capacity, mycorrhizal type, storage, root respiration, etc.). Sampling biases can make the detection of empirical correlations between traits difficult (Tables 2.A1 and 2.A2), and this reduces the number of 'multiple trait' sets available for explanation of observed effects. Traits of cultivated plants in agriculture, in particular, deserve much more attention in databanks like TRY. In principle, machine learning and data mining could be used to fill, at least in part,
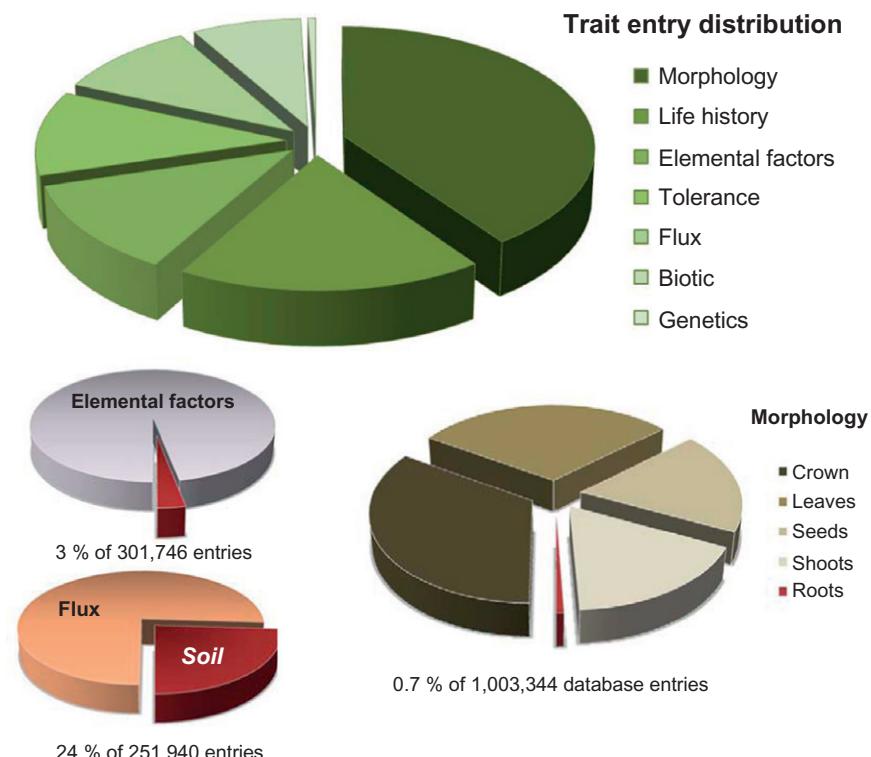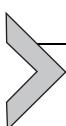
Figure 2.3 Distribution of 2,496,849 entries and 681 plant traits as recorded in the TRY database (accessed 1 December 2012), weighted according the number of observations (cf. Kattge et al., 2011a). The contributions of measurements relevant for ecological processes in the soil compartment are given as percentage of the three main groups (morphology, elemental factors and flux). More details in Tables 2.A1 and 2.A2.

these gaps by establishing multiple trait sets from existing data (Bohan et al., 2011; Shan et al., 2012; Tamaddoni-Nezhad et al., 2012, 2013). These authors have proposed grammatical and probabilistic factorisation, using background phylogenetic information, to fill gaps in trait prediction. Such approaches could markedly improve the standardisation and comparison among data sets and, hence, the resolution of ecological networks (Tammadoni-Nezhad et al., 2013), but this does not obviate the urgent need for more below-ground trait observations (Table 2.A2) in wild plants and crops.

3.2. Stoichiometric plasticity of autotrophs

Foliar N is involved in both respiration and photosynthesis and can be present in non–respiratory structures and compounds (Reich et al., 2008). Respiration rates at a given N concentration are, on average, consistently lower in leaves than in roots (Reich et al., 2008). Considering the model of N flow consisting of shoots, roots, labile and resistant substrates, and living soil organisms as originally conceptualised by Coleman (1985), all the plant categories besides shoots belong to the soil food web as defined by Hunt et al. (1987). From this perspective, we recognise different N allocation patterns and connections between the green (living leaves) and the brown world (leaf litter and plant roots). Some of the environmental–driven changes in this continuous N flow from leaves to litter to soil and then back to plants through their roots will be discussed in the next sections. Craine et al. (2009) showed clear macroecological scaling for 555 plant species, where the fractionation of $\delta^{15}N$ between foliar tissues and soil was related to the difference in delta values, scaling with $\Delta^{15}N$ [$\delta^{15}N$ (leaf) $-\delta^{15}N$ (soil)] against foliar $\delta^{15}N$. The positive correlation between the site-averaged foliar $\delta^{15}N$ and the $\Delta^{15}N$ supports a slow increase of foliar $\delta^{15}N$ as $\Delta^{15}N$ increases: plants with lower foliar N content will be less enriched in ^{15}N (Craine et al., 2005, 2009). In Fig. 2.4, we see also a slight but consistent difference in foliar $\delta^{15}N$ between all plant species and N_2 fixers. These higher foliar $\delta^{15}N$ values in N_2 fixers (plants in association with N_2-fixing bacteria expected to have low $\delta^{15}N$ being atmospheric N their source of N) seems explainable by mycorrhizal symbionts (Craine et al., 2009; Quispel, 1974).

4. THE ADVANTAGES OF STOICHIOMETRIC PLASTICITY

Carbon is fixed from the atmosphere via photosynthesis, transformed into carbohydrates, allocated to different plant tissues and transferred to the soil via root respiration, exudation, mycorrhizae, endophytes and herbivory (Bahn et al., 2010, 2013; Brüggemann et al., 2011; Denef et al., 2009; Epron et al., 2012; Jones et al., 2009; Ostle et al., 2007). There can be a strong differentiation between woody and herbaceous plants, with woody species having foliar C contents around 45% or more (percentages fluctuate according to the seasons, see Tognetti and Peñuelas, 2003), in contrast to herbaceous species whose leaves tend to have lower C contents ($\sim$40%).

A slower major pathway of C from the plant to the soil is related to litter deposition and its subsequent decomposition if moisture is not limiting, a
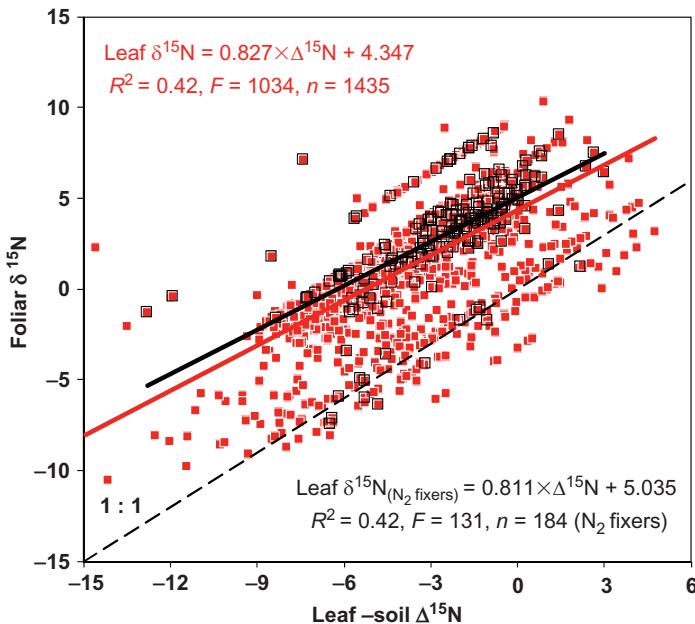
Figure 2.4 Measurements of $\delta^{15}N$ in the foliar tissues of plants (Craine et al., 2009) in comparison to the $\Delta^{15}N$ trophic enrichment from the soils they are growing on (trophic enrichment *sensu* Caut et al., 2009). To obtain trait values from the TRY database, we averaged species by contributing author and environmental conditions to account for possible disproportionate contributions to species-rich communities. Correlations are provided for the entire dataset (in red) and for the plants with N_2-fixation capacity; the latter data points are embedded in black boxes. With linear regression slopes of 0.8267 ± 0.0257 SE (all the taxa together) and 0.8110 ± 0.0710 SE (only the N_2 fixers), these scaling relationships share the same trend (confidence interval 95%). *Data mining from* Wright et al. (2004), *their supplementary material, and, to a lesser extent, from* Quispel (1974).

pathway that is affected by litter chemistry and related to the chemical composition of the above-ground biomass (Cotrufo et al., 2009; Fontaine et al., 2004). Fire can alter this pathway, reducing the flow of litter C to the soil and changing the forms in which C enters the soil and the atmosphere (Certini, 2005; Lavorel et al., 2007). The pathways have been suggested to be linked through priming effects that exemplify the interaction between the green and the brown world: the mineralisation of SOM is influenced (mostly enhanced, but sometimes reduced) by inputs of fresh organic compounds (Blagodatskaya and Kuzyakov, 2008; Kuzyakov, 2010).

Annually, ∼98 billion tonnes of C are estimated to be emitted globally by all soils, an amount which is likely to rise due to global warming (Bond-Lamberty and Thomson, 2010; Smith and Fang, 2010). Soil C stocks are suggested to decline during intensification of land use, particularly as natural and seminatural ecosystems are converted to agroecosystems (Don et al., 2011; Guo and Gifford, 2002). The (im)balance between soil C and nutrients is subtle, as atmospheric N deposition drives the global soil C:N ratio, whereas human-induced leaching from croplands affects C:N and C:P ratios at the local scale (De Vries et al., 2011).
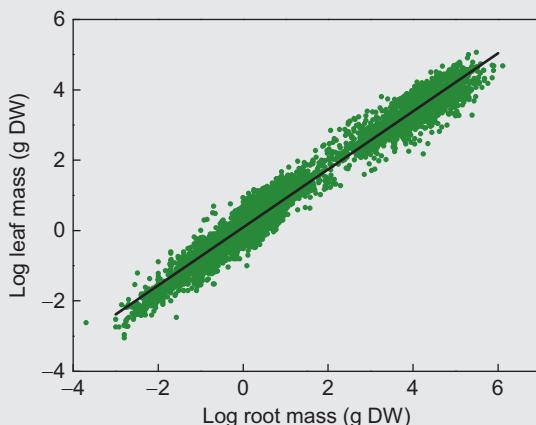
The two macronutrients N and P, obtained from the soil through roots, are crucial components in nutrient cycling. The strong positive correlations in grasses between the N concentrations in the phyllosphere and in the rhizosphere, and between the δ^{15}N values of leaves and of soils (Craine et al., 2005), are examples of a direct linkage across the boundary of the green and the brown worlds. Moreover, there is a strong connection between leaves and roots, whose mass-related traits tend to scale allometrically (e.g. Craine et al., 2005; Poorter and Sack, 2012). Species with fast-growing leaves generally have fast-growing roots (cf. Yu et al., 2012); consequently, both leaf and root life-spans are longer in harsh environments (Box 2.2).

Fast-growing species adapted for higher metabolic activity, show higher N and P contents. Consequently, the fast (slow) growth syndromes differentiate plant species that have inherently low (high) C:N ratios (a classical trade-off), often with effects at a higher trophic level, as for N-rich plants with increased leaf damage by invertebrate herbivory (e.g. Loranger et al., 2012). Finally, shoot and root N:P ratios tend to scale allometrically (Kerkhoff et al., 2006), although the question of whether terrestrial plants have optimal N:P ratios comparable to the Redfield's Ratio from phytoplankton remains unanswered (Sardans et al., 2012a).

Many questions of nutrient allocation in plants can be posed allometrically (Weiner, 2004): for instance, regardless of plant N:P thresholds, do we expect foliar and litter C:N:P ratios to co-vary allometrically? If so, a trait-driven predictability of soil C:N:P ratios would be of highest importance for an efficient management of agroecosystems, including a better fertilisation regulation. N and P are seen as indicators for the nutrient leaching from agricultural soils. The EU Nitrates Directive obliges EU Member States to limit the yearly use of manure to maximal 170 kg N ha^{-1} (Zwart et al., 2011) and this is slightly more than the mean N excreted by one cow in one year (161 kg N ha^{-1}). On small scales like at farm level in the Netherlands, for instance, there is a 12 kg gap between the use of

BOX 2.2 Biomass allocation between the brown and the green world

Especially as seedlings, inherently fast-growing species generally show a suite of traits that allow for such high growth rates: high metabolic rates of photosynthesis and respiration when expressed per total plant mass (Poorter et al., 1990), high rates of nutrient uptake per unit root mass (Drew and Saker, 1975; Reich et al., 1998a), and leaves with higher specific leaf area, protein concentration, but less investment in cell walls (Poorter and Villar, 1997). Further, fast-growing species have mostly, but not always (traits correlations in larger plants can be far less consistent, see Peñuelas and Estiarte, 1998; Wright et al., 2010), low concentrations of lignin and other secondary compounds and show organs that are characterised by low dry matter contents (Lambers and Poorter, 1992; Reich et al., 1998b). Inherently slow-growing species form the other side of the spectrum, and generally show opposite characteristics. For slow-growing tree species, this suite of traits is complemented by a high wood density (Wright et al., 2010). The resulting trait differentiation is reflected in the overall composition of leaves, stems, roots and seeds, and influences the litter quality and the microflora, as reported by Agnelli et al. (2007), Boström et al. (2007), Peuke et al. (2006), Lindahl et al. (2007), Risk et al. (2009) and Ascher et al. (2012). These suites of traits are associated with precitable differences in plant performance under different environmental conditions. For example, species adapted towards a faster growth generally have a much higher competitive ability when nutrients are abundant (Yu et al., 2012); but, when nutrients are scarce, inherently fast-growing species are outcompeted by inherently slow-growing species, which generally are better able to conserve nutrients, for example, by having slower rates of tissue turnover and by withdrawing leaf nutrients to lower levels prior to leaf fall (Aerts and Chapin, 2000; Wardle, 2002).

Continued

> **BOX 2.2 Biomass allocation between the brown and the green world—cont'd**
>
> Hence, when nutrient availabilities change, for instance, because of increasing atmospheric N deposition, shifts in vegetation are expected due to consistent leaf–root linkages. These linkages support direct relationship between leaf and root nutrient contents, given that the leaf and root masses are positively correlated (García-Palacios et al., 2013). In contrast to stem and root dry weights (DW), which seem to scale isometrically (Ordinary Least-Squares (OLS) regression exhibiting 1.055), leaf and root DWs scale allometrically by 0.834 (OLS).

plant–available N and the nitrogen application standards (Zwart et al., 2011). Therefore, regardless of the existence of a kind of soil Redfield's Ratio, harvesting crops allocating N could affect the long-term stoichiometry of agroecosystems.

Given the source of N and P, the kind of allometric co-variation between litter N:P ratio and leaf N:P ratio depends on whether N or P is more limiting in a given habitat (Liebig's 'Minimum Law'). If neither of these elements is more clearly limiting, then foliar and litter N:P scale isometrically (Fig. 2.5). But, if P is strongly limiting, the slope will be <1, and if N is strongly limiting, the slope will be >1. Wright and Westoby (2003) investigated eastern Australian evergreens (ca. 70 species in pristine conditions) and showed that, where soil P was the major limiting factor, foliar and litter N% scaled isometrically, otherwise foliar and litter P% scale allometrically (bigger difference between leaf and litter P% for those species with lower leaf P), with consequences for the allometric co-variation between the leaf and the litter N:P ratios.

It is intriguing that as the leaf N:P ratio increases, the litter N:P ratio becomes proportionally higher, suggesting that plants retranslocate N and P not only as a function of the concentration of each nutrient separately, but also depending on the relative availability of the other. Hence, it will be N (or P) which will determine if either a C:N or a C:P leaf to litter ratio will scale isometrically. Briefly, N:P ratios are higher in litter than in leaf biomass, indicating relatively more retranslocation of P than of N in leaves. Under nutrient-rich conditions, high foliar concentrations of N and P are mostly accompanied by low N:P in litter (cf. Cornelissen et al., 2004; Quested et al., 2003), and when the foliar concentrations of N and P are higher, less P is retranslocated while translocation of N seems independent of foliar N (Fig. 2.5). As a result there will be lower N:P ratios, with
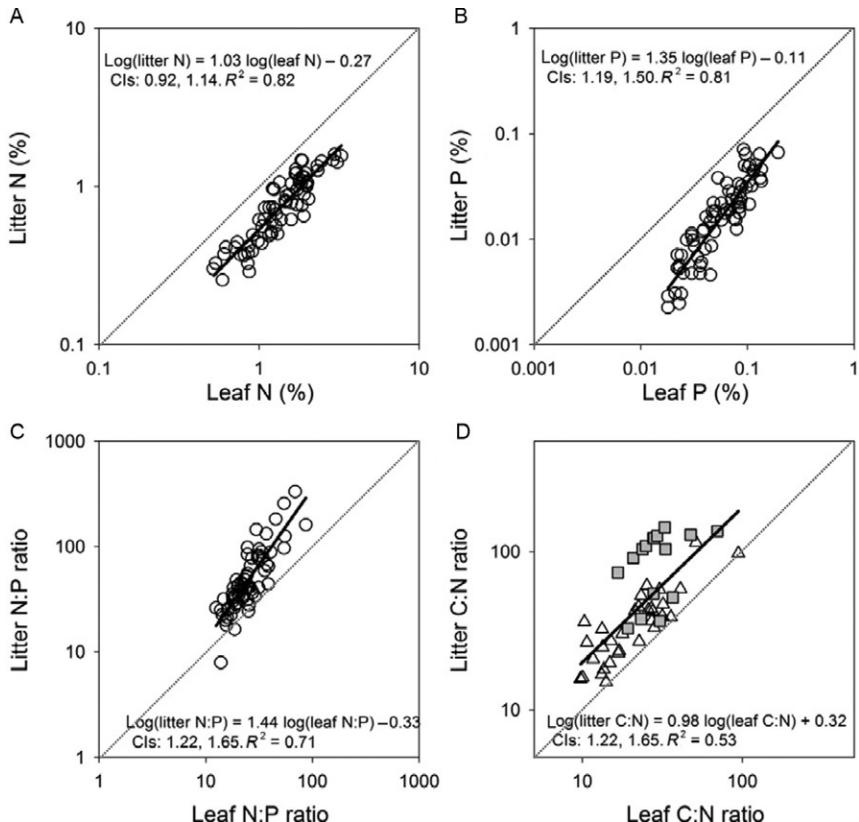
Figure 2.5 Allometric (blue 1:1 line) and isometric (red 1:1 line) correlations between nutrient ratios in leaves and litter. Isometric correlations occur between N% and the C:N ratio in the green world (living foliar tissues) and in the brown world (dead litter), in contrast to allometric correlations between P% and the N:P ratio. Trait measurements (as circles: plots A, B and C) of N%, P% and N:P in the foliar tissues of plants and in the litter beyond them from Wright and Westoby (2003); C and N measurements (plot D) from Díaz et al. (2004) and Pérez-Harguindeguy et al. (2000), triangles, and White et al. (2000), boxes.

implications for ecosystem services and processes in, among others, agroforestry (like nutrient cycling and decomposition rate, respectively) and plant–arthropod(s) multitrophic interactions such as insect herbivory and natural pest regulation (cf. Cohen et al., 2005).

With a linear regression of 0.980 ± 0.135 SE, the slope between the two C:N ratios ($p < 0.0001$) is undistinguishable from unity; the elevation is not

significant (intercept $p = 0.094$), although the litter seems carbon-enriched: the 'brown' C:N ratio (Pérez-Harguindeguy et al., 2000), was slightly higher than the 'green' C:N ratio (Díaz et al., 2004) and much higher in White et al. (2000), being the latter brown ratio on average 3.16 times higher than the corresponding green ratio. The isometric correlation between the elemental composition of living leaves and their respective litter as shown by the C:N ratios (Fig. 2.5D) suggests a potential universal scaling for plants as consumer–resource fluxes in the green and the brown worlds act in comparable ways.

To test this suggestion we will focus on the stoichiometry of both the above- and below-ground resources, starting with a literature survey. We used Web of Science (WoS, Institute for Scientific Information, Thompson Reuters, New York) and ran a cited reference search to compile data on the soil nutrient ratios and the stoichiometric C:N:P balance (Fig. 2.A1). With 67.5% of all the WoS records until 2012 (>5000 records over >25 years, including double entries), C:N was the most common descriptor/predictor in soil ecology, followed by N:P (20.3%), C:N:P (7.1%) and C:P (only 5.1%). As autotrophs can be stoichiometrically plastic (e.g. Hall, 2009; Taylor and Townsend, 2010; Vitousek, 1982), we aimed to gauge the extent to which nutrients can be stored for organisms belonging to the lowest trophic level. We also sought to identify whether environmentally driven variations in the C:N:P ratios result in pervasive elementary *mismatches*.

4.1. Above-ground evidence for plasticity from the Catalan Forest Inventory

Most trees cultivated in temperate plantations naturally occur in Mediterranean areas. Field data from such biodiversity hotspots may therefore provide a better insight in agroforestry also for temperate Europe. Empirical data from the Catalan Forest Inventory (Sardans and Peñuelas, 2013) show how the annual biomass growth and the C, N and P in foliar tissues are strongly correlated with the above-ground plant total mass (Fig. 2.6). All the three linear regression slopes of the log-shoot (growth, N_{tot} and P_{tot}, respectively) as a function of the log-foliar C concentration were undistinguishable from each other and equal to the theoretically expected ¾ slope, being for above-ground growth 0.796 ± 0.025, for above-ground N 0.788 ± 0.021 and for above-ground P 0.771 ± 0.030 standard error (SE) of estimate. However, N and P, both elements obtained from the soil and accumulated in foliar tissues, scaled in a very different way from the scaling of the foliar C obtained from air (Fig. 2.6): unlike C, only the linear regression slope (Fig. 2.6) of log-shoot above-ground P as function of the log-foliar
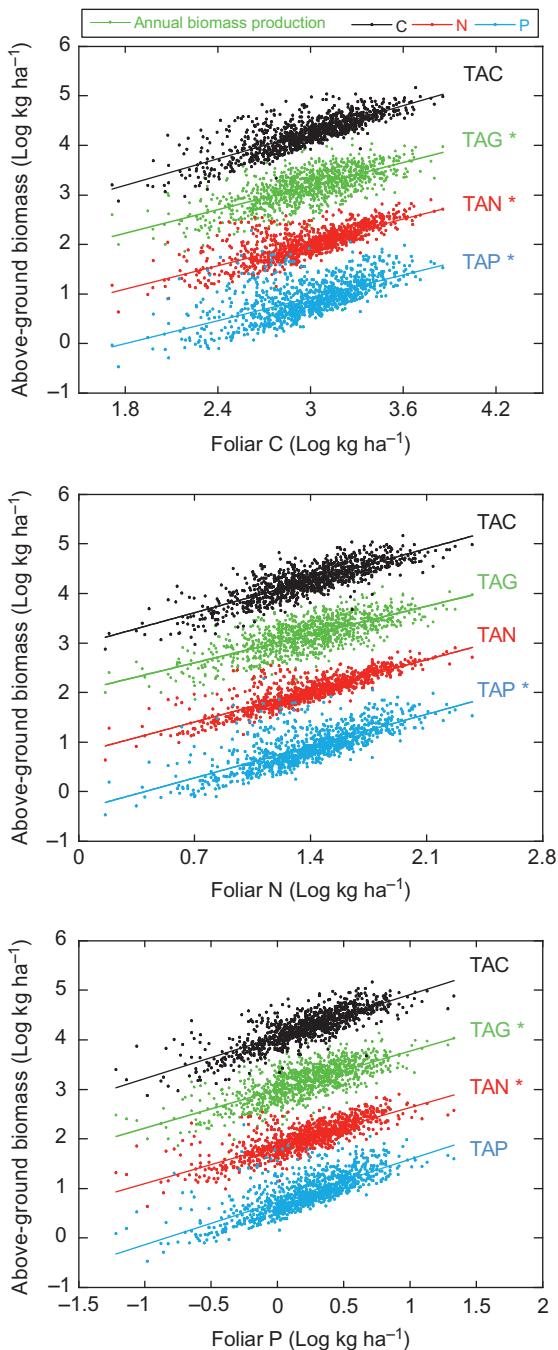
Figure 2.6—See legend on next page.

concentration N (0.739 ± 0.026 SE) was statistically close to ¾, but not for either above-ground growth (0.815 ± 0.025 SE) or above-ground N (0.896 ± 0.016 SE).

Conversely, log–foliar P concentration for both the above-ground growth (0.775 ± 0.022 SE) and the above-ground N (0.767 ± 0.018 SE) were undistinguishable from ¾, but not for above-ground P (0.861 ± 0.024 SE). Ultimately, the ¾ power law linking foliar C with above-ground P, N and plant growth is not surprising, as the non–power relationship with above-ground C can be explained by an increasing fraction being sequestered in tissues during plant growth (cf. Weiner, 2004). The data from Catalan Forest Inventory supported this suggestion, exhibiting a negative relationship between above-ground tree biomass and tree leaf/wood biomass ratio: with increasing tree size there was also a proportional increase of the biomass allocation to wood (with high C:N and C:P ratios) and therefore a decrease of biomass allocation to leaves (with low C:N and C:P ratios) (Sardans and Peñuelas, 2013).

Kerkhoff et al. (2005) pointed out how nutrient stoichiometry in plant tissues affects growth efficiency, and allometric relationships between total plant biomass and the annual biomass production rate are well known (e.g. Cannell, 1982; Enquist, 2002; Enquist et al., 2007). Assessed individually, foliar N did not show a latitudinal trend (Elser et al., 2007, 2010; Reich and Oleksyn, 2004), unlike foliar P and foliar and litter N:P ratios, which tend to increase with latitude (Kerkhoff et al., 2005; McGroddy et al., 2004; Reich and Oleksyn, 2004; see also Chen et al., 2013; Hedin, 2004; Sardans et al., 2012a, for discussions). However, different elemental profiles of foliar tissues not only directly reflect plant–environment interactions (e.g. Baxter and Dilkes, 2012; Ordoñez et al., 2009; Salt et al., 2008), but have also indirect consequences for related insects at higher trophic levels (Fagan and Denno, 2004; Fagan et al., 2002; Woods et al., 2004). Some

Figure 2.6 Constrained stoichiometrical composition across the Catalan Forest Inventory (Sardans and Peñuelas, 2013) for the total above-ground carbon (TAC), the total above-ground nitrogen (TAN), the total above-ground phosphorus (TAP) and the total above-ground growth (TAG) as predicted by the foliar C (upper plot), N (middle plot) and P (lower plot) contents (dry weight). All correlations are highly significant ($p < 0.0001$; confidence interval 95%). Allometric exponents close to the three-quarter law are marked by asterisks (*, ANOVA $p = 0.00023$). Based on a log–log analysis, only %P in foliar tissues was a significant predictor for the above-ground growth mass ($R^2 = 0.127$, $p < 0.0001$). More explanations in the text.

bottom-up effects on invertebrates during the early spring, when young foliar tissues are richer in nutrients, and top-down effects on nutrient cycling after the vegetative season are already known from literature (e.g. Lambers et al., 2008; Slansky and Rodriguez, 1987).

To illustrate some possible multitrophic implications, we scrutinised differences in the elemental concentrations of the leaves over one order of magnitude. If foliar N increases from 0.5% to 5%, above-ground N is expected to increase from 52 to 215 kg ha^{-1}, and above-ground P from 4 to 29 kg ha^{-1} (implying a shift from a ratio of 13 to 7.4, hence a decrease of −43%). However, if foliar P increases from 0.05% to 0.5%, above-ground N is expected to increase from 85 to 210 kg ha^{-1}, and above-ground P would increase from 4.9 to 39 kg ha^{-1} (implying a shift from a ratio of 17 to 5.3, hence a decrease of −70%). The latter scenario means that it will be less efficient for herbivores to graze foliar tissues with a higher N% as they would get much less P for the same amount of consumed plant resource. Although herbivores tend to consume resources much poorer in P than those consumed by predatory invertebrates, herbivores are less efficient as they consume *per capita* greater quantities of food (Woods et al., 2004). It seems very likely that the effects of a relative retranslocation of P will affect the behaviour of more specialised above-ground invertebrates (including pollinating insects) in a different way from those inhabiting litter or soil.

4.2. Below-ground evidence for plasticity from Irish grassland ecosystems

Due to lower levels of variation in plant stoichiometry relative to soils (Fig. 2.6; Sardans et al., 2012a), shifts in leaf palatability for above-ground invertebrate herbivores may force consumers to change diet (i.e. plant species), life history (e.g. voltinism) or behaviour. Further, given the (isometric) correlations shown in Fig. 2.5 between the leaf tissue chemistry and the composition of litter, elemental shifts in the phyllosphere—including compounds such as tannins that affect simultaneously above-ground herbivory and below-ground decomposition—are likely to be manifested in the rhizosphere and to influence detritivores as well (Aerts, 1996, 1997; Grime et al., 1996; Killingbeck, 1996). Moreover, if such stoichiometrical shifts occur in the rhizosphere, the following question arises: do heterotrophic soil microorganisms in the brown world react to their environment in a comparable way to plants in the green world?

Fig. 2.7 shows that on average (1) stoichiometric shifts also occur below-ground, (2) microbial biomass P content is positively related to substrate
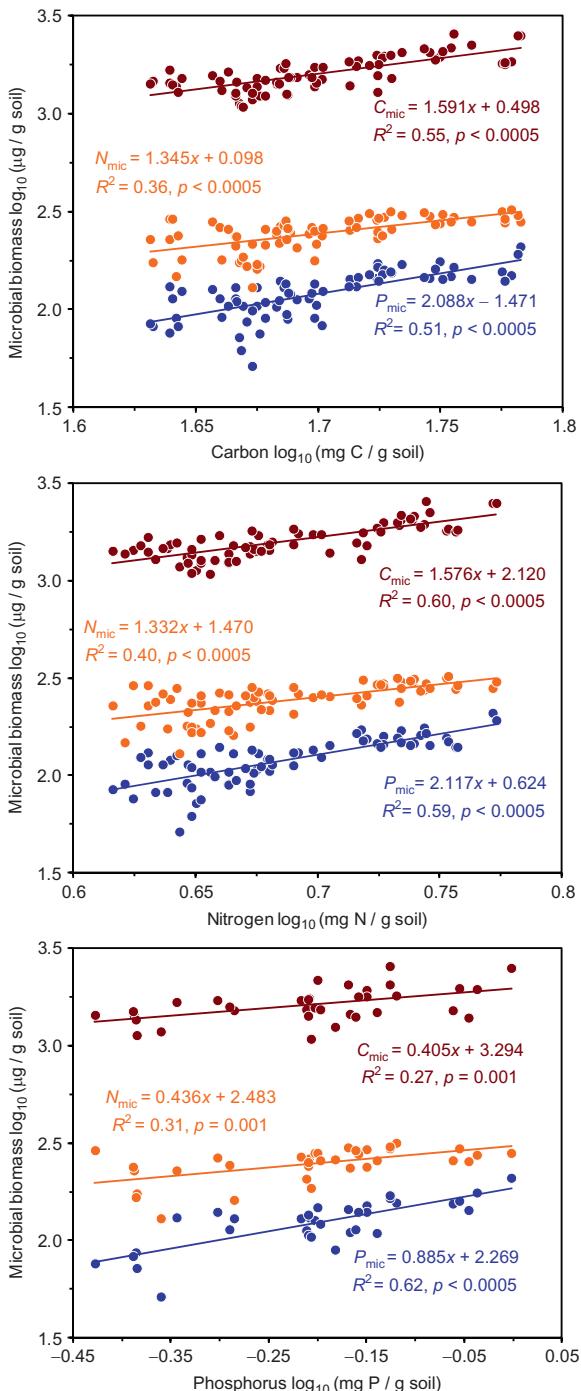
**Figure 2.7**—See legend on next page.
Figure 2.7 Stoichiometrically explicit plasticity (*sensu* Klausmeier et al., 2004) of microbial biomass from soils of the 'Cowlands Field', with an upper scatter (soil P vs. microbial

C and N (environmental factors, *x*-axes) to a larger extent than microbial biomass C and microbial biomass N, and (3) microorganisms (C, N, P) contents change according to substrate P much less than with substrate C and N, although biomass P content increases significantly more than biomass C (or N) content (Table 2.3). A study on Irish grassland ecosystems showed that the bacterial:fungal ratio increased with P fertilisation (Tan et al., 2013). These empirical trends have significant implications since the microbial biomass C:P and N:P ratios change consistently more than the microbial biomass C:N ratios, irrespective of bacterial:fungal ratios in soil.

Ferris et al. (1997) demonstrated that the C:N of isolates of soil bacteria and *Escherichia coli* ranged between 3.65 and 4.92 (with a mean of 4.12) and Makino et al. (2003) demonstrated a strong stoichiometric homeostasis in biomass P (and related biomass C:P and N:P) for *E. coli* K-12, independently of external conditions and under a wide range of nutrient concentrations and growth rates. In general, P accounts for up to 3% of the bacterial dry mass, and in particular, fast-growing bacteria contain ∼25% of their dry weight as RNA and DNA (Herbert et al., 1971). As decoupling of P from RNA allocation and growth rate require particular supply (i.e. high food C:N with low N:P, extremely low food levels), the close correlation between RNA and P contents indicates that ecosystem processes influence the expression of rRNA synthesising genes (Elser et al., 2000a, 2003; Sterner and Elser, 2002). Griffiths et al. (2012) plotted the microbial biomass C:P as predicted by the available C:P molar ratio and obtained a log–log linear regression slope of 0.15, significantly different from the 1:1 isocline, indicative of constrained (homeostatic) stoichiometry for microbes (cf. Makino and Cotner, 2004).

(C, N, P) elemental profiles), a middle scatter (soil N vs. microbial (C, N, P) elemental profiles), and a lower scatter (soil C vs. microbial (C, N, P) elemental profiles). These Irish grasslands had different fertility treatments (Griffiths et al., 2012). Elemental profiles of microbial biomass and soil nutrient availability were—as expected—strongly correlated (confidence interval 95%), but the microbial enrichment in terms of P biomass was always the most efficient in comparison to the microbial enrichments in either C or N, as shown by increased slopes of the log–log lines. With a coefficient of variance (CV) of 24.9%, the independent predictor soil P was much more variable than the predictors soil C and soil N (9.5% and 10%, respectively); also within the dependent variables, the CV for microbial P (25.4%) was much higher than for microbial C or N (20.7% and 18.9%, respectively). Soil C and soil N were twice as high as for soil P (72 and 35, respectively).

Table 2.3 Empirical evidence of management-driven changes in the elemental ratios (averages $\pm$ SD, $n = 6 \times 12$, randomised design) of microbial biomass from treated grasslands (material and methods in Griffiths et al., 2012)
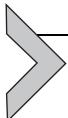
Grassland P treatment (since 1968)	C:N:P microbial ratios (mass:mass)			C:N:P microbial ratios (mol:mol)		
	C:N	C:P	N:P	C:N	C:P	N:P
Never P fertilised (control treatment)	7.30 $\pm$ 1.32	17.05 $\pm$ 2.32	2.42 $\pm$ 0.60	7.91 $\pm$ 1.43	44.05 $\pm$ 5.99	5.76 $\pm$ 1.42
Decreased P (15 kg reduced to 5 kg ha^{-1} year^{-1} in 1999)	5.98 $\pm$ 0.70	13.60 $\pm$ 1.13	2.30 $\pm$ 0.36	6.48 $\pm$ 0.76	35.12 $\pm$ 2.91	5.49 $\pm$ 0.85
Intermediate P fertilisation (15 kg ha^{-1} year^{-1})	6.27 $\pm$ 0.65	13.12 $\pm$ 1.19	2.11 $\pm$ 0.21	6.79 $\pm$ 0.71	33.90 $\pm$ 3.08	5.02 $\pm$ 0.50
Maximal P fertilisation (30 kg ha^{-1}year^{-1})	6.60 $\pm$ 1.10	10.90 $\pm$ 1.76	1.66 $\pm$ 0.21	7.15 $\pm$ 1.19	28.16 $\pm$ 4.55	3.97 $\pm$ 0.49
Abruptly increased P (0–30 kg ha^{-1} year^{-1} in 1999)	6.99 $\pm$ 1.16	12.97 $\pm$ 0.73	1.91 $\pm$ 0.35	7.57 $\pm$ 1.26	33.50 $\pm$ 1.88	4.55 $\pm$ 0.82
Interrupted high P (30 reduced to 0 kg ha^{-1} year^{-1} in 1999)	6.72 $\pm$ 1.00	13.32 $\pm$ 1.36	2.00 $\pm$ 0.16	7.28 $\pm$ 1.08	34.41 $\pm$ 3.51	4.77 $\pm$ 0.39

The background of the three experimentally derived conversion factors for the microbial (C, N, P) estimates has been discussed in Cleveland and Liptzin (2007). The microbial C:N:P ratios were derived as follows: C_{mic} was estimated as $C = EC/k_{EC}$, where EC equals organic C extracted from fumigated soil minus organic C extracted from nonfumigated soils and $K_{EC} = 0.45$ (Jenkinson et al., 2004); N_{mic} was estimated as $N = EN/k_{EN}$, where EN equals total N extracted from fumigated soil minus total N extracted from nonfumigated soil and $k_{EN} = 0.45$ (Brookes et al., 1985); P_{mic} was estimated as $P = E_P/k_{EP}$, where $E_P = [(F - U)/(S - U)/25]$, being F equal to PO$_4$-P extracted from fumigated soil, U to PO$_4$-P extracted from nonfumigated soil, S to PO$_4$-P extracted from spiked soil, and $k_{EP} = 0.40$ (Brookes et al., 1982, 1984).

Abundance and diversity of the bacterial community as a whole increased, whereas the activity of bacterial phosphatases declined, with increased chemical P fertiliser input (Tan et al., 2013). These data indicate a shift in the bacterial:fungal ratio towards bacteria, and a decline in bacterial investment to enzymes for P-solubilisation with increasing P availability and are consistent with comparable shifts in bacterial:fungal ratio and decreased abundance of fungal phosphatases (Keiblinger et al., 2012; Schneider et al., 2012). Using control plots, Griffiths et al. (2012) found a molar C:P ratio of the soil microbial biomass of 45, close to the global C:P average of 47 for grasslands (Brookes et al., 1984; Cleveland and Liptzin, 2007).

Microbial activity, decomposition rate and likely the whole below-ground food web are limited by the availability of low-molecular-weight carbon compounds (Albers et al., 2006; Fontaine et al., 2007; Hättenschwiler et al., 2011; Pollierer et al., 2007; Tiunov and Scheu, 2004); focusing only on the C and N budgets is a too narrow aspect of soil food webs (as currently done in agroecology) considering the importance of available P for organisms at the basal level of food webs. As the microbial C:N ratio varies widely (e.g. Cherif and Loreau, 2009; Daufresne and Loreau, 2001; Klausmeier et al., 2007; Taylor and Townsend, 2010), keeping the microbial parameter C:N ratio constantly equal to 4 (De Ruiter et al., 1993; Hunt et al., 1987; Moore and De Ruiter, 2012) might no more be appropriate for food-web modelling.

Our empirical data in Table 2.3 show that the microbial biomass C:N ratio fluctuates between 4.78 and 9.37 and differ significantly from the supposedly fixed C:N parameter of 4, and, as expected, long-term P-application led to increasing soil C and N, with cascading effects on microbial elemental content (Griffiths et al., 2012). These contrasts between observed and modelled C:N ratios could explain why divergent trends have been detected between observed soil fertility declines and expected soil fertility increases from detrital soil food-web models (Holtkamp et al., 2011; Kardol et al., 2006). The mentioned differences are probably caused by underestimation of the microbial C:N ratio, with consequent error propagation across trophic levels. Better food quality (microbial biomass with low C:P or N:P ratios can be regarded as more palatable for microfauna) is likely to affect feeding preferences of invertebrate herbivores. This occurs more often for microbial biomass C:P ratios (63.9% of the samples) than for N:P ratios (55.6% of the samples), suggesting that C:P is a statistically and stoichiometrically robust predictor for environmental soil quality, independent of the soil bacterial:fungal ratio (Fig. 2.7).

5. CONSTRAINED RESOURCES, ISOTOPIC SIGNATURES AND NETWORKS

Scaling the allometry and energy demand of heterotrophic organisms in the brown world seem more difficult than in the case of (photo)autotrophs in the green world. At the community level, allometric scaling and predator–prey relationships mirror the biotic demand of metazoans. In addition, multitrophic interactions among invertebrates from different size classes are apparent from the isotopic signatures. The $\delta^{13}C$ value is commonly used to determine the resource (i.e. the prey), whilst the $\delta^{15}N$ value is used to assign both predators and preys to trophic levels (Traugott et al., 2013 and literature therein). Although the consumer–resource body-mass ratio is the most frequently used type of food-web metrics, other indices, such as the predator–prey size ratio, the numerical abundance ratio and the biomass ratio are used also. All species can be size-structured according to specific traits and their trophic height can be measured in relation to their isotopic signatures.

5.1. Consumer–resource body-mass ratios and isotopic signatures

In Fig. 2.8, we set the height of size-structured nodes in proportion to the mean $\delta^{15}N$. As far as we know, it is the first time that allometric relationships, tritrophic interactions and isotopic signatures have been stoichiometrically scaled on the same ecological network at the same time, despite many previous examples of investigations of individual components of this suite of measures (e.g. Jennings and Warr, 2003; Jennings et al., 2002; Layman et al., 2005; Ponsard and Arditi, 2000). In general, $\Delta^{13}C$ is expected to be higher among invertebrates consuming plant tissues (hereafter, herbivores) than among predators and omnivores that have consumed other invertebrates (McCutchan et al., 2003). However, in these studies, the $\Delta^{13}C$ signal was not linked to all the expected trophic links and in our study area $\Delta^{13}C$ is strongly predictable by the complete predator–prey scaling, that is, all the possible consumer–resource body-mass ratios.

Invertebrate tissues assimilate carbon isotopes at different rates: fat and reproductive tissues reflect diet C signatures almost instantaneously, compared to other 'structural' tissues (e.g., Focken and Becker, 1998). The $\delta^{13}C$ value of the individual as a whole reflects its average resource C signature given that most $\delta^{13}C$ values change little between trophic levels (Fig. 2.9). Focusing on our litter food web, the enrichment factor for C is more conservative than

Taxon	ID#
Lycosidae spp.	1
Atheta sp.	2
Nemastoma spp.	3
Liogluta sp.	4
Formica spp.	5
Pardosa spp.	6
Geophilus insculptus	7
Gnathonarium spp.	8
Trogulus spp.	9
Lithobius mutabilis	10
Neobisium spp.	11
Camponotus spp.	12
Acaridae spp.	13
Roncus spp.	14
Chthonius spp.	15
Ptinus italicus	16
Xylophagus spp.	17
Megalothorax spp.	18
Calliphoridae spp.	19
Phyllobius romanus	20
Tomocerus spp.	21
Philoscia muscorum	22
Polyxenus spp.	23
Echinodera spp.	24
Kyklioacalles spp.	25
Lampyris noctiluca	26

Figure 2.8 As one emblematic example of a food web from the brown world, we show here the soil and litter arthropod network of the Monte Venere beech forest (Lake Vico, Italy) plotted using *Network*3D. Representative taxa are directly reported, other taxa are coded (IDs **1–26**) and shown in the upper legend. Node diameters of each taxon are proportional to the specific log-transformed body-mass average (μg dry weight); the mass of primary producers, leaf litter and microbes are arbitrarily set to 10 μg to improve the graph readability. Node heights are proportional to the mean δ^{15}N value of each taxon. The δ^{15}N signature of leaf litter is set at -2.13, corresponding to the signature of decaying *Fagus sylvatica* leaves sampled in the upper soil layer. An identical signature was assumed for all basal resources (i.e. primary producers, bacteria and fungi) for demonstrative purposes. The vegetation of the entire study area has been described in Scoppola et al. (1989).
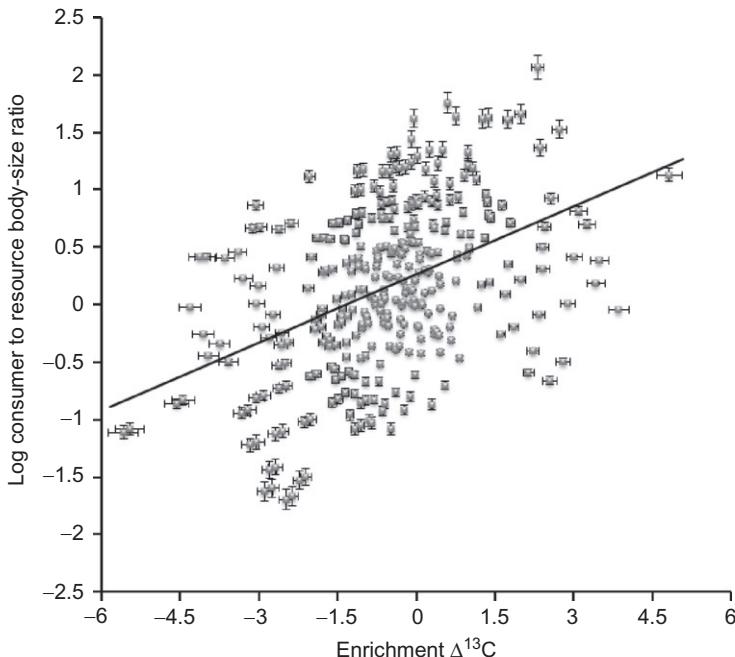
Figure 2.9 When all the invertebrates of the Vico brown web (Fig. 2.8) were examined together (plotted with error bars at 5%), the discrimination factor $\Delta^{13}C$ (horizontal axis) exhibited a positive correlation with the consumer–resource ratio of the log-transformed body-mass averages (vertical axis). This direct relationship can be regarded as very robust ($n = 336; p < 0.0000001$). Any positive $\Delta^{13}C$ indicates an enrichment of the consumer in ^{13}C against its resource, whereas any positive consumer–resource body-mass ratio indicates a (much) larger consumer (predator) than its prey.

the enrichment factor for N when we split the signal into the three energy channels: predatory invertebrates feeding on detritivores, predatory invertebrates feeding on herbivores, and predatory invertebrates feeding on other predators (depending on which guild they were assigned to according to Chinery, 1986; Demange, 1981; Dindal, 1990; Du Chatenet, 1990; McEwan Kevan, 1962; Perrier, 1923, 1929, 1930; Petersen and Luxton, 1982; Thiele, 1977). Hence, the relationship between $\Delta^{13}C$ and consumer–resource body-mass ratios is driven by predatory body-mass variation, whereas other sources of variation can influence $\Delta^{15}N$ values (Mancinelli, 2012; Traugott et al., 2013; Vanderklift and Ponsard, 2003).

In Fig. 2.10 the different types of relationship between $\Delta^{13}C$ (upper plot) and $\Delta^{15}N$ (lower plot) and the predator's body mass are shown according to
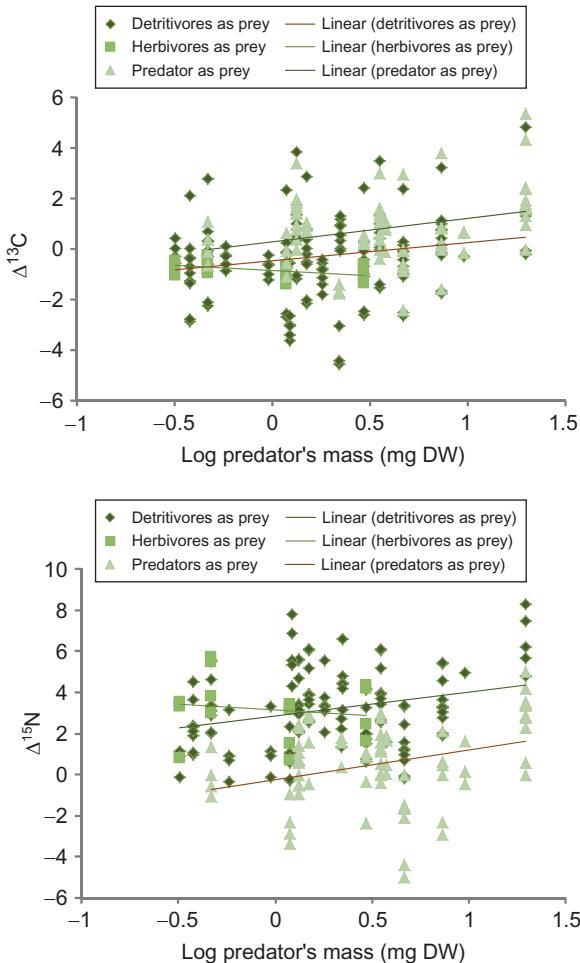
Figure 2.10 Correlations between the log-transformed body-mass values of the predatory invertebrates of the two previous figures (in mg dry weight, plotted on the horizontal axis) feeding on detritivores (filled circles), herbivores (open circles) and other predators for $\Delta^{13}C$ (upper plot) and $\Delta^{15}N$ (lower plot). Please note the inverse axes for the discrimination factors in comparison to Fig. 2.9.

the guild the prey belong to, that is, whether they are detritivores, herbivores or predators (including cannibals). Predatory arthropods tend to have a higher N content and a lower C:N ratio than their potential herbivorous prey (Martinson et al., 2008), as a negligible relationship of N content with the body size of herbivore arthropods—in contrast to a sharp inverse

relationship of C content with body size—has been reported for Cedar Creek, Minnesota (Denno and Fagan, 2003; Siemann et al., 1996; unpublished data from Siemann and Elser at the NCEAS repository). Many predators are N limited and intraguild predation may allow them to increase their N intake and growth (Denno and Fagan, 2003; Fagan and Denno, 2004; Loranger et al., 2012; Matsumura et al., 2004).

If so, the observed relationship between the enrichment factor $\Delta^{13}C$ and the consumer–resource body-mass ratio is (contemporaneously) determined by traits and behaviour: an increase in the weight (body mass) of predators occurs in parallel with an increase in the amount of prey catchable by predation. In other words, an increase in intraguild predation and cannibalism scales positively with $\Delta^{13}C$ and appears to explain the correlation in Fig. 2.9. This provides indirect evidence for increasing omnivory (Naeem and Wright, 2003): generally, large and abundant predators imply much more target prey species (Cohen, 1977; Klarner et al., 2013), in opposition to small and rare parasites (Cohen et al., 2005).

Comparable patterns are also expected to occur in below-ground trophic networks, even within a part of the soil fauna, namely the free-living nematodes. On average, consumer–resource body-size ratios are expected to be larger in aquatic systems than in terrestrial systems (Brose et al., 2006; Nakazawa et al., 2011) and indeed our ratios are rather small, although mostly positive. The consumer–resource body-size ratios along environmental gradients in Fig. 2.11 show much larger consumers than resources at either very low C:N or C:P ratios in the soil (corresponding respectively to high soil N and P values), but on average there was no consistent difference between predatory nematodes and their prey across three environmental gradients. Although the analysis by Brose et al. (2006) was based only on above-ground and aquatic organisms and did not incorporate below-ground organisms, the consumer–resource ratios for our invertebrates are consistent with the ratios for terrestrial invertebrates shown by Brose et al. (2006). This lack of large-scale fluctuations in the consumer–resource body-size ratio is not surprising. Gilljam et al. (2011) have reported consistent under- or overestimations in predator–prey systems when using species trait averages such as 'species body-size average', rather than individual body mass.

5.2. Abiotic constraints on population dynamics

Richer soils are characterised by a much greater occurrence of larger soil invertebrates, and this increasing trend in larger soil mesofauna *versus* the
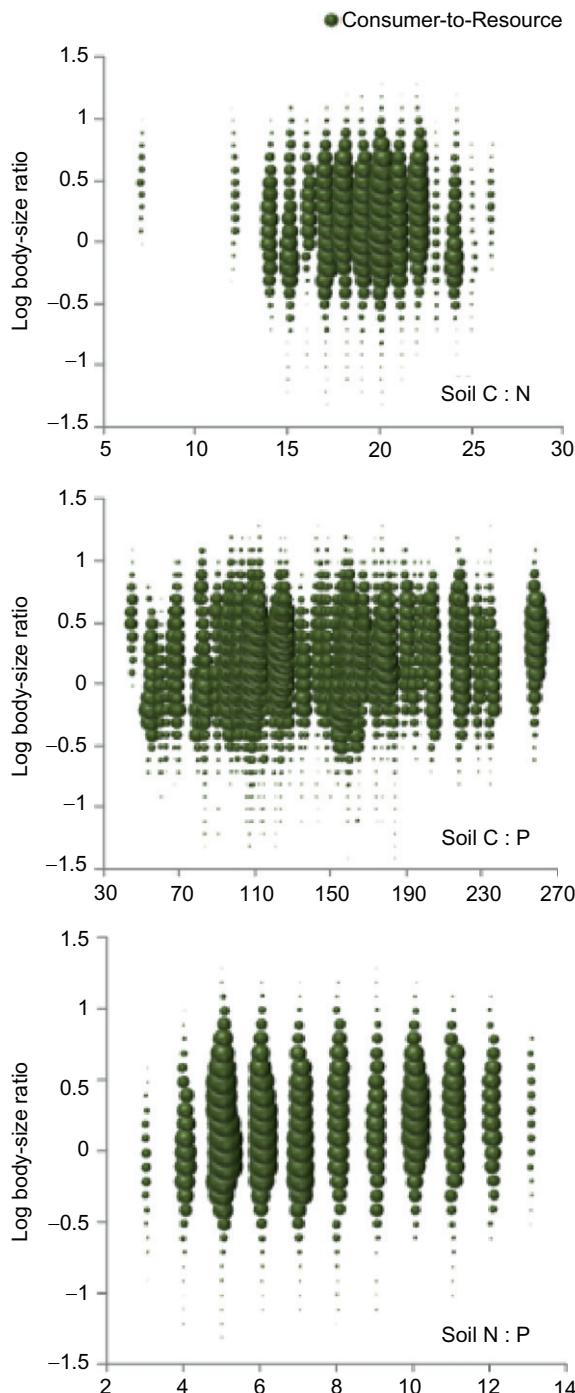
Figure 2.11—See legend on next page.
Figure 2.11 Soil food-web consumer–resource body-mass ratios computed for the
nematofauna of 75 Dutch agroecosystems on sandy soils against site-specific soil

smaller microfauna has been recorded for organic C, total N, total P (Mulder and Elser, 2009), Zn and Cu (Mulder, 2010) and soil acidity (Mulder et al., 2012). Proportions of C, N and P, soil pH and microbial and faunal abundances are closely correlated: when P was limiting, as in more acidic soils, fewer large invertebrates and more small invertebrates have been recorded on average. Such robust size dependence of the soil food web on soil nutrient contents is also expected to reflect the so-called 'threshold elemental ratio', that is, the nutrient:C ratio of a given resource below which the growth rate of the related consumer will be limited by food quality (Doi et al., 2010; Elser et al., 2000b; Mulder et al., 2009, 2011b; Sterner and Elser, 2002). Comparable increases in body size and in diversity when limiting nutrient increases are clearly recognisable also in some community evolution models (Brännström et al., 2011; Loeuille and Loreau, 2005).

The finding that such major variations in the occurrence of invertebrates can be ascribed to elemental drivers raises two important questions of relevance to agroecosystems: with increasing soil pH and higher N and P contents (lower C:element ratios), do larger-sized invertebrates become more abundant (or bigger), or do smaller-sized invertebrates become less abundant (or smaller)? And if so, what mechanisms cause the departure from common linear relationships between size and abundance, as shown by Mohr (1940)? To our knowledge, almost no previous studies have investigated intraspecific variability in soil invertebrate body shapes, aside one morphometric investigation of a single nematode species in relation to humus type and season by Arpin et al. (1988). Intraspecific variability represents a notable and important limitation to a straightforward understanding of the linkage among environmental factors, individual traits and population-scale processes (Zaccarelli et al., 2013 and literature cited therein). To understand this variability in a broader context, Mulder and

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nutrients (molar ratios). Due to the huge number of possible body-mass ratios, the high omnivory degree within a single taxocene (as here the free-living soil nematodes) seems to mask direct elemental responses, weakening their trait-driven predictability. In contrast to the litter mesofauna, where in the case of phosphorus, the detrital P production by larger invertebrates can require 20 times as much [P] as entered in the food web in form of litter (McBrayer, 1977), our soil microfauna shows no dramatic shifts in interactions. Positive log-transformed body-mass ratios imply larger consumers than resources.

Vonk (2011) built a publicly accessible database of individual measurements of >29,500 soil nematodes. Among other results, their comprehensive data show that variability in body sizes according to gender and life stage (adults or juveniles) reflects the diet and feeding behaviour of free-living nematodes and is thus an underestimated key factor that influences the multitrophic interactions of soil biota. Data from agroecosystems on sandy and clay-rich soils were used to investigate the intraspecific variability of the nematodes according to environmental drivers and life history.

Different types of eco-stoichiometrical responses can be distinguished: none (a frequent outcome for free-living nematodes with a wide ecological niche), linear positive or negative, exponential, optimum quadratic curve with $x^2 < 0$, and quadratic curve with $x^2 > 0$. Some nematodes, such as juveniles of *Aporcelaimellus* (Fig. 2.12), exhibited optima within the observed elemental range for N and P (in contrast to their nearly exponential trend along an increasing C content of their soils). Others showed either a steep linear or a log-logistic descending trend, suggesting a minimum outside the investigated environmental range.

Fungivore nematodes did not show any response to soil C, N or P, in contrast to bacterivore nematodes (*Acrobeles, Anaplectus, Eumonhystera, Panagroilaimus, Plectus*), predatory and omnivore nematodes (*Dorylaimoides, Aporcelaimellus*) and some plant-feeding nematodes. Further, the number of taxa that react to soil P was much higher than those that reacted to either C or N (Fig. 2.12). Empirical examples from literature on the P, C and N contents of detrivores show a remarkable split between the positive skew of the left-tailed distribution of P observations *versus* the negative skews of the right-tailed distributions of C and N observations (Cross et al., 2003). Hence, terrestrial invertebrates not only react directly (by foraging interactions) and indirectly (trait-mediated biotic interactions) to the environment (Moya-Laraño and Wise, 2007) and to average soil C:N:P ratios (as observed here), but are also likely to reflect in their body tissues the external P-deficiency, as predicted by ecological stoichiometry (Elser et al., 1996; Sterner and Elser, 2002).

These contrasting responses of soil nematodes to elemental factors like C, N and P help to explain why the consumer–resource body-mass ratio of nematodes shown in Fig. 2.11 did not vary markedly, as taxa can replace one another within the same functional guild. For instance, across the soil N gradient (Fig. 2.12) and to a lesser extent for C and at lower P contents, predatory nematode juveniles of the large-sized *Dorylaimoides* and the very large *Aporcelaimellus*, appeared avoid each other, with consequences
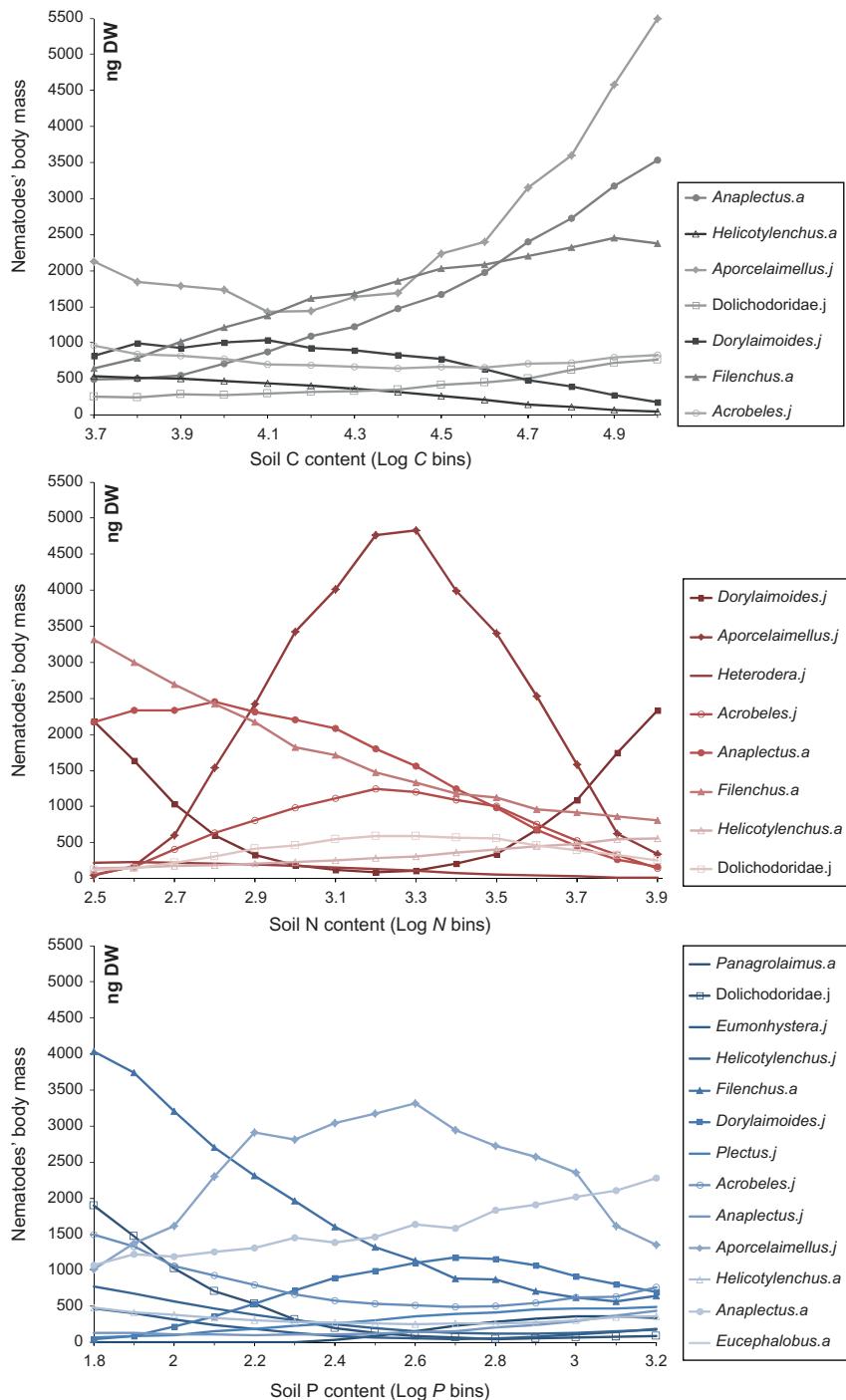
Figure 2.12—See legend on next page.
Figure 2.12 Generalised Linear Model (GLM) of dry body mass (ng) for nematodes as a function of soil C, N and P contents as log mg kg^{-1} dry matter. In contrast to Fig. 2.11,

that cascade down to consumer–resource body-mass ratios. For instance, weighted averages of the body mass of juvenile nematodes decrease significantly with increasing soil C:P ratio ($R^2 = 0.50$) and mean predatory nematodes plotted along the soil N:P ratio are significantly greater than mean detritivores (Mulder and Vonk, 2011), suggesting trait–mediated interactions between soil invertebrates under environmental limitation that may modulate the overall size distribution of the entire food web (Box 2.3).

5.3. Environmentally driven and trait-mediated networks

Most of the trophic links in agroecosystems food webs show animals preying on (abundant) organisms with a much smaller body mass than their own, but these roles vary significantly with changes in the environment, such as for mesofauna, which increases disproportionately in enriched systems (Mulder and Elser, 2009). Focusing on their faunal records from ten abandoned agroecosystems, soil nematodes (28 nodes on average) are by far the largest contributors at genus level to the network structure (47% of the edaphic food web), followed by microarthropods (16 nodes for mites and 6 for collembolans) and oligochaetes (6 nodes for enchytraeids and 3 for earthworms). Historically, network structure and interaction stability have been investigated as a function of consumer–resource body-mass ratios. In Cohen et al. (2009), the link length of a trophic chain from (eaten) resource to (predating) consumer within a food web is the number of orders of magnitude of difference in body-mass average plus the number of orders of magnitude of difference in numerical abundance between the resource and the consumer (Fig. 2.13).
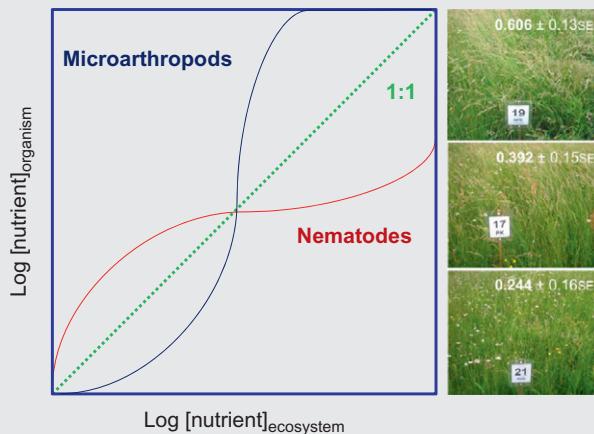
Under mesic conditions, the average trophic link length between the resource and the consumer was more than two orders of magnitude and pointed to a long bacterial pathway, *versus* a short fungal pathway under

where besides at low nutrient ratios the consumer–resource body-mass ratios of nematodes seem in most cases not sensitive to environmental predictors, the binned body-mass average of soil nematodes strongly reflects the soil C, N and P. We run a Monte Carlo simulation based on 5559 individuals measured in sandy soils and 5523 individuals measured in clay-rich soils. Please note the different responses for a same genus (in italics) according to life-history traits ('j' for juveniles and 'a' for adults).

BOX 2.3 Soil nutrients influence the size distribution of soil biota

The fate of C in both organisms and ecosystems is regulated by mass-balance and the availability of key nutrients such as N and P (Sardans et al., 2012a; Sterner and Elser, 2002). Generally, autotrophs and decomposers have higher C:nutrient ratios, and consumers have lower C:nutrient ratios (Martinson et al., 2008). All the issues previously discussed show that these factors operate at both the organismal level as well as the environmental level, and hence explain the eco-physiological and the life-history traits of not only autotrophs, but also of heterotrophs. The physiological understanding of the extent to which threshold C:nutrient ratios of a food resource (prey) above which the consumer's growth rate will be limited by the N and/or P contents of the prey may modulate the effects of stoichiometric food quality on species at different trophic levels is more important than ever (Urabe et al., 2010). Vexing interactions between any consumer's C:nutrient ratios and its maximal growth efficiency for many nutrients are known for freshwater ecosystems (Elser et al., 1988; Sterner, 1997; Sterner and Elser, 2002), although comparable evidence is rising from terrestrial ecosystems. In the case of autotrophs, Matzek and Vitousek (2009) find no clear link between N:P ratio in their tissues and the (pine) growth rate. However, in the case of many soil heterotrophs, such a link is according to Mulder and Elser (2009) not implausible and deserves further investigation under controlled environmental conditions, such as in the Ecotrons (Naeem et al., 1995; Stewart et al., 2013, and references therein). Being possibly the first test for a trait-mediated association of terrestrial webs with C:N:P stoichiometry (Peñuelas and Sardans, 2009), Mulder and Elser (2009) focused in fact on the potential size dependence of heterotrophs. As soon environmental C:P ratios decrease, a shift between smaller invertebrates (here: nematodes) and larger invertebrates (mites, collembolans and enchytraeids), differing in productivity and turnover rate, seems to occur. Hence, low productivity, infertile ecosystems, like heathlands, had on average much more nematodes than microarthropods, in contrast to high productivity, fertile ecosystems, such as abandoned meadows or managed grasslands, where much more microarthropods occurred. Besides these effects in the food-web structure, a response trait can also be detected in the life history of nematodes, whose juveniles are coping almost three times better with P-limited soils than their adults (Mulder and Vonk, 2011). Lower growth rates for juveniles under soil P-deficiency are supported by decreases in herbivory through less plant-available P (cf. Schade et al., 2003; Woods et al., 2004) and can be detectable in experimental plots: in Ossekampen (Van der Wal et al., 2009), the trait-mediated increase of total faunal biomass was more than 50% higher for NPK addition than for PK alone.

BOX 2.3 Soil nutrients influence the size distribution of soil biota—cont'd

acidic conditions (Mulder et al., 2005b). The association between trophic link length and soil pH (Fig. 2.13) is comparable to the association between faunal biomass–size scaling and soil pH (Mulder and Elser, 2009) and the robust correlations of soil taxocenes' densities with pH (Mulder et al., 2005b). Each association is more than the summary of chemical reactions to a relative concentration of $[H^+]$-ions, since soil acidity has a strong impact on nutrient availability, making pH the best independent predictor for allometric investigations in the brown world (Table 2.4). Ultimately, all together these chemical reactions act as ultimate energetic subsidy. Given that the soil is only one part of any terrestrial ecosystem, it should be stated that both heterotrophs and (above-ground) autotrophs react in a comparable way—but at different rates—to changes in their energetic subsidy. Hence, within any terrestrial ecosystem, (below-ground) biota and (above-ground) vegetation respond to the same soil stoichiometrical conditions and apparent direct responses of soil biota to vegetation or agroecosystem types should be treated with caution.

It is striking the extent to which invertebrate biodiversity, allometric scaling and food-web properties correlate with (that is, react directly to) environmental factors like pH, atmospheric N deposition, cattle manure, macronutrients like P and micronutrients like Cu. As part of the Dutch
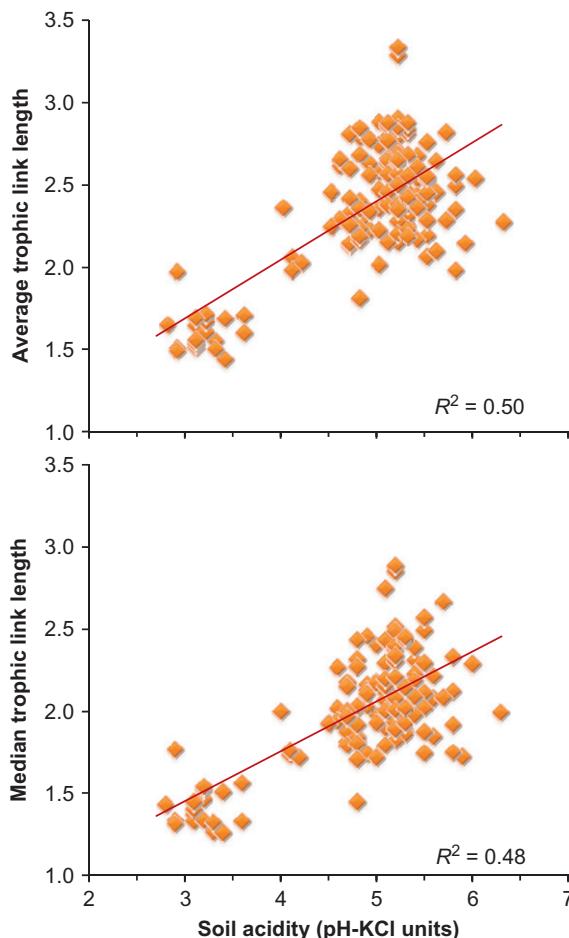
Figure 2.13 Direct correlations between soil acidity and the average (upper scatter) and the median (lower scatter) of all the possible trophic link lengths expected in 135 edaphic food webs of the same agroecosystems of Table 2.4. In a comparable way to that of Reuman and Cohen (2004), but with inversed axes, we plotted all the nodes and trophic links on ordinate $\log(N)$ and abscissa $\log(M)$. Then the length l of any trophic link from prey (resource) r to predator (consumer) c will be: $l = |\log(M_c) - \log(M_r)| + |\log(N_c) - \log(N_r)| = |\log(M_c/M_r)| + |\log(N_c/N_r)|$. This absolute length, measuring the Manhattan square-block distance between consumer c and its resource r (Cohen et al., 2009; Mulder et al., 2009, 2011a), is strongly environmentally driven ($p \leq 10^{-20}$).

Table 2.4 Empirical evidence of environmental-driven changes in taxonomic diversity, functional metrics allometric scaling and food-web structure in the edaphic webs from 135 Dutch agroecosystems belonging to the novel SIZEWEB inventory (Cohen and Mulder, 2013)

Predictors	Taxa	Pearson	Slope	Elevation	Significance	Links	Density	5th TLL	Average TLL	95th TLL
Soil pH	**−0.64287**	**−0.58288**	**−0.5031**	**0.60639**	**0.53646**	**−0.54326**	**−0.35567**	**0.41167**	**0.70636**	**0.50969**
	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Organic matter	**−0.24188**	**−0.15571**	**−0.21962**	**0.07127**	**0.17081**	**−0.28354**	**−0.3727**	**0.01287**	**0.31177**	**0.32519**
	0.0047	0.0713	0.0105	0.4114	0.0476	0.0009	<0.0001	0.8822	0.0002	0.0001
Airborne nitrogen	**0.27514**	**−0.04823**	**0.16322**	**0.18662**	**0.05045**	**0.37465**	**0.49533**	**0.13708**	**−0.16928**	**−0.13968**
	0.0012	0.5785	0.0586	0.0302	0.5612	<0.0001	<0.0001	0.1129	0.0497	0.1062
Total soil nitrogen	**0.02277**	**−0.24729**	**−0.03394**	**0.30176**	**0.22297**	**0.1304**	**0.25267**	**0.22825**	**0.12397**	**0.08669**
	0.7933	0.0038	0.6959	0.0004	0.0093	0.1317	0.0031	0.0078	0.152	0.3174
Manure input	**0.01905**	**−0.24804**	**−0.03642**	**0.30097**	**0.22354**	**0.12596**	**0.24727**	**0.2276**	**0.12708**	**0.08921**
	0.8264	0.0037	0.6749	0.0004	0.0092	0.1455	0.0038	0.0079	0.1419	0.3035
Water P content	**−0.44831**	**−0.3413**	**−0.39314**	**0.15414**	**0.30813**	**−0.3765**	**−0.3108**	**0.02833**	**0.41095**	**0.46839**
	<0.0001	<0.0001	<0.0001	0.0743	0.0003	<0.0001	0.0002	0.7443	<0.0001	<0.0001
Soil P	**−0.46615**	**−0.4954**	**−0.42739**	**0.3512**	**0.45232**	**−0.35264**	**−0.19987**	**0.17237**	**0.4776**	**0.4148**
	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.0201	0.0456	<0.0001	<0.0001

Continued

Table 2.4 Empirical evidence of environmental-driven changes in taxonomic diversity, functional metrics allometric scaling and food-web structure in the edaphic webs from 135 Dutch agroecosystems belonging to the novel SIZEWEB inventory (Cohen and Mulder, 2013)—cont'd

Predictors	Taxa	Pearson	Slope	Elevation	Significance	Links	Density	5th TLL	Average TLL	95th TLL
Soil Cr	−0.28416	−0.23598	−0.21602	0.31707	0.21235	−0.22367	−0.12466	0.15418	0.28138	0.15585
	0.0008	0.0059	0.0119	0.0002	0.0134	0.0091	0.1497	0.0742	0.0009	0.0711
Soil Cu	−0.45042	−0.35174	−0.44273	0.2101	0.3069	−0.3876	−0.31429	0.09858	0.49042	0.4449
	<0.0001	<0.0001	<0.0001	0.0145	0.0003	<0.0001	0.0002	0.2553	<0.0001	<0.0001
Soil Hg	−0.11262	0.00309	−0.15635	−0.07575	−0.0228	−0.11985	−0.16776	−0.16242	0.07357	0.0438
	0.1934	0.9716	0.0702	0.3826	0.7929	0.1662	0.0518	0.0598	0.3964	0.614
Soil Pb	0.12485	0.23142	0.04717	−0.31519	−0.25484	0.08619	−0.01032	−0.25854	−0.16532	−0.10552
	0.1491	0.0069	0.587	0.0002	0.0029	0.3203	0.9054	0.0025	0.0553	0.2232
Soil Zn	−0.36638	−0.28751	−0.32546	0.32115	0.24002	−0.28775	−0.19462	0.20789	0.41724	0.34614
	<0.0001	0.0007	0.0001	0.0001	0.005	0.0007	0.0237	0.0155	<0.0001	<0.0001

Relevant predictors (environmental drivers) at the left column, web descriptors at the upper row: Taxa (taxonomically identified soil invertebrates), Pearson's correlation of the mass–abundance scaling of the taxa occurring within one edaphic food web, log–log linear regression slope of the mass–abundance values of the taxa within one edaphic food web, elevation (intercept) of the aforementioned linear regression, significance (R^2) of the aforementioned linear regression, expected trophic links to be realised, linkage density (ratio of the expected trophic links divided by observed taxa), 5th TLL percentile of the trophic links' lengths, average TLL of all possible trophic links' lengths, 95th TLL percentile of the trophic links' lengths.

Predictors	Min. log(N)	Log (average N)	Max. log(N)	Log (summed N)	Min. log(B)	Log (average B)	Max. log(B)	Log (summed B)
Soil pH	−0.34251	0.72265	0.57073	0.64926	0.30127	0.54955	0.36408	0.43102
	<0.0001	<0.0001	<0.0001	<0.0001	0.0004	<0.0001	<0.0001	<0.0001
Organic matter	−0.07302	0.28468	0.32963	0.24438	0.04114	0.0202	−0.01247	−0.03705
	0.4	0.0008	<0.0001	0.0043	0.6357	0.8161	0.8859	0.6697
Airborne nitrogen	−0.2336	−0.03451	−0.08109	0.06247	0.12077	0.27369	0.31887	0.3435
	0.0064	0.6911	0.3498	0.4717	0.1629	0.0013	0.0002	<0.0001
Total soil nitrogen	−0.341	0.22577	0.14936	0.28472	0.11573	0.485	0.48509	0.50521
	<0.0001	0.0085	0.0838	0.0008	0.1813	<0.0001	<0.0001	<0.0001
Manure input	−0.33965	0.22762	0.15138	0.28557	0.11473	0.48409	0.48354	0.50344
	<0.0001	0.0079	0.0797	0.0008	0.1852	<0.0001	<0.0001	<0.0001
Water P content	−0.21547	0.38452	0.41108	0.30201	0.15277	0.15677	0.03664	0.06404
	0.0121	<0.0001	<0.0001	0.0004	0.0769	0.0694	0.6731	0.4606
Soil P	−0.36243	0.50029	0.42865	0.44285	0.24972	0.40243	0.26464	0.31659
	<0.0001	<0.0001	<0.0001	<0.0001	0.0035	<0.0001	0.0019	0.0002

Table 2.4 Empirical evidence of environmental-driven changes in taxonomic diversity, functional metrics allometric scaling and food-web structure in the edaphic webs from 135 Dutch agroecosystems belonging to the novel SIZEWEB inventory (Cohen and Mulder, 2013)—cont'd

Predictors	Min. log(N)	Log (average N)	Max. log(N)	Log (summed N)	Min. log(B)	Log (average B)	Max. log(B)	Log (summed B)
Soil Cr	−0.12525	0.36746	0.35383	0.34533	0.09868	0.2336	0.12687	0.18191
	0.1478	<0.0001	<0.0001	<0.0001	0.2548	0.0064	0.1426	0.0347
Soil Cu	−0.22463	0.55229	0.59741	0.50357	0.08665	0.24499	0.13173	0.15595
	0.0088	<0.0001	<0.0001	<0.0001	0.3176	0.0042	0.1278	0.0709
Soil Hg	0.08874	0.1537	0.26432	0.13869	−0.00448	−0.11898	−0.15137	−0.14808
	0.3061	0.0751	0.0019	0.1087	0.9589	0.1693	0.0797	0.0865
Soil Pb	0.17922	−0.0579	0.16125	−0.02905	−0.1927	−0.19172	−0.16273	−0.17036
	0.0375	0.5048	0.0617	0.738	0.0251	0.0259	0.0593	0.0482
Soil Zn	−0.12743	0.52556	0.53456	0.50308	0.12885	0.35265	0.24281	0.28504
	0.1408	<0.0001	<0.0001	<0.0001	0.1364	<0.0001	0.0045	0.0008

Relevant predictors at the left column, same drivers as before, but other web descriptors at the upper row: Min. log(N) as smallest log population density recorded ($\#m^{-2}$), log(average N) of all recorded population densities ($\#m^{-2}$), max. log(N) as largest log population density recorded ($\#m^{-2}$), log(summed N) as log of the total number of all the soil invertebrates recorded in one square metre, min. log(B) as smallest log estimated biomass ($\mu g\ m^{-2}$), log(average B) of all estimated biomass ($\mu g\ m^{-2}$), max. log(B) as largest estimated biomass ($\mu g\ m^{-2}$), and log(summed B) as log of the total estimated biomass values of all the soil invertebrates (μg dry weight m^{-2} soil).

All Pearson's correlation values are given in bold, p–values in the corresponding cells below. There is no evidence for any kind of 'universal' allometric scaling in these 135 food webs under different environmental conditions, being soil pH (F-ratio 93.68, $p < 0.0001$) and airborne N (atmospheric) deposition (F-ratio 23.14, $p < 0.0001$) the best predictors forecasting soil biodiversity in a stepwise regression. All computations performed in SAS 9.3.

Soil Quality Network (Mulder et al., 2011b; Rutgers et al., 2009), we recorded the occurrence of 258 soil invertebrates in agroecosystems under different types of land-use management, together with community and environmental descriptors for each site and selected 135 edaphic food webs (Table 2.4); the complete data and individual cases will be discussed elsewhere. These data directly link chemical soil composition and atmospheric N deposition to the mass–abundance scaling of differently sized soil invertebrates and demonstrate for the first time that the allometry of entire soil biota definitively *relates* to soil abiotics and, hence, *changes* according to the local energetic subsidy.

6. ANTAGONISM ABOVE, MUTUALISM BELOW: NATURE OR AGRICULTURE?

Interannual fluctuations in soil C:N:P ratios have been described in previous work (Parton et al., 1988; Schimel et al., 1991, 1996) and confirmed at global scales by meta-analyses (Cleveland and Liptzin, 2007; Sardans et al., 2012a,b). Hence, the global amount of mobilisable stocks, and the sufficiency and long-term capacity of P reserves to support food productions (Pretty et al., 2010), in addition to local, patchy occurrences of soil, litter and foliar P (ranging in dry foliar tissues between 0.001‰ and 0.419‰) should be of concern for ecosystem functioning and productivity. Organisms react to (and reflect the) elemental availability of their environment in several ways. Mutualism below-ground occurs (i) when stoichiometric constraints of different organisms are governed by independent components (e.g. mycorrhizae, rhizobia and even parasitic plants influencing below-ground properties, as those described in Bardgett et al., 2006) and (ii) where a trophic level can be excluded by commensalism (microbial symbionts of leaf cutter ants, termites; cf. Mueller et al., 2005). For instance, mycorrhizae not only envelop roots and help plants to acquire nutrients, receiving carbon from their hosts in return, but they also enable arthropods to deal better with resources of low elemental profile and provide resources to hyphal-feeders. In the brown world, the entire fungal network is by far the largest-sized taxon. For any mycelium, the most important macroscopic parameter is biomass, as hyphal length is hard to measure although it is mostly seen as proportional to total fungal biomass (Moore et al., 2005). Mycelia are important exceptions to the classical food–web theories of size-mediated trophic distribution of organisms occurring in the brown world.

6.1. Stoichiometry and mutualism in an exploited world

Plant growth in terrestrial systems is limited by light, water and nutrients. N availability in soils plays a particular role among these constraints because it is of biogenic origin and, as can be seen in succession studies, it is more economical for plants to gather N that has been fixed by other organisms. Only a few microorganisms have evolved to fix N from the atmosphere via an energy-demanding process, so N pools in ecosystems accumulate slowly. When inorganic N finally becomes available during decomposition processes, it is highly mobile and prone to be lost through leaching. Available P is regulated in a comparable way, since inorganic P regulates organic matter accumulation only in the initial stages of soil formation, and P is being recycled in its organic form during progressive stages of soil formation (Cole and Heil, 1981; Walker and Syers, 1976).

As nutrient availability governs ecosystem productivity under a given climate, maintenance and conservation of the nutrient pool remains a fundamental driving force during the evolution of ecosystems. If we compare ecosystems at high and low latitudes, the size and conservation of nutrient pools are strikingly different, given that the accumulation of organic matter in soils becomes an increasingly important reservoir at higher latitudes (Heal and Ineson, 1984). As a result of N and P turnover process (Heal and Ineson, 1984; Schlesinger, 1977), despite a roughly comparable litter input in temperate grasslands and temperate forests (7.3 vs. 8.5 t ha^{-1} year^{-1}, respectively), grasslands have double the amount of SOM as temperate forests (220 vs. 120 t ha^{-1}, respectively), whereas tropical forests have by far the highest litter input (15.8 t ha^{-1} year^{-1}) but share with the desert biome one of the lowest SOM (80–85 t ha^{-1}).

The extremely low SOM average of tropical forests, despite their high litter input, makes the worldwide deforestation in a desperate attempt to gain land for human and agricultural purposes hardly understandable. Under tropical conditions, a year-round biologically active temperature regime together with intensive precipitation speeds up decomposition processes (Woomer et al., 1994, Aerts, 1997). Therefore, dead organic matter does not accumulate in large quantities and nutrients are released rapidly in tropical humid ecosystems (Lodge et al., 1994). Consequently, soils in tropical humid systems are often highly weathered and prone to nutrient leaching (Kuyper, 2012), surely after logging roads (cf. Struebig et al., 2013). In general, in many tropical ecosystems the degree of N retention has achieved a stage where productivity is limited by the availability of P instead of N,

a plant–soil interaction supported by the dominance of particular mycorrhizal types in different biomes (Read, 1991; Vargas et al., 2010), but mostly not in their fragile agroecosystems.

The great majority of net primary production enters the soil system as plant litter, rather than being consumed by herbivores (Cebrian, 1999; McNaughton et al., 1989). Goverde et al. (2000) observed that plant N concentrations differed between mycorrhizal-infected and non-mycorrhizal legumes and in combination with C and P, these factors affected the larval development of Lepidoptera that fed on leaves of mycorrhizal N_2-fixers. The general understanding of successful mutualism as in the case of plant–mycorrhizae associations is of greatest importance for land-use management, agroforestry and biological control. Such infections may affect plant efficiency, leaf chemical defences and species competition, with cascading effects at higher trophic levels. Arbuscular mycorrhizae (AM) are possibly the most widely investigated symbiontic fungi. On one hand, AM fungi are applied in silviculure and agriculture, as they enhance the biomass productivity and reduce pathogenic diseases (Jeffries and Dodd, 1991; Sharma et al., 2005), where on the other hand the biodiversity of AM fungi is known to decrease in agroecosystems (Helgason et al., 1998; Johnson, 1993). Hence, the recent overview by Chagnon et al. (2013) on the trait-mediated consequences of AM traits for ecosystem functioning in the perspective of the well-known C-S-R plant strategies of Grime (1979) will help to understand how to increase on a sustainable basis crop yields and keep restored plant communities stable (Fig. 2.14).

After an extensive analysis of global relationships between N availability and foliar $\delta^{15}N$, Craine et al. (2009) suggest that (i) warm and dry sites have higher N availability than cold and wet sites, (ii) plants with high N concentrations are expected to occur in locations with high N supply and (iii) N availability tends to become high in sites with low P availability. To a certain extent, this reflects in part the biogeography of mycorrhizal-dominanted vegetation types (Read, 1991; Vargas et al., 2010). In the Mediterranean areas, decomposition is often hampered by climatic conditions and a larger fraction of dead plant material accumulates (Jobbágy and Jackson, 2000), forming a humus layer with low but constant nutrient release. There, high SOM contents have enabled the evolution of stronger consumer–resource interactions between plants and nutrient pools, which are facilitated by plant–fungus–soil interactions (Tahovská et al., 2013). Tree species have been shown to create soil conditions that enhance decomposition of their own litter (Ayres et al., 2009a,b; Vivanco and Austin,
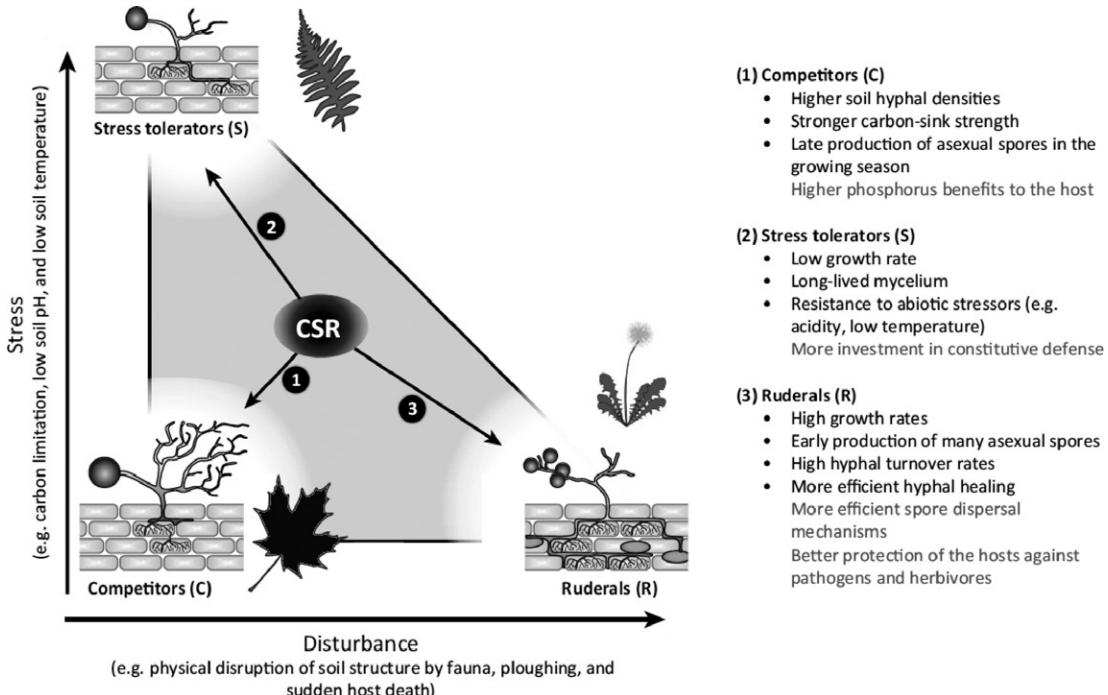
Figure 2.14 Grime's Competitors–Stress tolerators–Ruderals triangle for arbuscular mycorrhizal (AM) fungi according to their resistance to stress and disturbance factors as well as their phenotypic traits. At the right, traits empirically observed with a bullit; other traits expected by Chagnon et al. (2013) in light grey. *Figure reprinted with permissions from the authors and from Cell.*

2008). Symbioses with ericoid- and ecto–mycorrhizae, which have the ability to break down organic matter, enable certain plants to monopolise their litter resources at higher latitudes, whereas this ability is absent in AM fungi at lower latitudes (Hättenschwiler and Vitousek, 2000; Kraus et al., 2003).

6.2. Antagonism and mutualism: Implications for agroforestry

In the absence of earthworms, such as in boreal forests, the largest part of fresh organic matter consists of soil microbes (Högberg and Högberg, 2002). Coniferous forests of higher latitudes, where only few plant species dominate, may have >1000 species of ectomycorrhizal fungi (ECM). The narrow range of plant hosts and the high diversity of ECM can be assumed to enable a more efficient utilisation of resources by the host plant (Perry et al., 1989). In contrast, <25 species of AM fungi have been found in deciduous forests of lower latitudes that contain more than 1000 plant species (Allen et al., 1995; Janos, 1992). Since different species may be linked by the same mycorrhizal network, resources may be transferred from one plant to another through hyphal linkages. It seems plausible that shifting resources from one plant to another may decrease competition between different host plants (Read et al., 1985). This is important since the release of enzymes by ECM increases the uptake capacity of organically bound nutrients (Allen and Allen, 1990) and directly links the host plant to the N sources in organic soils (Cleveland and Liptzin, 2007; Hättenschwiler and Vitousek, 2000; Michelsen et al., 1996; Vargas et al., 2010). Although AM fungi are not able to mineralise N from organic matter on their own, their extraradical hyphae are highly efficient in the acquisition and translocation of inorganic N to host plants (Govindarajulu et al., 2005; Hodge and Fitter, 2010). In addition, AM fungi can be spread by soil microarthropods, some of which are known to be specialised dispersal agents (Klironomos and Moutoglis, 1999). On the other hand, the network of AM fungi can become disrupted with damage for the seedlings of tree hosts by invasive herbs and forbs colonising the understory (Stinson et al., 2006), with dramatic and unclear consequences for agroforestry.

Mycorrhizal root N concentration and root respiration vary across tree hosts (Trocha et al., 2010) and vary even more with root depth (Lindahl et al., 2007), as changes in soil N availability with soil depth have been reported in boreal coniferous forests (Fig. 2.15). Divergent soil C:N ratios in C-rich soils in boreal Europe are also supported by previous studies addressing the mean annual temperature, as forests in cooler climates leach
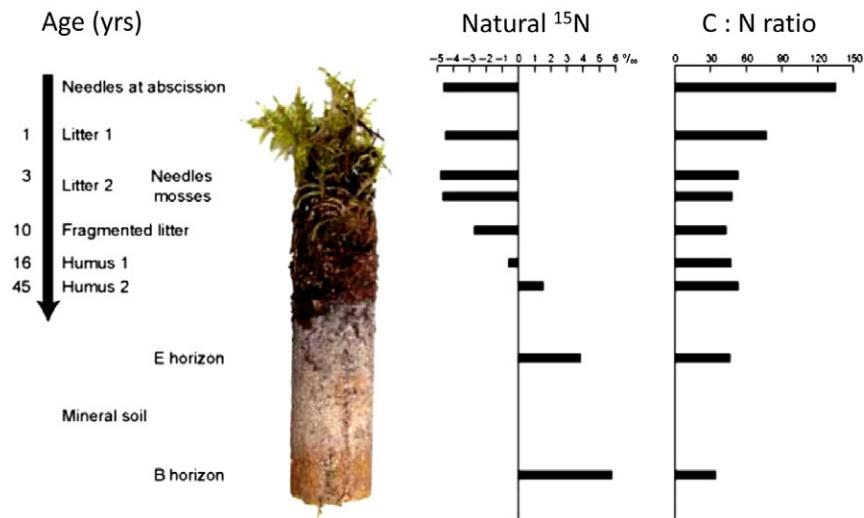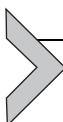
Figure 2.15 Changing of litter and soil elemental qualities throughout an upper soil profile from one boreal forest in Swedish Jädraås at 60°49′ N 16°30′ E. From left to right, age in years, increasing with depth (estimated from the ^{14}C-average of three samples from each horizon), litter and soil C:N ratios and natural ^{15}N abundance. *Redrawn from Lindahl et al. (2007).*

more N than forests in warmer climates (Dise et al., 2009). A soil C:N ratio changing further with depth (Jobbágy and Jackson, 2000; Lindahl et al., 2007) can explain the vertical differences in δ^{15}N values observed by Scheu and Falca (2000) and Uchida et al. (2004) between epigeic earthworms (exploiting fresh litter) and endogeic earthworms (exploiting decomposed resources) and is likely to influence nutrient cycling. One caveat regarding nutrients changing vertically is the co-variance with other parameters that vary with depth, such as moisture, temperature, pH and soil texture (Jobbágy and Jackson, 2000), although such trends in nutrients are less evident in agroecosystems due to tillage and ploughing.

Simple but comprehensive models, like the carbon–nutrient balance hypothesis, show the lack of evidence for an optimal plant defence due to allocation to secondary metabolites and decreased palatability (Hamilton et al., 2001), but the complexity of multitrophic interactions occurring in the green world, especially in the presence of specialised networks or at extreme environments, may re-open the discussion on the role of secondary

metabolites in plant tissues. Further, C:N changes with soil depth (Fig. 2.15), vertically stratified foliar δ^{13}C changes in trees (e.g. Crowley et al., 2012) and significant increase in δ^{13}C values with soil depth under grasslands (e.g. Briones and Bol, 2003) are all consistent with the idea of several trait-mediated horizontal levels of co-existing networks with independent eco-stoichiometry and specific mutualism or antagonism. For instance, direct and indirect interactions between fine plant roots and organisms at different soil depth stimulate growth of plants and invertebrate herbivores (Bonkowski, 2004; Hausmann et al., 2003; Moles et al., 2011; Scheu and Setälä, 2002), in a comparable way to plant–arthropod interactions above-ground (e.g. larvae feeding on foliage but adults pollinating flowers).

7. SCALING STOICHIOMETRY PROVIDES A BRIDGE TO ECOSYSTEM PROCESSES

In the previous sections, attention has been given to the stoichiometry of the green world (including leaves, stems, fruits and related invertebrates) and the brown world (including litter, seed bank, living roots and soil organisms). As shown, the stoichiometric approach is a useful framework to understand relationships between various trophic levels: this can be relevant for the energy that becomes available when heterotrophic organisms from one trophic level consume organisms belonging to lower levels (Coleman, 1985; Hunt et al., 1987). Shortly, it turns out that there is a strong correlationship between ecological stoichiometry and traits associated with resource use, acquisition strategy, enhanced transport and nutrient supply in the soil.

One of the main outcomes in our overview is the potential to use stoichiometric parameters as key biological indicators of community composition and functioning in soil food webs, facilitating the assessment and prediction of possible responses of soil systems to (human–induced) changes in nutrient availability. Hence, in contrast to the assumption that allometric scaling is not useful for understanding small differences among similarly sized plants (cf. Enquist et al., 1998, 1999), we show that within comparable sites, merging allometry with ecological stoichiometry provides an invaluable tool for understanding diverse phenomena like individual growth and nutrient cycling in soil biota. Our results on the chemical composition of autotrophs and heterotrophs lead us to believe that as soon as these resources are subject to elemental changes in their environment, cascading effects at higher trophic level might occur.

7.1. Top-down or bottom-up: The squaring of the nutrient cycle

Contrasting empirical trends between pristine ecosystems and agroecosystems lead to a friction between ecologists dealing with either the 'bottom–up' view or the 'top–down' view. Size distribution and habitat–response relationships of plants, fungi, bacteria, protists and animals in terrestrial ecosystems have traditionally been studied separately, making the general detection of responses difficult. Can actually body size forecast how organisms are enhancing nutrient fluxes or become affected by stoichiometric imbalances according to ecological stoichiometry? Based on the recent overview by Sardans and Peñuelas (2012), where acidification as a driver was supplemented with the expected cascading effects in the soil biota (Tables 2.4 and 2.5), the strong correlations between environmental drivers, plant traits, soil parameters and faunal traits are undeniable. Besides global warming and invasive plants, N eutrophication due to agricultural intensification and atmospheric deposition is a very important driver (Box 2.4).

Decomposition of the organic material is dependent on litter C:N ratio (Gundersen, 1991), litter and foliar N content and C:N ratios are correlated with each other (Fig. 2.5) and both C and N provide isotopic signatures to the food web (Figs. 2.8–2.10). However, this cycle is disturbed by external N, such as N from livestock manure—which varies depending on grazing intensity, livestock species and breed and has a European mean of $40 \, \text{kg N ha}^{-1}\text{year}^{-1}$ (De Vries et al., 2011; ERM, 1999)—and also from atmospheric deposition (Box 2.4). High N deposition can affect supporting ecosystem services by reducing biodiversity and enhance some provisioning ecosystem services by increasing wood production (Aherne and Posch, 2013). Changes in soil C:N:P ratios, such as those driven by increasing atmospheric N deposition, CO_2, and torrential rainfall (Hunt and Wall, 2002; Sardans and Peñuelas, 2007; Wardle et al., 1998), are robust predictors for trait-mediated cascading effects in faunal biomass distribution (Table 2.5). Likely, it is time to stop with the idea of a 'donor system' dominated by microbial processes, as microbial biomass as a whole is highly sensitive to ecological stoichiometry (Fig. 2.7). Thus, it is no more a chicken-and-egg caveat between the green and the brown world, but one single global process.

Detritus-based, edaphic food webs are considered to be donor-controlled (*sensu* Pimm, 1982), with their basal resources regulating primary consumers abundances (e.g. Tiegs et al., 2008; Wallace et al., 1999). As such,

Table 2.5 Major couplings between global warming, plant invasion, soil acidification and N eutrophication (change drivers), plant responses and soil biota (meta-analyses by Sardans and Peñuelas, 2012 (vascular plant–soil interactions), Sardans et al., 2012a,b (change drivers and responses), Bobbink and Hettelingh, 2011 (critical loads of N), and Naeem et al., 1995; Reich et al., 2005; Mulder and Elser, 2009; Griffiths et al., 2012; Vasseur et al., 2012; Cotrufo et al., 2013; Vonk and Mulder, 2013 (empirical data and frameworks))

Change drivers	Vascular plant responses	Elemental changes in soil	Cascading effects in soil
Warming (temperate and cold/wet environments)	↑ Plant production and growth (but the effects can be negative in short, extreme warming events)	↑ Soil enzyme activity, counteracting the negative effect of litter production with higher C:N and C:P ratios	↑ Bacterial population and microbial C, increased fungal sporulation, plant pests
	↑ Plant C:N and C:P ratios	↑ Soil C:N and C:P ratios	↓ Earthworms in extreme warming events
	↑ Plant investment in N and P uptake	↓ Decrease of N and P availability	↓ Microarthropods and enchytraeids
Warming (hot/dry environments)	↑ Plant growth	↓ Soil enzyme activity and nutrient cycling	↑ Bacterial population and microbial C
	↑ Plant C:N and C:P ratios by increase in the presence of C-rich structures linked to water stress avoidance; no significant effects on plant N:P ratio	↑ Soil C:N and C:P ratios	↓ Earthworms
		↓ Decrease of N and P availability	↓ Microarthropods and enchytraeids
Invasive plants on nutrient-rich soils	↑ Success of (weed) species with higher growth rates, low C:N and C:P ratios, fast plasticity in resource acquisition, and high reproductive investment	↑ N and P soil concentrations and availability as well as nutrient cycling	↑ Macroarthropods (carabids), seed consumption by granivorous beetles
		↑ N leaching	↑ Ammonia-oxidising bacteria and archaea
Invasive plants on nutrient-poor soils	↑ Success related to conservative use of resources	↓ P availability reduces the	↓ Microarthropods and consequently less (passive)

Continued

Table 2.5 Major couplings between global warming, plant invasion, soil acidification and N eutrophication (change drivers), plant responses and soil biota (meta-analyses by Sardans and Peñuelas, 2012 (vascular plant–soil interactions), Sardans et al., 2012a,b (change drivers and responses), Bobbink and Hettelingh, 2011 (critical loads of N), and Naeem et al., 1995; Reich et al., 2005; Mulder and Elser, 2009; Griffiths et al., 2012; Vasseur et al., 2012; Cotrufo et al., 2013; Vonk and Mulder, 2013 (empirical data and frameworks))—cont'd

| Change drivers	Vascular plant responses	Elemental changes in soil	Cascading effects in soil
		probability of success by N_2-fixing plants	dissemination of microbes with consequences on soil decomposition rate
Acidification	↓ Plant growth, decrease of foliar Ca	↓ P and Ca biologically available, counteracting in part the increased availability of Al (enhanced by acidity)	↓ Bacteria and plant–parasitic nematodes (but higher relative contribution of nematodes to the total fauna), earthworms tend to disappear in acidic soils, and enchytraeids become rare
	↑ Plant competition intensity and mycorrhizal symbioses	↑ C sequestration, less soil fertility	↑ Total fungal biomass (incl. melanised hyphae) and total arthropods, with increased feeding preferences of grazing microarthropods
N eutrophication	↑ Above-ground growth and increase in shoot/root ratio	↑ Soil respiration and accumulation of recalcitrant C	↓ Extramatrical mycelium, reduced total microbial biomass
	↑ Plant investment in P uptake	↑ P availability, increasing P-limiting role	↓ Mesofaunal abundance (oribatids, gamasids, collembolans), but higher biodiversity
	↑ Plant N:P ratio (↓ C:N ratio)	↑ Soil N:P ratio (↓ C: N ratio)	↓ Earthworms
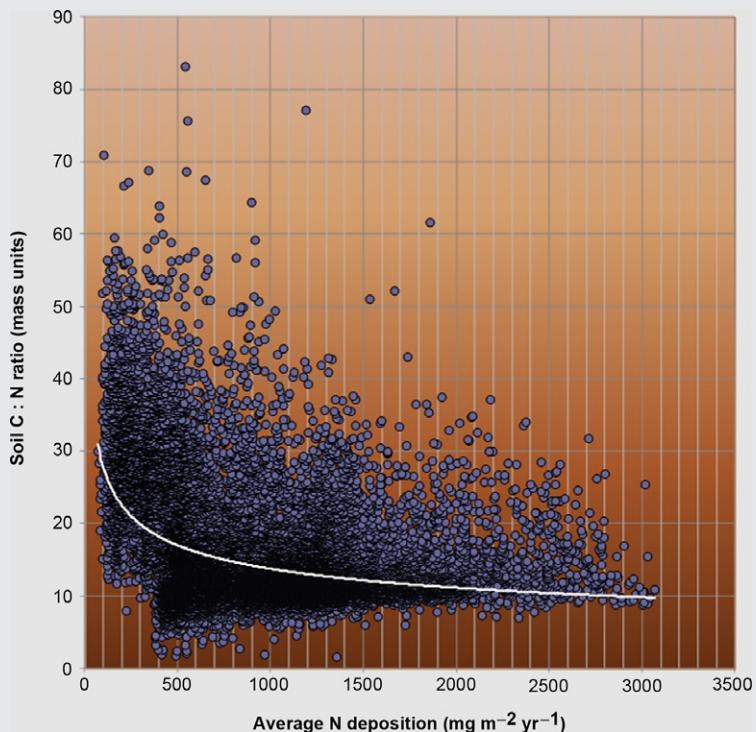
BOX 2.4 Atmospheric N deposition and soil C:N ratios

Identification of empirical C:N values that are supposed to be critical for life-supporting functions as described in ecological stoichiometry is challenging, surely at a continental scale. Nutrient cycling, in fact, is closely related to the elemental composition of living biomass (Elser, 2006) and energy flows in the brown and green worlds differ considerably. Given for example the huge differences in the C:N ratio of mycorrhizal tissues and woody stems (from 10 up to 400, Sterner and Elser, 2002), the synergy between biological and ecological stoichiometry is expected to provide novel tools to show how tolerant a consumer of a given size can be for a resource of poor elemental quality (Elser et al., 2000a,b; Urabe et al., 2010). To achieve this, we selected C:N data from a European Soil Survey of 2009 known as LUCAS (Land Use/Cover Area frame statistical Survey). During this field survey of the European Commission, collected samples, weighing in total ~11 tonnes, were sent to JRC (Ispra, Italy) and stored in the European Soil Archive Facility. The total C and N concentrations were measured in soils of 30 cm, including >8000 agroecosystems. As in other parts of our chapter, we recorded strongly fluctuating soil C:N ratios (coefficient of variation > 50%), but the C:N ratio approaches the overall average of 16.2 in mass units. In temperate European grasslands, as in the case of vegetation belonging to the class E of the European Nature Information system (EUNIS), N is typically seen as limiting element in meta-analysis depicting production under N enrichment (González et al., 2010). Hence, given that a negative effect of atmospheric N deposition on soil C:N is likely and seen that soil C:N contributes to determine the physiological success of forbs, herbs and grasses, it seems to us valuable to verify the extent to what the soil is 'buffering' the atmospheric N deposition. A correlation between atmospheric N deposition and soil C:N would be a stoichiometric constraint which might affect the productivity of ecosystems and hence the entire conversion efficiency from resources to consumers. Following the tradition of using data to refine and strengthen ecological models, we merged two continental data sets together, mining ~19,500 geo-referenced soil samples from croplands and other locations collected in 2009 across Europe for LUCAS (vertical axis) with average atmospheric N deposition values at the same sites (horizontal axis) estimated over a decade (2000–2009) calculated according to the emission and deposition values of www.emep.int (Hettelingh et al., 2013; Posch et al., 2012). The EMEP chemical transport model developed at the Meteorological Synthesizing Centre (MSC-W), hosted at the Norwegian Meteorological Institute, was concerned with the regional atmospheric dispersion and deposition modelling of acidifying and eutrophying compounds (here: nitrogen). This model allows not only forecasting either a site-specific N eutrophication or an increasing N limitation (De Vries and Posch, 2003), but also trait-mediated species-specific elemental changes in organismal tissues and in their community. Chapin (1980) and Wright et al. (2001) have shown that plant species from nutrient-poor soils generally have lower foliar N (and P) than those from nutrient-rich soils. In addition, in our Section 2.4.2 a certain degree of microbial plasticity has been reported (microbial biomass C, N and P contents reflect environmental changes in the soil), as in the studies by Tezuka (1990) and Griffiths et al. (2012). Assuming that all organisms depend on a steady nutrient to carbon supply, the negative power fit between

Continued

BOX 2.4 Atmospheric N deposition and soil C:N ratios—cont'd

the modelled driver N deposition and the empirical soil C:N ratios can be interpreted as a kind of 'site sensitivity distribution' for almost 20,000 locations. Despite the scatter due to the log-normal distribution common in large datasets (Cleveland and Liptzin, 2007; Kattge et al., 2011a), a global atmospheric signal beyond different ecosystems (croplands, grasslands, heathlands, woodlands) becomes detectable. As soon as we remove the Studentized outliers (Residuals $> |2|$), the entire statistical significance increases from 21% up to 32.4% (R^2), providing a method that can be helpful for detecting sites below growth-limiting threshold elemental ratios across Europe (Fig. 2.A2). If we can ascribe a certain location to either an ongoing N eutrophication or to an increasing N limitation, such an approach might be useful for European Commission policy-decision makers and stakeholders and it will be a true challenge to explore whether ecological stoichiometry can provide the necessary endpoints for a trait-based assessment of environmental effects of atmospheric N deposition on both nature as agriculture. Such a widespread atmospheric N deposition could among others inhibit the light isotopic signature of N fixation *in situ* (Elser, 2011), with consequences for (legume) crops, even causing nutrient imbalances in trees (Schulze, 1989; Vitousek et al., 1997).

they appear incompatible with cascade propagation, at least down to the basal trophic level. Such a phenomenon becomes particularly evident in above-ground food webs, as claimed by White (2005), because of nutritive constraints for plants. Interestingly, this reductive view has long been challenged in many soil food webs (e.g. Hines and Gessner, 2012; Lensing and Wise, 2006; Mikola and Setälä, 1998; Santos et al., 1981; Strong, 1992; Wardle et al., 2009; Wise et al., 1999) by acknowledging that autotrophic and heterotrophic compartments are intimately linked, as most generalist predators include detritivore and herbivore prey in their diet, and can exert density-dependent control on their prey (cf. Naeem et al., 2000).

In addition, (i) changes induced in organic matter decomposition reflect C:N:P ratios, and ultimately influence the growth of primary producers; (ii) trophic relationships between detritivores and detrital resource are sensitive, and reciprocal consumer–resource interactions take place at the base of food webs, since the activity of the heterotrophic microflora depends on its growth rate, which in turn is potentially influenced by detritivores preying on the microflora itself; and (iii) primary consumers control the standing stock of producers and decomposers, their assimilation rate into the system, as well as the key ecosystem processes they perform, such as production, decomposition and mineralisation.

These ecological processes at the base of the food web highlight the huge importance of the photoautotrophic component (i.e. plants) for linking the green and the brown worlds. On one hand, identifying the trade-offs in above-ground plant traits, such as leaf and shoot traits, allows the scaling-up of primary (natural) and secondary vegetation to ecosystem properties and finally to ecosystem services, such as crop or timber production (Lavorel and Grigulis, 2012). On the other hand, comparable trade-offs can be expected below-ground, even in polluted or managed systems such as soils of temperate grasslands under atmospheric N deposition. On average, in the scrutinised ecosystems the N deposition largely exceeds the critical load of $10 \text{ kg N ha}^{-1}\text{year}^{-1}$ given in Bobbink and Hettelingh (2011) and despite this amount remains only a fraction of the manure N input in most agroecosystems (each grazing cow excretes $>160 \text{ kg N ha}^{-1}\text{year}^{-1}$), this exceedence is detectable in intensively managed areas across Northwest Europe (Fig. 2.A2).

If any predator–prey link can affect growth or reproduction of the particular predator through food N limitation (Sterner and Elser, 2002), knowing the N requirements and the efficiency in retaining N and C enables us to estimate the Threshold Elemental Ratio above which a consumer is showing

growth or reproduction penalty (Fagan and Denno, 2004). Since basal resources like plants and microbes reflect soil C:N due to their stoichiometric plasticity, any N input affecting soil C:N ratio will influence all animals seeking for their N requirements in plants and microbes. Such a reproduction penalty is evident in flower and pollen traits of plants (Mulder et al., 2005c), with cascading effects on pollinating invertebrates. A decline of specialist insects due to habitat fragmentation or replacement by exotic (alien) species induced by global warming (Aizen et al., 2008; Ashworth et al., 2004; Cannon, 1998; Hagen et al., 2012; Kaaber and Nielsen, 1988; Parmesan et al., 1999; Roy et al., 2001) might be threatened further by trait-specific sensitivity of host plants to pollution (Cox, 1988). As most long-term monitoring studies show decreasing trends in SO_4, NO_3 and NH_4 and an amelioration in acidity, supporting the idea of an effective European policy in the emission reduction (Hildrew et al., 2013; Reis et al., 2012; but see Hettelingh et al., 2013), it seems that the pressure of xenobiotics on plants and related invertebrates has to be ascribed both to soil pollution and to (cattle or atmospheric) N deposition. In both cases, the lower nutritional quality of resources will act as a kind of environmental filtering.

Grigulis et al. (2013) underpinned top-down effects (above-ground) and bottom-up effects (below-ground) for plants and microbes on ecosystem processes and services. They quantified the relative effects of plant and microbial functional properties on key processes and showed that there is a continuum from above-ground plant trait-mediated to soil microbial trait-mediated effects on productivity, potential N mineralisation and leaching rates of soil inorganic N (Cotrufo et al., 2013; De Vries et al., 2011). In contrast, vegetation assimilates and delivers organic matter to the soil compartment, allowing commensurate increases in microbial C (Mulder, 2006). In Fig. 2.16, we added to the framework by Grigulis et al. (2013) the soil faunal contribution with its interactions and processes, enabling at a glance the visualisation of multitrophic relationships in line with the predictions of stoichiometry theory.

According to Wardle et al. (2004) and Grigulis et al. (2013), productivity, C sequestration and N retention are related to plant and microbial traits (three upper arrows), in parallel to elemental factors, here as 'stoichiometric templates' *sensu* Schade et al. (2005), referring to the magnitude of drivers characteristic of the scale of interest, which in our case determine the traits that enable soil biota to operate through ecosystem services (Table 2.5). When organic matter enters the soil, either as surface litter (dead leaves) or as fragmented root litter (Cotrufo et al., 2013), the heterotrophic respiration starts with converting the organic C in the litter to CO_2, making N available for plants. Typical residuals of organic
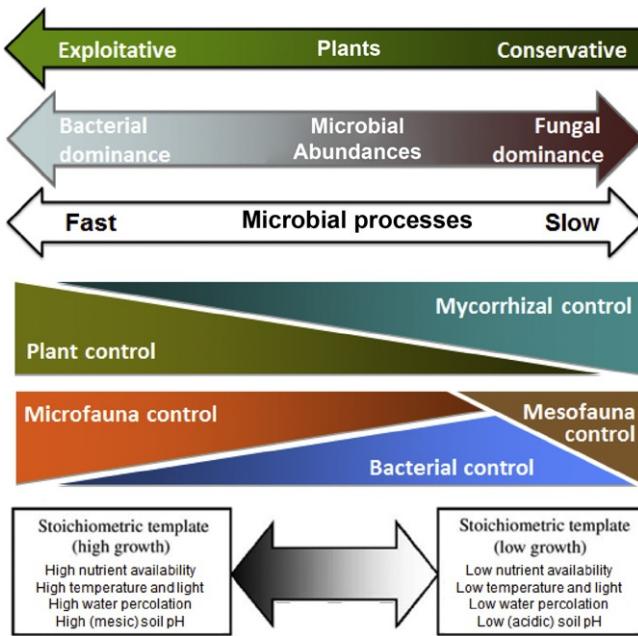
Figure 2.16 Main mechanisms underpinning top-down effects (above-ground) and bottom-up effects (below-ground), strongly supporting the relevance of leaf stoichiometry for litter pools, soil processes and multitrophic interactions as expected from ecological stoichiometry. *Upper panel modified from* Grigulis et al. (2013); *lower template panel from* Schade et al. (2005).

C include sugars, starch, hemicellulose and proteins, cellulose, lignin, suberin, cutin (Begon et al., 2006; Schmidt et al., 2011); other litter components, such as cork and plant cuticles, can even resist microbial attack and decomposition for millions of years (Mulder et al., 2000; Schmidt et al., 2011). Such a complexity for the residual C resource might contribute in part to explain both (i) the lower sensitivity of C compared to N and P and (ii) the high sensitivities of soil C:N and C:P ratios—hence, the high sensibilities of soil N and P to environmental and biotic changes.

7.2. Our expectations: Absence of evidence or evidence of absence?

Element–driven habitat–response relationships are an emerging research priority for generating 'general ecosystem models' (*sensu* Purves et al., 2013). Given the strong correlations between ecological stoichiometry and traits,

developing such models seems feasible. In fact, trait ecology enables the modelling of dynamic responses to environmental changes, since traits *continuously* reflect resource quality, and resources are easily influenced by environmental changes, as in the case of airborne N deposition. Moreover, the fast-growth *versus* slow-growth syndromes further differentiate plant species that have inherently different C:N ratios; and higher competitive ability when nutrients are abundant and turn over rapidly is traded-off against relatively poor performance in low-nutrient environments with slow turnover (Fig. 2.16). Similarly in trait-mediated interactions, larger invertebrates, such as soil microarthropods, perform poorly in low-nutrient environments with slow nutrient turnover in comparison to smaller-sized invertebrates, such as nematodes (Fig. 2.16). Soil invertebrates show distinct effect and response traits, as in Mulder et al. (2011b: their fig. 2.10) where shifts in the abundance of nematodes in soils under livestock pressure ('response trait', here to manure) are expected to influence other trophic levels in the food web (effect trait). Nematodes are sensitive to livestock pressure (cattle grazing, soil trampling and especially nitrification) and shows sigmoidal-like decreasing trends (Mulder et al., 2011b). Only two nematode genera show increasing trends, the bacterivorous *Chiloplacus* and the predatory *Thonus* under conventional and intensive management. The steepest decrease is shown by *Metateratocephalus* and *Teratocephalus*, taxa that appear extremely sensitive to livestock density at the boundary between low-pressure and high-pressure grassland farming.

This has several implications at different observational scales. In the green world, for example, increasing meat production fodder quality increases grazing pressure that in turn favours the growth of less-palatable species with more tannin-rich leaves (Cingolani et al., 2005; Del Val and Crawley, 2005; Rusch et al., 2009). At higher trophic levels, tannins can deter consumption by birds (Butler, 1982) and may act as antifeedants for bacterial fermentation in ruminants (Ellis, 1990). As 'functions effect traits', defence mechanisms in response to herbivore damage (Dicke et al., 2003) result in more tannins in leaf epidermal cells which directly affect herbivory and indirectly enhance natural vegetation succession (bottom-up). At the same time, rumen microflora are affected (Mosquera et al., 2006), as microbial bindings in the rumen alter enteric fermentation, and manure will influence fodder quality (top-down). Selective facilitation for specific bacterial communities, with cascading effects for soil invertebrates, can be reflected in greenhouse emissions from soil biota, especially in agroecosystems (cf. Hunt and Wall, 2002; Lubbers et al., 2013).

There will always be both a suite of traits that determines the success of single species in a given environment and a species assemblage that

determines the suite of dominant functional traits. Hence, traits are not only descriptors of dominant properties of entire communities to determine ecosystem services, but also predictors of the capacity to support ecosystem services (Expectation I). The extent to which these expectations are interwoven is suggested by Wright et al. (2005), who concluded that foliar traits are patterned according to plant's growth syndrome and functional type, rejuvenating *de facto* the classical Raunkiær life forms according to climatic and environmental conditions. Since sophisticated predictive models are necessary to inform policy, with results frequently required quickly for immediate application to rapidly changing socio-economic-political scenarios (Raffaelli and White, 2013; Sutherland and Freckleton, 2012), mining large datasets like TRY and LUCAS is a powerful and fast approach for assessments of ecological processes. The statistically robust allometric co-variation between many traits (and the stoichiometric plasticity of many organisms) is a new reality that fulfils Expectation II.

It is probably the first time that this coupling of ecological stoichiometry with allometric scaling and food-web theory has offered relatively simple but accurate summaries of the kind of ecosystem functioning that policymakers seek. With this method, existing patterns between and within food webs appear to be in clear agreement with functional differences at higher trophic level between species-poor and species-rich ecosystems reacting to multiple elemental drivers. Comprehensive data mining can limit the drawbacks of currently used key parameters (which were derived from literature or guessed by expert judgement), because only a data-rich world enables us to explore a huge range of parameter values for better calibration of our models.

8. BE EXPLICIT: CAN WE REACH A CONSENSUS?

Drawing on recent empirical examples from a wide range of terrestrial (agro)ecosystems, we discussed the diversity of insights that can be gained from a trait-based predictability, including community responses to altered environmental conditions. We described practical and statistical methods that can be used to connect networks, both above- and below-ground, and considered what can be learned from antagonistic networks (besides classical food webs, biocontrol involving species addition or community alteration facilitating the loss of agricultural pests) and from mutualistic networks (plant–pollinator and plant–mycorrhizal interactions). We also addressed the recent introduction of trait-based frameworks (Chagnon et al., 2013; Grigulis et al., 2013; Lavorel et al., 2013) to resolve multitrophic interactions and their ecological implications.

8.1. Implementing current knowledge
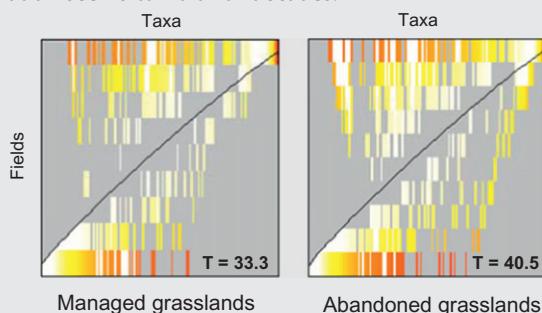
Biodiversity loss due to N deposition and increased acidification have been reported by, among others, Clark and Tilman (2008) and Sardans and Peñuelas (2012). In Northwestern Europe, many terrestrial ecosystems are under N eutrophication, especially in intensive rural areas (Fig. 2.A2). Given the evidence for negative responses of plant species to N deposition (Payne et al., 2013), it is not unlikely to expect comparable responses for soil invertebrate species. Emerging evidence shows that even after ecological restoration of agroecosystems, the human footprint of land-use management inflates the structure of the soil metacommunity (Box 2.5). Elemental factors regulating the occurrence and the abundance of plants and invertebrates are therefore the key to quantifying ecosystem services. Despite data fluctuating from observed values (soft traits) to inferred values (hard traits), and uncertainty existing along this continuum (cf. Osnas et al., 2013), for stoichiometric and allometric relationships environmental constraints are undeniable.

For instance, observing a faunal mass–abundance slope less negative (respectively, more negative) suggests that larger animals absorb more (respectively, less) energy from the environment than smaller animals, and such nutrient use efficiency (*sensu* Lloyd et al., 2013) could be translated into different mass–abundance scalings for heterotrophs and autotrophs. The fact that for soil heterotrophs mass–abundance slopes deviate from $-\frac{3}{4}$ is evidence that species of different body size (which in terrestrial ecosystems is less related to the trophic position than in aquatic ecosystems) acquire different amounts of energy (e.g. Brown and Gillooly, 2003; Cohen et al., 2003, 2009; Reuman et al., 2009; Yvon-Durocher et al., 2011), implying an inefficient trophic transfer for the food webs whose slopes will be less (i.e. steeper) than $-\frac{3}{4}$.

Understanding population dynamics and forecasting their changes are obviously crucial issues (Begon et al., 2006). In their recent meta-analysis, Martin et al. (2012) recognised that there is little scientific justification for prioritising ecological investigation of unmodified biomes. Published investigations in the peer-reviewed journals of the Ecological Society of America (*Ecology, Ecological Monographs* and *Ecological Applications*) or the American Society of Naturalists (12.8% and 12.5%, respectively) have even fewer studies dealing with non-rural areas than the journals of the British Ecological Society (*Journal of Ecology*, *Journal of Animal Ecology* and *Journal of Applied Ecology*) or the Society for Conservation Biology (23.5% and 25.5%, respectively). Due to this ongoing research focus on unmodified habitats, stakeholders and policy-decision makers are faced with the difficult task of assessing ecosystem services in rural areas to provide the most basic information on the soil 'black box' (Fitter, 2005).

BOX 2.5 Order and disorder in restoration ecology

Site-specific averages of trophic link lengths provide a consumer–resource response of a food web as a whole. Nestedness is another computational approach that provides a description of groups of webs, although the classical nestedness is usually based on the binary occurrence of populations (presence or absence), in contrast to the continuum of traits for trophic link lengths and mass–abundance slopes. Although ordering of ecosystems in (species × sites) matrices according to environmental gradients (like soil chemistry) could result in different degrees of nestedness, this is not a caveat because it helps to detect the gradient that generated the nested pattern (Lomolino, 1996). In general, matrices of fixed (species × sites) sizes should be used (Ulrich et al., 2009) for maximal statistical performance, although Staniczenko et al. (2013) showed recently that nestedness can be computed for differently sized and non-binary (i.e. abundance weighted) metacommunities as well. According to Atmar and Patterson (1993), the computation of the nestedness of a presence–absence (fixed) matrix involves the following steps: (1) a curve has to be defined to separate all the matrix cells denoting the site-specific presence of a species from the cells denoting its absence; (2) the presence–absence matrix has to be reorganised to maximise its nestedness, permuting rows (fields) and columns (species); (3) the normalised distance to the isocline of step (1) has to be derived for each 'absence cell' recorded above the isocline and for each 'presence cell' recorded below the isocline; and (4) the sum of the normalised distances will be calculated, ranging between 0 for a 'perfectly nested matrix' and 100 for a 'completely unnested matrix' (Atmar and Patterson, 1993; Rodríguez-Girones and Santamaria, 2006). According to Rodríguez-Girones and Santamaria (2006), these T values, ranging from 0 to 100, should be seen as percentages, not as temperature degrees. Two brown world metacommunities, sized as 126 invertebrate taxa times 10 abandoned grasslands and 140 invertebrate taxa times nine managed grasslands, show that the 'heat of disorder' is much higher in the abandoned agroecosystem matrix [$T = 40.5$] than in the managed agroecosystem matrix [$T = 33.3$]. Abandoned agroecosystems which are characterised by waterlogging (creating anaerobic conditions that contribute to explain less fungal resources in comparison to other agroecosystems; see Kuramae et al., 2012), tend to have significantly higher levels of 'disorder' than do managed agroecosystems. Hence, we should rethink what is meant by this randomness, as high nestedness of grasslands abandoned 30 years ago might point to an intrinsic sensitivity to initial conditions. If so, it would be a kind of human footprint that even after ecological restoration seems to hold for decades.

Managed grasslands   Abandoned grasslands

8.2. Summary points and future issues

Amongst the emerging research foci that need to be addressed in the near future, we highlight the following ten issues, not presented in priority order:

- *The brown and the green worlds are ruled by the same elemental laws.* Unlike faunal communities, (steady-state) vegetation units tend to be dominated by similar-sized plants (Damuth, 2001; Enquist et al., 2009; West et al., 2009). Besides mass, other global plant functional relationships are widely recognised (Díaz and Cabido, 1997; Reich et al., 1997; Wright et al., 2004). Elemental factors co-vary with traits that are most likely the ones that are under selection and which matter during the evolutionary process. Air and soil compartments can be modelled in the same way as soon as separate C:N:P parameters are used to calibrate above- and below-ground resources.

- *Despite trait differences, most trait co-variances enable a quantification of ecosystem functioning.* Parameters derived from allometric (and/or isometric) co-variations between traits characterising the above- and below-ground parts of plants are essential to quantify ecosystem services. Given the skewed distribution of some trait suites, more attention has to be devoted to the below-ground part, although the possibility that the brown world with its distinct boundaries is buffered more than the green world against environmental harshness should be taken into account to explain the observed distribution skewness.

- *Chronic nutrient addition in engineered ecosystems will provide novel evidence and can validate models.* Long-term nutrient addition experiments and intensive agriculture are appropriate study areas for those seeking evidence for (co)limitation of plants and animals. Such areas also offer unique possibilities to investigate the human influence on soil formation and to apply molar weathering ratios, with consequences for all organisms (Table 2.4). Besides stoichiometric studies on C and macro- and micronutrients, elements such as S, Fe, Mg, Ca, K, Mn, Cd and rare earth metals deserve much more attention.

- *More research in extreme and engineered ecosystems can provide concrete information for a fine-tuned forecasting model.* Martin et al. (2012) recommended considering *all field sites*, including novel ecosystems too. This implies among others that not only the trait of native species, but also the traits of cultivated species (including insecticidal crystal proteins, glucosinolates, etc.), should be observed and measured, and first attempts to correlate traits at crop level were recently published (Poorter et al., 2013).

- *Laboratory studies are needed to delineate dietary relationships of soil invertebrates.* Elemental fluxes across soil food webs can be addressed with stable isotope signatures ($\delta^{13}C$ and $\delta^{15}N$) but not yet with fatty acids, whose profiles can only be interpreted when numbers of profiles of resources and consumers increase (Pollierer et al., 2012; Traugott et al., 2013). Isotope labelling could be used to address issues from behavioural ecology, for instance if social insects interacting with fungi can deal more easily with resources with a low elemental profile (bad food quality) than expected from ecological stoichiometry.
- *Consumer–resource stoichiometry shapes the composition and the structure of terrestrial food webs.* The historical discrepancy between above-ground data sampling and below-ground soil monitoring has driven terrestrial food-web models in different directions. No dynamic food-web model has directly evaluated the relative importance of continuous changes in C: N:P ratios in relation to trophic sensitivity of invertebrates to changes of C:P and N:P contents, although indirect evidence is rising (Box 2.3).
- *Stoichiometric plasticity of the resources is widespread.* Agroecosystem models differ greatly, but although the classical food-web model of Coleman (1985) and Hunt et al. (1987) offered an initial and brilliant starting point, despite some attempts to integrate the stoichiometric and trophic theories into a more comprehensive framework, almost three decades later most soil food-web models still continue to ignore P and place great emphasis on fixed parameters for microbial C:N ratios (Moore and De Ruiter, 2012).
- *Environmental drivers such as atmospheric nitrogen deposition influence the soil and resource C:N compositions.* Effects of climate on foliar trait relationships have been regarded as modest (Wright et al., 2004), but little is known about the effects of newly reactive N and atmospheric N deposition (cf. Sardans et al., 2008, 2012b). It is evident that airborne N is decreasing the soil C:N ratio (Box 2.4), with cascading effects above-ground on plant traits and the performances of plant-related invertebrate herbivores and invertebrates predating herbivores; and below-ground on microbial traits and microbial-grazing soil invertebrates.
- *Rural changes alter the $\Delta^{15}N$ signature of ecosystems.* Although much less than industrial N fixation (Vitousek et al., 1997, 2002), anthropogenic N fixation by enhancing the cultivation of clover, peas, soybeans, and alfalfa alters the background $\delta^{15}N$ values of their companion crops and/or the $\delta^{15}N$ of the natural communities replaced by the introduced N_2-fixing

crops with cascading effects on insect herbivores. Also some invasive plant species, whose success has been attributed to their N$_2$fixation and novel traits, can contribute to altered δ^{15}N values of invaded soils.

• *Although a policy priority, knowledge on elemental thresholds is lacking.* Although it seems still hard to detect threshold events at which changes in ecosystems are likely to be irreversible or the restoration far too expensive, such a knowledge would be of great value for the prioritisation of agencies to decline the introduction of new species (Fleishman et al., 2011) and to reach a consensus regarding sustainable implementation of land use.

8.3. Perpetuum mobile

Priority in conceptualising and assessing ecosystems is to be sure that we agree on all terms we use. Alas, despite an existing consensus on interactions between organisms, consensus on the major determinants of food-web assemblages that limit or facilitate component species is lacking. Moreover, good agricultural practises are usually defined for only specific aspects of European land-use management due to the claimed complexity of the relationships between agriculture and environment. Only integrating the brown and the green world across their boundaries within one general framework based on ecological stoichiometry and quantified by allometric scaling will enable us for a better (mechanistic) understanding of ongoing processes in (agro)ecosystems that contributes to improve land-use management, agroforestry, restoration ecology, and conservation biology. As a matter of fact, abiotics govern food webs by shaping biodiversity, allometric scaling and energy equivalence; management of agroecosystems is simply fastening changes in elemental factors.

Summarising, the balance between C, N and P drives microbes, vascular plants (and hence vegetation, thus co-determining different ecosystem types), and soil invertebrates and finally shapes ecological networks in both natural and managed ecosystems. The focus on experimental and natural sites—instead of managed, disturbed or even polluted locations—makes direct comparisons among ecological networks difficult, because modelling can become biased either by fixed food-web parameters or by too different sampling protocols. Any mechanistical correlation of species with their observed responses to drivers or along environmental gradients requires in either case traits from a wide variety of organisms, across multiple trophic levels, from as many different habitats as possible (Naeem and Bunker, 2009). Many below-ground examples of environmental pressure favouring particular trait combinations are still unknown for Eukarya (in particular

from agroecosystems), although we present novel evidence that even in restored areas the former management and the effects of N deposition on the soil C:N ratios are long-term processes that cannot be reversed as easily as commonly thought. Such a balance between soil biota and their environmental conditions is subtle, dynamic and surely not stochastic.

Hence, we must put an end to our Anthropocene view that we can get every kind of ecosystem type we wish by intensification, deforestation or restoration, as even the soils of many natural ecosystems are already overexploited. Given the well-documented decomposition process enhanced by litter fauna, obtaining more invertebrates' growth efficiencies and assembling more soil food webs in agroecosystems under stoichiometrically different conditions are important goals. In such a way, we will really become capable to contribute to a single mechanistic framework for the globally demanded development of sustainable agricultural policies.

ACKNOWLEDGEMENTS

> *It is a recognized principle of ecology that the interactions of organisms and environment are reciprocal.*
>
> **Alfred C. Redfield (1958)**

> **APPENDIX**
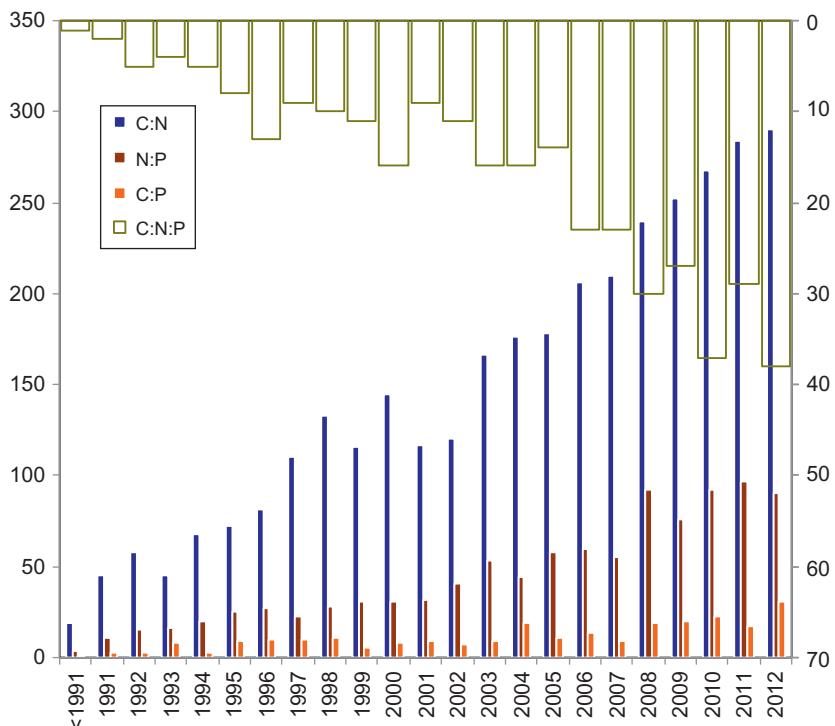
Figure 2.A1 To rank the most widespread elemental proxies in terrestrial research, we used Web of Science and ran a cited reference search to collect data on soil nutrient ratios till 31 December 2012. A Web of Science search for all articles published on the TOPIC 'soil' AND 'ratio' AND either 'C:N', 'C:P' or 'N:P' (bottom part diagram, left vertical axis), or 'C:N' AND ('N:P' OR 'C:P') (top part diagram, reversed vertical axis on the right) provided a total amount of 5036 records over the years, including double entries. Nitrogen is by far the most widely used soil predictor.
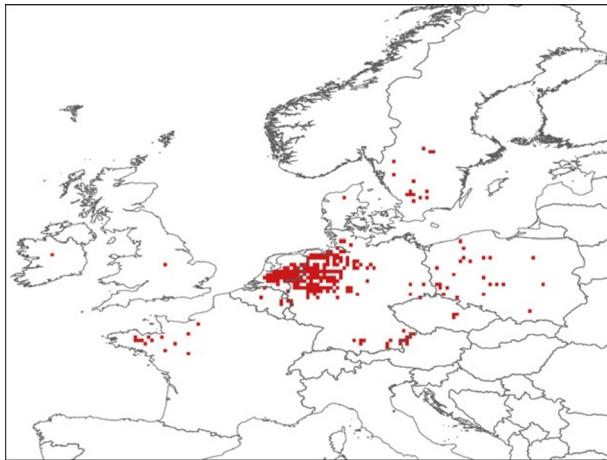
Figure 2.A2 In temperate grasslands, N is typically seen as limiting element. Assuming the direct effect of atmospheric N deposition on soil C:N (as in Box 2.4) and seen that soil C:N ratio co-determines the success of the plant and animal species occurring in natural grasslands and agroecosystems, it seems to us valuable to detect rural areas where the empirical soil C:N ratio is much lower than expected from the negative correlation between atmospheric N and soil C:N.

Table 2.A1 Overview of the above-ground plant traits sorted by the number of multiple entries [in brackets]

Plant architecture: height of lowest branch *versus* total plant height (furcation index) [331588], Plant growth form [134214], Leaf area [108945], Plant height vegetative [81946], Phenology: vegetative [73456], Specific leaf area (SLA) [65157], Plant life form (Raunkiær life form) [64949], Woodiness [44506], Leaf nitrogen (N) content per dry mass [43125], Leaf angle [41450], Photosynthesis pathway [40603], Leaf type [40327], Phenology: reproductive [38136], Plant functional type [37256], Leaf dry mass [36260], Leaf dry matter content (LDMC) [33589], Species distribution: climate type [29427], Stem specific density (SSD) [29246], Dispersal syndrome [29239], Plant commercial use [27358], Leaf compoundness [25297], Plant tolerance to fire [23388], Plant height generative [23282], Leaf phosphorus (P) content per dry mass [20544], Plant propagation [19665], Plant lifespan [18641], Pollination syndrome [16367], Leaf lamina width [14733], Leaf nitrogen (N) content per area [14333], Dispersal unit type [13975], Leaf nitrogen/phosphorus (N/P) ratio [12599], Germination efficiency [12387], Leaf fresh mass [12173], Plant tolerance to human impact [12070], Leaf carbon (C) content per dry mass [11565], Species distribution: continentality [11464], Leaf lamina length [11284], Species distribution: native *versus* invasive [11248], Leaf δ^{15}N [11115], Leaf

Continued

Table 2.A1 Overview of the above-ground plant traits sorted by the number of multiple entries [in brackets]—cont'd

distribution along the axis [10751], Specific leaf area (SLA) based on fresh mass [10380], Plant palatability [9753], Stem diameter at 1.3 m (DBH) [9730], Dispersal unit length [8511], Flower colour [7992], Plant heterotrophic nutrition mode [7885], Leaf lamina thickness [7814], Species phytosociological group [7477], Leaf lamina density [7359], Vital attributes of persistence and establishment [7357], Specific leaf area (SLA) of leaf lamina [7335], Leaf respiration per dry mass [7122], Dispersal unit width [6966], Plant tolerance to soil texture [6555], Leaf density [6491], Photosynthesis per leaf area [6340], Flower pollinator and type of reward [6317], Leaf texture (sclerophylly) [6299], Leaf carbon (C) content per area [6219], Mating system [6124], Leaf petiole length [6006], Dispersal unit thickness [6000], Stem conduit density (vessels and tracheids) [5562], Leaf shape [5494], Leaf carbon/nitrogen (C/N) ratio [5475], Leaf phosphorus (P) content per area [5391], Dispersal kernel [5320], Leaf petiole fresh mass [5107], Leaf petiole diameter [5097], Leaf petiole dry mass [5082], Plant tolerance to high temperatures [4965], Plant architecture: shoot branching [4879], Leaf physical strength [4780], Dispersal unit heteromorphy [4725], Species distribution: endemism [4624], Photosynthesis per leaf dry mass [4597], Plant tolerance to frost [4502], Leaf porosity [4440], Germination requirement [4420], Leaf potassium (K) content per dry mass [4256], Plant tolerance to precipitation [4235], Plant tolerance to soil pH [4221], Flower sex [4202], Photosynthesis leaf intercellular CO_2 concentration [3958], Fruit type [3903], Leaf calcium (Ca) content per dry mass [3853], Leaf aluminium (Al) content per dry mass [3691], Species reproduction type [3668], Leaf $\delta^{15}N$ *versus* soil $\delta^{15}N$ ($\Delta^{15}N$) [3664], Dispersal unit dry mass [3614], Flower self–incompatibility [3608], Leaf magnesium (Mg) content per dry mass [3583], Flower type [3563], Leaf zinc (Zn) content per dry mass [3382], Leaf manganese (Mn) content per dry mass [3366], Specific leaf area (SLA) of leaf lamina per fresh weight [3354], Plant tolerance to planting density [3336], Stem conduit diameter (vessels and tracheids) [3330], Leaf sodium (Na) content per dry mass [3278], Plant tolerance to drought [3233], Leaf iron (Fe) content per dry mass [3227], Wood vessel bars per perforation plate [3152], Leaf thickness [3150], Stem conduit area (vessels and tracheids) [3050], Wood vessel element length [3049], Plant tolerance to shade [3043], Wood fibre lengths [3023], Leaf length [2946], Plant tolerance to waterlogging [2945], Flower sex timing [2911], Plant relative growth rate (RGR) [2812], Leaf respiration per area [2793], Flower UV reflectance [2781], Flower insemination: autogamous or xenogamous [2777], Stomata conductance per leaf area [2776], Plant strategy type according to Grime [2750], Species distribution: altitude of origin [2726], Species distribution: origin zonal [2726], Leaf palatability [2719], Species distribution: number of floristic zones [2657], Plant resprouting capacity after disturbances [2655], Leaf barium (Ba) content per dry mass [2604], Plant growth rate [2509], Plant resprouting capacity after fire [2451], Photosynthesis carboxylation capacity (Vc_{max}) per leaf area (Farquhar model) [2418], Leaf cobalt (Co) content per dry mass [2404], Leaf strontium (Sr) content per dry mass [2391], Leaf dry mass per plant dry mass (leaf weight ratio, LWR) [2300], Stem conduit lumen area (vessels and tracheids) per sapwood area [2280], Plant defence mechanisms: allelopathy [2198], Stem nitrogen (N) content per dry mass [2188], Flower conspicuous [2185],

Table 2.A1 Overview of the above-ground plant traits sorted by the number of multiple entries [in brackets]—cont'd

Fruit/seed conspicuous [2185], Leaf colour in fall conspicuous [2185], Plant is a small grain [2185], Leaf color [2167], Leaf bromine (Br) content per dry mass [2153], Flowering requirement (requirement for fertility) [2140], Plant tolerance to salinity [2115], Leaf chlorine (Cl) content per dry mass [2101], Plant tolerance to CaCO$_3$ [2092], Leaf scandium (Sc) content per dry mass [2090], Leaf rubidium (Rb) content per dry mass [2086], Fruit/seed colour [2073], Plant tolerance to hedges [2055], Vegetative regeneration [2040], Plant moisture use [2037], Vegetative reproduction: spread rate [2034], Plant age of maturity (first flowering) [2024], Metamorphoses and morphological adaptations: seed or dispersal unit [2017], Fruit/seed abundance [2001], Seedling vigor [1989], Crown diameter along the longest axis [1961], Crown diameter perpendicular to first axis [1929], Leaf lifespan [1926], Shoot green tissue carbon/nitrogen (C/N) ratio [1925], Leaf samarium (Sm) content per dry mass [1836], Leaf lanthanum (La) content per dry mass [1781], Germination temperature [1740], Leaf chromium (Cr) content per dry mass [1702], Leaf caesium (Cs) content per dry mass [1555], Stem carbon (C) content per dry mass [1530], Photosynthesis electron transport capacity (J$_{max}$) per leaf area (Farquhar model) [1520], Leaf cerium (Ce) content per dry mass [1473], Stem dry mass per plant [1437], Stomata conductance per leaf dry mass [1431], Photosynthesis net assimilation rate (NAR) [1407], Leaf number of leaflets per leaf [1398], Stem phosphorus (P) content per dry mass [1283], Leaf antimony (Sb) content per dry mass [1220], Shoot nitrogen (N) content per dry mass [1212], Species US Wetland Indicator [1202], Leaf sulphur (S) content per dry mass [1186], Photosynthesis carboxylation capacity (Vc$_{max}$) per leaf dry mass (Farquhar model) [1178], Shoot dry mass [1173], Leaf transpiration per area [1114], Photosynthesis electron transport capacity (Jmax) per leaf dry mass (Farquhar model) [1105], Leaf silica (Si) content per dry mass [1092], Leaf perimeter length [1089], Wood vessel scalariform perforations [1075], Leaf δ^{13}C [1064], Leaf europium (Eu) content per dry mass [1053], Leaf nickel (Ni) content per dry mass [1032], Species distribution: mode of introduction [1017], Leaf copper (Cu) content per dry mass [1015], Leaf nitrogen (N) content [1006], Plant defence mechanisms: chemical defence compounds [984], Germination stimulation [965], Leaf thorium (Th) content per dry mass [944], Bud frequency per bud bank layer [939], Shoot phosphorus (P) content per dry mass [910], Leaf titanium (Ti) content per dry mass [903], Leaf boron (B) content per dry mass [901], Plant spininess or thorniness [894], Stem respiration per dry mass [844], Leaf dry mass per plant [804], Leaf lignin content per dry mass [801], Plant light requirement [749], Bark density [737], Shoot vegetative dry mass [726], Leaf epidermis volume per leaf volume [723], Metamorphoses and morphological adaptations: aerenchym [716], Leaf area per plant dry mass (leaf area ratio; LAR) [714], Leaf vanadium (V) content per dry mass [677], Leaf ytterbium (Yb) content per dry mass [676], Shoot carbon/nitrogen (C/N) ratio [675], Photosynthesis per leaf transpiration (water use efficiency: WUE) [667], Plant tolerance to grazing [667], Plant tolerance to mowing [667], Plant tolerance to

Table 2.A1 Overview of the above-ground plant traits sorted by the number of multiple entries [in brackets]—cont'd

trampling [667], Leaf selenium (Se) content per dry mass [666], Leaf molybdenum (Mo) content per dry mass [659], Stem length (height) [658], Stem diameter [625], Plant dry mass [618], Leaf terbium (Tb) content per dry mass [612], Leaf chlorophyll content per area [607], Leaf inrolling of lamina [598], Reproductive dry mass per plant [585], Wood secretory elements [584], Leaf mesophyll palisade parenchym volume per leaf volume [579], Vegetative reproduction: distance between ramets [570], Plant hairiness [562], Leaf mesophyll spongiophyll volume per leaf volume [548], Leaf intercellular volume per leaf volume [507], Leaf mercury (Hg) content per dry mass [493], Shoot carbon (C) content per dry mass [483], Wood dry mass per plant dry mass [475], Leaf phenolics content per dry mass [471], Leaf tannins content per dry mass [471], Vegetative reproduction: clonal growth organ [469], Stomata density [450], Leaf phosphorus (P) content per dry mass [444], Plant carbon (C) allocation to root, stem, leaves [440], Bark carbon (C) content per dry mass [439], Bark nitrogen (N) content per dry mass [438], Bark phosphorus (P) content per dry mass [425], Leaf arsenic (As) content per dry mass [422], Leaf light absorption (extinction) [417], Leaf lutetium (Lu) content per dry mass [400], Leaf mesophyll palisade parenchym volume per spongiophyll volume [398], Bud source [370], Leaf gold (Au) content per dry mass [345], Leaf cadmium (Cd) content per dry mass [340], Leaf pH [321], Plant specific area (surface per dry mass of all green parts) [320], Leaf neodymium (Nd) content per dry mass [314], Species distribution: neophyte status [312], Leaf hafnium (Hf) content per dry mass [307], Leaf starch content per dry mass [307], Leaf sugar content per dry mass [307], Leaf area per plant [306], Flower pollen per ovule [302], Wood silica (SiO_2) bodies [301], Stomata conductance model parameter (Ball-Berry, Jarvis, Leuning) [296], Leaf cellulose content per dry mass [293], Leaf hemi–cellulose content per dry mass [293], Leaf respiration temperature dependence [293], Leaf soluble components content per dry mass [293], Crown area [290], Leaf epidermis cell length [290], Stem dry mass per plant dry mass [282], Leaf intercellular volume [280], Leaf tissue volume [280], Leaf volume [280], Plant secondary compounds [267], Leaf gadolinium (Gd) content per dry mass [249], Plant clonal growth form [245], Stem carbon/nitrogen (C/N) ratio [245], Leaf non–structural carbon (C) content per dry mass (TNC) [242], Leaf potassium (K) content per area [240], Vegetative reproduction: clonality of ramets [230], Leaf inclination [228], Leaf volume per leaf area [225], Leaf epidermis thickness [216], Leaf epidermis cell area [209], Shoot nitrogen (N) mass vegetative [196], Stem volume [195], Stem nitrogen/phosphorus (N/P) ratio [191], Bark thickness [183], Photosynthesis light use efficiency (LUE) [180], Vegetative reproduction: lateral spread [179], Leaf epidermis cell wall thickness [178], Leaf mesophyll cell area [171], Leaf hypodermis volume per leaf volume [164], Leaf vascular bundle volume fraction: sclerenchym [160], Leaf vascular bundle volume fraction: phloem [160], Leaf vascular bundle volume fraction: xylem, phloem, sclerenchym [160], Leaf vessel diameter [160], Leaf total area per leaf projected area [155], Leaf mesophyll palisade parenchyma cell area [150], Leaf respiration in light

Table 2.A1 Overview of the above-ground plant traits sorted by the number of multiple entries [in brackets]—cont'd

per leaf area [149], Leaf osmotic potential at full turgor [146], Leaf nitrogen (N) content organic per dry mass [145], Leaf sclerified tissue per midrib [143], Leaf nitrogen (N) NO_3^- content per dry mass [142], Stem diameter at base [141], Stomata distribution [141], Plant defence mechanisms: physical defence structures [140], Reproductive structure nitrogen (N) content per dry mass [138], Leaf chlorophyll content per dry mass [136], Leaf and fine root turnover [131], Leaf silver (Ag) content per dry mass [126], Shoot necromass [126], Stem area at base [122], Leaf mid vein thickness [121], Leaf dysprosium (Dy) content per dry mass [118], Leaf sclerified tissue per leaf lamina tissue [117], Plant architecture: height of lowest branch [117], Shoot relative growth rate [117], Branch dry mass per plant [116], Leaf mesophyll area per leaf area [115], Plant resprouting capacity after clipping [113], Leaf mesophyll thickness [110], Stomata area [109], Stomata index (stomata/epidermis cells) [107], Branch respiration per dry mass [104], Reproductive structure phosphorus (P) content per dry mass [101], Branch respiration per surface area [100], Leaf mesophyll cell volume [94], Leaf mesophyll density [94], Leaf number of chloroplasts per mesophyll cell [94], Leaf vein density [94], Leaf volume of chloroplasts [94], Vegetative reproduction: number of ramets [93], Leaf vascular bundle cell size: phloem (area) [89], Paracotyledon dry mass [89], Leaf lead (Pb) content per dry mass [88], Species distribution: characteristical ecological distribution [88], Species distribution: invasiveness [88], Leaf mid vein support tissue thickness [87], Dispersal distance [83], Stomata pore area per leaf area index (LAI) [83], Leaf area per metamer dry mass [82], Leaf dry mass per metamer dry mass [82], Leaf petiole mass per metamer mass [82], Stem internode area [82], Stem internode area per leaf area [82], Stem internode length [82], Stem internode mass per metamer mass [82], Stem specific internode mass [82], Branch respiration temperature dependence [80], Shoot calcium (Ca) content per dry mass [80], Shoot iron (Fe) content per dry mass [80], Shoot magnesium (Mg) content per dry mass [80], Shoot manganese (Mn) content per dry mass [80], Shoot potassium (K) content per dry mass [80], Stem area other tissues but pith and xylem [80], Stem area pith [80], Stem area xylem [80], Stem fraction of pith [80], Stem fraction of xylem [80], Stem fraction tissues other than pith or xylem [80], Stem total area of cross section [80], Reproductive structure nitrogen/phosphorus (N/P) ratio [79], Leaf respiration per nitrogen (N) content [78], Specific leaf area (SLA) per leaf nitrogen (N) content [78], Leaf xanthophyll and carotene content [77], Leaf vascular bundle cell size: xylem (area) [74], Nitrate reductase activity [74], Photosynthesis per leaf nitrogen (N) content (nitrogen use efficiency: PNUE) [73], Stem diameter at base of crown [73], Leaf area per sapwood area [71], Plant architecture: number of branches per tree [71], Crown depth [69], Leaf protein content per dry mass [69], Paracotyledon dry mass per plant dry mass [68], Leaf elastic modulus [67], Leaf osmotic potential at turgor loss [67], Germination lag time [63], Germination maximum rate per day [63], Species US Federal T/E Status [61], Stem respiration per surface area [60], Vegetative reproduction: role of clonal growth organ in plant

Table 2.A1 Overview of the above-ground plant traits sorted by the number of multiple entries [in brackets]—cont'd

growth [59], Stem respiration per nitrogen (N) content [58], Flower heterostyly [56], Photosynthesis carboxylation capacity (Vc_{max}) per leaf nitrogen (N) content (Farquhar model) [56], Photosynthesis electron transport capacity (J_{max}) per leaf nitrogen (N) content (Farquhar model) [56], Stomata area per leaf area [56], Branch respiration per nitrogen (N) content [54], Stem cavitation risk [52], Leaf cell volume [50], Leaf uranium (U) content per dry mass [50], Stomata guard cell length [50], Leaf light reflectance [48], Leaf RUBISCO content per area [48], Leaf soluble phenolics content per dry mass [48], Stem fraction of total area: xylem cell wall [48], Dispersal unit colour [47], Stem fraction cell wall in xylem [47], Vegetative reproduction: persistence of connection between clonal growth organs [46], Plant architecture: number of offspring shoots per parent shoot per year [45], Photosynthesis light response curve [44], Shoot number of mature leaves [43], Shoot number of non–mature leaves [43], Fraction of ground area covered by projected canopy [42], Leaf water content at full turgor [42], Photosynthesis CO_2 compensation point [42], Stem respiration per volume [42], Stem respiration temperature dependence [42], Leaf carbon/phosphorus (C/P) ratio [41], Seeding frequency [41], Branch dry mass per plant dry mass [40], Leaf hydraulic conductance [40], Leaf insertion [40], Stomata conductance: leaf osmotic potential at final reduction [40], Stomata conductance: leaf osmotic potential at initial reduction [40], Fine stem carbon (C) content per dry mass [39], Fine stem carbon/nitrogen ratio (C/N) [39], Fine stem dry matter content per fresh mass [39], Fine stem lignin content per dry mass [39], Fine stem nitrogen (N) content per dry mass [39], Fine stem pH [39], Leaf mid vein mean vessel diameter [37], Stomata conductance: vapour pressure deficit at final reduction [37], Stomata conductance: vapour pressure deficit at initial reduction [37], Plant architecture: bifurcation ratio [36], Plant architecture: relationship of stem mass, height and diameter [35], Leaf mid vein conductivity [34], Leaf dry mass per ground area [32], Leaf respiration in light per dry mass [32], Leaf tantalum (Ta) content per dry mass [32], Leaf water content per area [32], Stem fraction of total area: cell wall [32], Stem fraction of total area: collenchyma cell wall [32], Stem fraction of total area: pith cell wall [32], Stomata pore length [32], Crown surface roughness [31], Leaf cuticula thickness [30], Photosynthesis electron transport capacity (J_{max}) temperature dependence (Farquhar model) [30], Stem dry mass per unit ground area [28], Branch nitrogen (N) content per dry mass [27], Plant tolerance to windthrow [27], Branch dry mass per unit ground area [26], Leaf mesophyll cell height [25], Leaf vascular bundle cell size: sclerenchym (area) [25], Leaf water content at turgor loss point [25], Fern spore length [24], Leaf cuticula conductance [24], Leaf nitrogen (N) content per total leaf area [24], Plant respiration per nitrogen (N) content (different organs combined) [24], Cotyledon carbon (C) content per dry mass [20], Cotyledon nitrogen (N) content per dry mass [20], Leaf ash content per dry mass [20], Leaf cell lumen area per leaf area [20], Leaf nitrogen (N) content per plant nitrogen (N) content [20], Plant growth per leaf nitrogen (N) content [20], Plant growth per plant nitrogen (N)

Table 2.A1 Overview of the above-ground plant traits sorted by the number of multiple entries [in brackets]—cont'd

content [20], Plant nitrogen (N) content per dry mass [20], Stem nitrogen (N) content per plant nitrogen (N) content [20], Stem non–structural carbon (C) content per dry mass (TNC) [20], Stem fraction of collenchym [19], Photosynthesis temperature dependence [18], Leaf dry matter content per volume [17], Leaf mesophyll palisade parenchym thickness [17], Leaf mesophyll spongiophyll thickness [17], Leaf mid vein xylem conduit number [17], Leaf mineral content per dry mass (summing all major minerals) [17], Leaf nitrogen (N) fraction in RUBISCO [17], Leaf structural dry matter content per dry mass [17], Leaf structural dry matter content per volume [17], Plant dry matter content per fresh mass [17], Plant dry matter content per volume [17], Wood dry mass per plant [17], Leaf respiration in dark minus respiration in the light, mass based [16], Leaf respiration in light per respiration in the dark [16], Photosynthesis oxygenation capacity (Farquhar model) [16], Plant architecture: stem empirical form factor to calculate sapwood carbon (C) content [16], Leaf chlorophyll content per nitrogen (N) content [15], Leaf dry mass fraction in given age class [15], Plant tolerance to soil type [13], Species understory *versus* overstory [13], Leaf area fraction in given age class [12], Germination establishment rate of young trees [11], Leaf area index of the whole leaves *versus* projected leaf area index [11], Plant basic mortality [11], Woody area index [11], Branch carbon (C) content per dry mass [10], Crown density [10], Crown mass per area [10], Fern spore mass [10], Fern spore radius [10], Fern spore volume [10], Leaf cell lumen width [10], Leaf cells per area [10], Leaf lamina volume [10], Leaf mesophyll cell lumen height [10], Leaf mid vein cross sectional area [10], Leaf mid vein length [10], Leaf mid vein vascular bundle diameter [10], Leaf solid volume per leaf volume [10], Leaf veins number of orders [10], Leaf water storage time constant [10], Leaf water storage transfer resistance [10], Leaf water volume fraction [10], Photosynthesis carboxylation capacity (Vc_{max}) temperature dependence (Farquhar model) [10], Photosynthesis light compensation point [10], Photosynthesis light saturation [10], Leaf cell lumen length [9], Leaf veins free ending density [9], Crown transpiration [8], Leaf epidermis conductance [8], Leaf hypodermis thickness [8], Plant hydraulic conductance [8], Stem sapwood volume per stem volume [8], Leaf carotenoid content per area [7], Leaf chlorophyll a/b ratio [7], Leaf veins number on first order [7], Stomata density: ratio of leaf adaxial to total stomatal density [7], Stomata pore area index [7], Branch nitrogen (N) content per unit ground area [6], Crown nitrogen (N) content per unit ground area [6], Crown radiation extinction coefficient [6], Leaf clumping factor [6], Stem fraction cell wall in collenchym [6], Stem nitrogen (N) content per unit ground area [6], Stem/wood aluminium (Al) content per dry mass [6], Stem/wood antimony (Sb) content per dry mass [6], Stem/wood arsenic (As) content per dry mass [6], Stem/wood cadmium (Cd) content per dry mass [6], Stem/wood calcium (Ca) content per dry mass [6], Stem/wood chromium (Cr) content per dry mass [6], Stem/wood copper (Cu) content per dry mass [6], Stem/wood iron (Fe) content per dry mass [6], Stem/wood lead (Pb) content per dry mass [6], Stem/wood magnesium (Mg)

Continued

Table 2.A1 Overview of the above-ground plant traits sorted by the number of multiple entries [in brackets]—cont'd

content per dry mass [6], Stem/wood mercury (Hg) content per dry mass [6], Stem/wood molybdenum (Mo) content per dry mass [6], Stem/wood nickel (Ni) content per dry mass [6], Stem/wood potassium (K) content per dry mass [6], Stem/wood sodium (Na) content per dry mass [6], Stem/wood sulphur (S) content per dry mass [6], Stem/wood thallium (Ti) content per dry mass [6], Stem/wood zinc (Zn) content per dry mass [6], Crown water interception coefficient [5], Fern spore width [4], Leaf nitrogen (N) content per plant [4], Stem fraction cell wall in pith [4], Stem nitrogen (N) content per dry mass vs foliage nitrogen (N) content per dry mass [4], Branch nitrogen (N) content per plant [3], Leaf anthocyanin content per area [3], Leaf anthocyanin content per dry mass [3], Leaf carotenoid content per dry mass [3], Leaf chlorophyll content per carotene content [3], Leaf nitrogen (N) retranslocation prior to leaf senescence [3], Leaf water content apoplastic [3], Stem nitrogen (N) content per plant [3], Stem surface area per dry mass [3], Branch respiration per volume [2], Leaf respiration coefficient growth [2], Leaf respiration coefficient maintenance [2].

TRY database accessed 1 December 2012.

Table 2.A2 Overview of the below-ground plant traits sorted by the number of multiple entries [in brackets]

Nitrogen fixation capacity [35843], Mycorrhizal type [14935], Seedbank lifespan [11463], Metamorphoses and morphological adaptations: shoot [7735], Metamorphoses and morphological adaptations: roots [4410], Metamorphoses and morphological adaptations: storage [3234], Rooting depth [2623], Seedbank location [2525], Root respiration per dry mass [2417], Litter potential decomposition rate [2120], Root nitrogen (N) content per dry mass [1492], Litter nitrogen (N) content per dry mass [1228], Root/shoot ratio [809], Litter phosphorus (P) content per dry mass [785], Root dry mass [677], Litter cellulose content per dry mass [503], Root δ^{15}N [441], Root radial oxygen loss [430], Litter SLA (litter leaf area per dry mass) [400], Root architecture [386], Root carbon (C) content per dry mass [378], Root exudation [363], Root porosity [358], Fine root length per dry mass (specific length) [352], Root cellulose content per dry mass [293], Root δ^{13}C [293], Root diameter [293], Root hemicellulose content per dry mass [293], Root lignin content per dry mass [293], Root soluble components content per dry mass [293], Root density [292], Root dry mass per plant dry mass [280], Litter lignin content per dry mass [255], Litter carbon (C) content per dry mass [216], Litter carbon/nitrogen (C/N) ratio [202], Fine root nitrogen (N) content per dry mass [189], Fine root carbon (C) content per dry mass [177], Root phosphorus (P) content per dry mass [169], Root nitrogen/phosphorus (N/P) ratio [161], Root alcohol dehydrogenase (ADH) activity [144], Fine root carbon/

Table 2.A2 Overview of the below-ground plant traits sorted by the number of multiple entries [in brackets]—cont'd

nitrogen (C/N) ratio [141], Litter tannin content per dry mass [110], Litter labile compound content per dry mass [102], Fine root phosphorus (P) content per dry mass [75], Root dry matter content per fresh mass (RDMC) [66], Coarse root dry mass per plant [64], Fine root dry mass per plant [62], Root respiration per nitrogen (N) content [48], Root respiration temperature dependence [48], Root sugar content per dry mass [48], Fine root lignin content [47], Coarse root carbon/nitrogen (C/N) ratio [46], Dead wood carbon/nitrogen (C/N) ratio [37], Fine root dry matter content per fresh mass [36], Fine root pH [35], Dead wood cellulose content [30], Dead wood lignin content [30], Fine root dry mass per unit ground area [30], Litterfall per ground area [27], Coarse root dry mass per unit ground area [26], Root nitrogen (N) uptake rate [24], Root phosphorus (P) uptake rate per root dry mass [23], Root nitrogen (N) content per plant nitrogen (N) content [20], Root non–structural carbon (C) content per dry mass (TNC) [20], Root dry matter content per volume [17], Coarse root nitrogen (N) content per dry mass [14], Root vessel diameter [13], Fine root cellulose content [12], Fine root labile carbon (C) compound content [12], Root area xylem [12], Coarse root dry mass per plant dry mass [10], Fine root dry mass per plant dry mass [10], Coarse root nitrogen (N) content per unit ground area [6], Fine root nitrogen (N) content per unit ground area [6], Litter water soluble carbon (C) content per dry mass [6], Coarse root carbon (C) content per dry mass [4], Root dry mass per ground area [3], Root nitrogen (N) content per dry mass *versus* leaf nitrogen (N) content per dry mass [3], Fine root nitrogen (N) content per plant [2], Root nitrogen (N) uptake rate per NPP [2], Root respiration per root surface area [2].

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