

Vegetation Functional Types and Traits at Multiple Scales

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Abstract Purpose and scale are the two main drivers that influence the description and classification of vegetation. Whereas the former can be relatively well defined, the latter is far more challenging where attributes that carry useful information at one scale often lack utility at another. Issues of scale dependency are widely discussed in theory but much less attention is given to their resolution in practice. This chapter considers how the advent of plant functional types and traits has added a new dimension to the study of scale dependence by replacing traditional, broad structural, species-based attributes with finer-scale trait characteristics and trait assemblages or ‘syndromes’ that reflect response-effect relationships of individuals and communities more explicitly along environmental gradients. Traditional scale-related aspects of vegetation classification are compared with recent advances involving plant functional types and traits, especially those expressed in holistic plant strategies. Case studies using global data sets illustrate a critical need for uniformity in data collection and analysis and address the question of scale dependency among specific sets of singular traits and trait syndromes at local, regional and biome scales.

Introduction

Purpose and scale are the two main drivers that influence the description and classification of vegetation. Whereas the former can be relatively well defined, the latter is far more challenging where attributes that carry useful information at one scale often lack utility at another. Issues of scale dependency are widely discussed in theory (Waide et al. 1999; Messier et al. 2010; Chakraborty et al. 2012; Chalcraft 2013; López-Martínez et al. 2013; Šímová et al. 2013), but much less attention is given to their resolution in practice. Most theoretical and empirical approaches invoke scale dependence between species richness and productivity, and for this reason there is a need for explicit consideration of scale in

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analytical studies of productivity and diversity (Waide et al. 1999). Yet such studies are rare. The advent of plant functional types and traits has added a new dimension to the study of scale dependence by replacing traditional, broad structural, species-based attributes with finer-scale trait characteristics and trait assemblages or ‘syndromes’ that reflect response-effect relationships of individuals and communities more explicitly along environmental gradients.

A key question concerns whether the relatively new trait-based ecology is better placed than traditional methods to cast light on how functional characteristics interact across varying environmental scales and whether functional types and traits can be exploited to improve our understanding of ecosystem dynamics. The aim of this chapter, therefore, is to review briefly the more traditional scale-related aspects of vegetation classification and then to compare these with recent advances involving plant functional types and traits, especially those expressed in holistic plant strategies. Case studies then address the question of scale dependency among specific sets of singular traits and trait syndromes at local, regional and biome scales.

Origins and Definitions

The nomenclature surrounding plant function is confused. ‘Functional type’, ‘functional trait’, ‘functional group’, ‘structure-function group’, ‘plant type’, ‘adaptive syndrome’, ‘strategy’ and ‘species group’ are but a few terms used to describe ecological groupings of species. Plant ‘function’, a term most often used to reflect adaptive behaviour, has its roots among the early ecologists, notably Alexander von Humboldt (1806), Eugenius Warming (1895, 1909) and his student Christen Raunkiær (1934). It was Andreas Schimper (1898) however, who established the connection between the physical environment and its physiological influence on vegetation at various global scales. Schimper reasoned that, across progressively finer scales, heat primarily controlled the flora, humidity the vegetation, with soil as a modifying factor. This hierarchical approach formed the basis for Schimper’s vegetation ‘**formations**’ within which he described groups of plants “of quite different modes of life”, namely ‘**guilds**’ (*Genossenschaften*) or plants that depend on others for their existence. Schimper’s guilds were restricted to lianes, epiphytes, saprophytes and parasites. Much later, Root (1967) extended the application of ‘guild’ to methods of resource use among birds (Rootian guilds), an essentially trophic concept that was modified by Wilson (1999) with further divisions (Alpha and Beta guilds) classified according to differences in resource use and environmental strategies respectively. More recently, Giordani et al. (2012) have allocated lichenized and lichenicolous fungi and bryophytes to “**functional guilds**”, based on growth form, reproductive strategy and photosynthetic traits.

Synusiae are frequently regarded as guild analogues but with a definite structural-functional connotation (e.g. moss layers). According to Pedrotti (2013), synusiae possess a dual significance: structural, as a concrete part of a phytocoenosis, and adaptive or functional, since they unite species with similar

adaptations (See also Barkman 1973). Much wider and less functional use of synusiae is applied to structural layers or strata, for example in rain forests (Williams and Adams 2010), although this usage lacks practical application in most structurally complex vegetation types. While guilds continue to be applied in faunal ecology, plant ecologists now are moving away from the use of guilds simply as trophic entities to a more complex response-effect ‘functional’ typology—a move presaged by Fosberg (1967). Much present-day functional ecology has its origins in the ‘**life form**’ (*livsform*) of Raunkjær (1934) (described below)—a ‘response’ type functional trait, based on the condition of the perennating organ during the most unfavourable season.

The need for mechanistic models of global classifications of structural-functional plant functional types (PFTs) was first recognized by Box (1981, 1996), who constructed a set of pheno-physiognomically defined plant types associated with ecophysiological functional traits that could be related directly to climate variables such as water balance and evapotranspiration. The first of its kind, the model proposed by Box provided a framework for subsequent finer-scale investigations of functional typology by Lavorel et al. (1997), who proposed four main types of functional classifications of plant species): (1) **emergent groups**—groups of species that reflect natural correlations of biological attributes; (2) **strategies**—species within a strategy have similar attributes interpreted as adaptations to particular patterns of resource use; (3) **functional types**—species with similar roles in ecosystem processes that respond in similar ways to multiple environmental factors; and (4) **specific response groups**—containing species that respond in similar ways to specific environmental factors. To these may be added specific **effect groups**—containing species that influence ecosystem performance either directly or indirectly (Díaz et al. 2002, 2007a, b; Lavorel et al. 2007). More recent applications now focus on functional traits as they apply to plant functional strategies that have attracted a diverse array of proposed models.

Plant Functional Strategies and Scale Dependency

Overview

When ecologically important plant traits are correlated, they may be said to constitute an ecological ‘strategy’ dimension when matched against trade-offs in investment (Westoby et al. 2002; Wright et al. 2007). More specifically, ‘**plant strategy**’ is usually taken to mean a combination of plant characteristics that optimize trade-off in resource allocation patterns in order to achieve maximum growth rate, maximum size and maximum age along with the plant’s growth response to different combinations of light and water availability (cf. Smith and Huston 1989). The different strategies manifested among species also contribute to the maintenance of diversity and hence ecosystem performance (Kraft et al. 2008; Bonser 2013), so that understanding plant ecological strategies and their application

Table 1 Summary of key plant functional strategies described in this chapter

Strategy	Main characteristics	Functional traits	Scale of application	Source
Leaf, Height, Seed size (LHS)	Parsimonious model of key elements of resource acquisition and return expressed primarily as tradeoffs between three main axes: SLA, H, S	SLA, LLS, seed mass (S) and fecundity, potential plant height at maturity (H), leaf size, shading, water use and response to disturbance, (LS) and twig size (TS)	Community to Biome. Excludes most succulent vegetation types	Westoby et al. (1998, 2002)
Leaf Economics Spectrum (LES)	Parsimonious model of quick-to-slow return on investments of nutrients and dry mass in leaves	LMA, Photosynthetic assimilation (A_{mass}), Leaf nitrogen (N), Leaf Phosphorus (P), dark respiration (R_{mass}), and leaf lifespan (LL).	Community to Biome. Excludes succulent vegetation types	Wright et al. (2004)
C-S-R	Characteristic developmental traits can be expressed within a triangular framework of competitor (C), stress-tolerator (S) and ruderal (R) strategists	Shoot morphology, leaf form, litter, max. potential RGR, leaf longevity, leaf phenology, flowering phenology, proportion of animal production devoted to seeds	Mainly herbaceous communities; limitations in complex woody vegetation	Grime (1977, 1979)
Life-form	Key adaptive strategies are indicated by the position of the perennating organ during the most unfavourable season	A set of Raunkiaëran life-forms.	Local to biome; all vegetation types	Raunkiaer (1934)
Vital attributes	Predicts successional changes in vegetation based on specific life history traits following disturbance	Propagule type, life stage, species presence	Communities subject to recurrent disturbance	Noble and Slatyer (1980)
Leaf, Life-form, Root (LLR)	Whole-plant combinations of functional traits are used to assess vegetation performance along biophysical gradients	36 generic functional traits based on leaf, life-form and above-ground root systems, combined according to a formal assembly rule	Any environment with potential for plant growth and survival. Local to biome	Gillison and Carpenter (1997), Gillison (2002, 2013)

across multiple scales has become one of the central facets of ecological research. This section introduces some of the better known plant strategies, the most significant of which are summarized in Table 1.

Three main directions of adaptive specialization are evident in the world flora, reflecting fundamental trade-offs between economics (conservative vs. acquisitive investment of resources) and size (Pierce et al. 2013). It is also argued (Lososová and Láníkova 2010) that two key processes affect the structure of trait values within

communities, namely competition and habitat filtering. Combined with traditional knowledge, these and other new insights are improving our ability to generalize broad strategic patterns and outcomes of competitive interactions among plants at various scales and to understand better the way functional traits and trait syndromes facilitate interactions among plants (Butterfield and Callaway 2013; Pierce et al. 2013). Across multiple scales, pattern and process remain elusive nonetheless.

Within the broad constraints of resource acquisition, four axes of specialization are considered pivotal to plant strategies (Westoby et al. 2002; Lavorel et al. 2007). These are contained within a well known strategy: the **Leaf, Height, Seed size** (LHS) model involving trade-offs between functionally independent traits. The related **Leaf Economics Spectrum** (LES) strategy (Wright et al. 2004) focuses on similarly parsimonious functional traits concerned with a quick-to-slow resource acquisition and return where functional relationships can be expressed along a biome-invariant scale (described later in this section). As well as the strategic dimensions outlined above, according to Craine (2009) all seed-plant diversity can be represented by four somewhat analogous central resource strategy axes: strategies for low nutrients, low light, low water, and low CO₂—with modifications for increases in resource supply. In the light of the above, for most practical purposes, a problem facing ecologists is the identification of a minimal set of factors among whole-plant trait syndromes and individual traits that best explain causal links within such an array of strategies and how these relate to scale. Most plant strategy models are fuelled by community-weighted means of species-related variables, with little attention to functional characterization at finer community or individual scale. At the level of the individual, the functional significance of leaf traits within the context of the entire plant becomes increasingly evident where plant responses along gradients of environmental adversity require coordinated responses of both whole plant traits and leaf traits alike (Bonser 2006).

The functional and strategic significance of leaf traits has analogues among root traits (Jackson et al. 1996; Craine et al. 2005; Roumet et al. 2006; Cornwell and Ackerly 2009; Liu et al. 2010; Laughlin et al. 2010), indicating clearly that not all trade-offs are above ground. Investment trade-offs between specific root length—the ratio of root length to root biomass (SRL)—and root nitrogen and lignin concentrations, indicate co-varying plant response (e.g. potential growth rate) along environmentally limiting gradients for overall plant growth (Comas and Eissenstat 2002; Craine and Lee 2003; Craine et al. 2005). Root structural and anatomical traits known to constrain relative growth rate and plant height at maturity are also considered potential links with hydraulic conductance, support and longevity (Hummel et al. 2007) and exert a feed-forward effect on stomatal conductance. Traits of woody roots in Neotropical tree species show, for example, close alignment with stem but not leaf traits. In their study of leaf, stem and woody-root traits in lowland South American forests Fortunel et al. (2012) identified two orthogonal axes of functional trade-offs: a first axis defined by leaf traits, corresponding to the LES, and a second axis defined by co-varying stem and woody-root traits, corresponding to a '**wood economics spectrum**'. These axes remain consistent when accounting for species evolutionary history with phylogenetically independent contrasts. A related study in subtropical forests in eastern

China, by Kang et al. (2013), found that leaf and wood traits varied differently across ecological scales, suggesting that trait variability is tissue-specific. More importantly, they concluded that these decoupled trait axes may increase the dimensionality of niche space and thus facilitate species co-existence in forest communities—until now a feature not regarded as significant.

Consistency between above-ground and below-ground trait strategies observed by Mokany and Ash (2008) suggests that below-ground traits may be predictable from above-ground traits, reducing the need to quantify root traits, at least in controlled conditions. On the other hand, Liu et al. (2010) have shown that, across multiple scales, while both root and leaf traits exhibited most of their variance among individuals and species within communities, variance in leaf traits tended to be relatively higher at coarser spatial scales than in root traits.

Among the more significant plant ecological strategies involving whole-plant functional types and individual traits is the **‘resource-ratio’ model** of Tilman (1982, 1985; cf. Clark et al. 2007) that views the spatial heterogeneity of resources as selecting for optimal foraging in chronically unproductive habitats. However, Tilman’s model requires precise ordering of trade-offs, for example, between life history and competitive ability in which data for the ability of multiple coexisting species may be limiting (Pierce et al. 2005). It is also argued by Miller et al. (2005) that additional validation is needed in many circumstances, although this is partly contested by Wilson et al. (2007). It is here that ecological context may play a significant role, as it is argued by Jabot and Pottier (2012) that the resource-ratio and **CSR theories** (Grime 1979) make different predictions regarding competition on poor soils, not because of their differing schemes of plant strategies, but because of the different disturbance types that they consider. In such cases Tilman’s predictions apply to marginally disturbed natural habitats, whereas Grime’s predictions target more disturbed conditions. Both approaches are based largely on temperate herbaceous communities and are yet to be tested in structurally and floristically rich communities such as those in humid lowland tropical forests.

In forecasting plant functional response along gradients of increasing abiotic stress, the **‘stress-gradient hypothesis’** (SGH) predicts that the frequency of facilitative and competitive interactions will vary inversely across abiotic stress gradients, with facilitation being more common in conditions of high abiotic stress relative to more benign abiotic conditions. Limitations in the way SGH had been studied led Maestre et al. (2009) to suggest differentiating between the original idea of how ‘common’ interactions might be along stress gradients and the ubiquitous empirical approach of studying shifts in the strength of pair-wise interactions. In line with this approach, a study of vegetation response (Gross et al. 2013) along a major aridity gradient in Spain at multiple scales (regional, community, neighbourhood) revealed that, despite their opposing influence, habitat filtering (trait convergence) and niche differentiation (trait divergence) acted simultaneously on species where competition and facilitation interacted with aridity in determining community structure. A key consequence of this finding is evidence that opposing traits (trait convergence and trait divergence) can interact effectively along regional gradients, suggesting further examination of the relative trait contributions to plant performance at individual trait level and with traits combined as a whole-plant syndrome (see also Armas et al. 2011; Maire et al. 2012).

The ‘**mass ratio hypothesis**’ (MRH) of Grime (1998) predicts that the effect of species or groups of species on ecosystem properties will depend on their proportional abundance in a community. The hypothesis is supported by empirical evidence (Díaz et al. 2007a; Garnier et al. 2004; Mokany et al. 2008; Laughlin 2011) and implies that the ecosystem function is determined to a large extent by the trait values of the dominant contributors to the plant biomass. According to the MRH, ecosystem properties should be predictable from the community-weighted mean of traits with proven links to resource capture, usage, and release at the individual and ecosystem levels. Díaz et al. (2007a) point to overwhelming evidence that the more abundant traits are major drivers of short-term ecosystem processes and their scale-related feedbacks onto global-change drivers. On the other hand, McLaren and Turkington (2010) argue that the effects of losing a functional group do not depend solely on the group’s dominance and that functional group identity plays a critical role in determining the effects of diversity loss—an argument that plays directly into the debate on functional redundancy.

Other, relatively well known but now less widely applied strategies include the ‘**Vital attribute**’ strategy of Noble and Slatyer (1980), which is based on the residence time of specific life-history traits following disturbance. This is one of the very few plant strategy models specifically geared to predict community outcomes in disturbance-related vegetation successional sequences. The strategy is better suited to community level rather than higher assembly scales where logistic and computational requirements unfortunately limit practical application. In a similar way, the well-known **r-K model** of MacArthur and Wilson (1967) (r indicating high rate of reproduction at low cost and K low rate of reproduction at high cost), while conceptually attractive, tends to oversimplify interaction between strategists. The r-K model also presents methodological limitations in many complex vegetation-successional sequences at local and regional scale where the indeterminacy of an r versus K characteristic detracts from its utility. This in turn reflects a general condition that the successful application of different strategies has as much to do with environmental context as it does with spatial scale. Other, less well known strategies are reviewed elsewhere (Westoby 1998; Lavorel et al. 2007; Gillison 2013).

Perhaps the most persistent and most successful plant strategy over the last century is that of Raunkiaer’s (1934) ‘**life-form model**’. Raunkiaer defined life form (*livsform*) theoretically as “The sum of the adaptation of the plant to the climate” (Du Rietz 1931) but in practice selected one of the most fundamental adaptations as a base for his systems of life forms, namely the survival of the perennating organ during the most unfavourable season. Although based primarily on sensitivity to winter temperatures, Raunkiaer’s strategy is applicable to ‘unfavourableness’ under other periodic or episodic, thermal, light, and moisture regimes including flood, fire and strong winds. The method (especially his ‘life-form spectrum’) has been applied widely across the globe with varying results, and a global physiognomic-ecological vegetation classification that includes the Raunkiaer model (Mueller-Dombois and Ellenberg 1974) is rarely applied in practice. It can be argued nonetheless that, as a plant ecological strategy, Raunkiaer’s system is consistent with a theoretical trade-off of carbon investment per individual

against tissue loss and reproductive and regenerative capacity under regimes of cyclic environmental extremes. Thus a gradient can be shown to exist between a dominance by woody phanerophytes in ‘optimal’ environments with corresponding decreases towards less optimal habitats accompanied by an increasing relative percentage of structurally reduced chamaephytes, geophytes and hemicryptophytes (Gillison 2013). Although frequently confused with the more physiognomic ‘growth forms’, Raunkiaer’s system remains attractive in its simplicity and its general application across many spatial and temporal scales. The system is greatly limited however, through an inability to account for critical adaptive elements related to plant physiological response to environmental change, in particular photosynthesis—a characteristic considered further in the ‘**LLR strategy**’ described below.

The following four strategies (CSR, LHS, LES and LLR) (Table 1) are described here in greater detail, as they share some common traits that are recognized determinants of plant growth, persistence and productivity. Together with primarily leaf-based features, they reflect a paradigm shift towards measureable evidence of cause and effect between functional traits and environment beyond the more loosely defined adaptive or ‘epharmonic’ Raunkiaer descriptors. With the possible exception of CSR, a feature in common with all of these strategies is their applicability across multiple scales.

The C-S-R Strategy

Apart from the Raunkiaer model, CSR is one of the best known plant strategy theories, which considers the interaction between competition (limitations to biomass production imposed by other species), stress (direct limitations to biomass production imposed by the environment) and disturbance (biomass removal or tissue destruction) in shaping phenotype. According to CSR theory, characteristic developmental traits are inherent to competitor (C), stress-tolerator (S) and ruderal (R) strategists, with apparent intermediate strategies (Grime 1977, 1979; Caccianiga et al. 2006). A fundamental aspect of CSR suggests that stress and indeterminate resource availability favour conservative phenotypes (Pierce et al. 2005). Although most theoretical support for CSR is derived from extensive studies on herbaceous vegetation in the UK, methodological limitations constrain its application in other countries containing especially species-rich, structurally and functionally complex woody vegetation (Gillison 2013). A partial solution to the methodological impasse (Hodgson et al. 1999; Hunt et al. 2004) is to allocate a functional type to an unknown subject using a few, simple predictor variables. Traits such as leaf weight, specific leaf area (SLA) and leaf dry matter content (LDMC) can be linked statistically with productivity traits that are relevant, for example, to the S type (slow-growing, stress-tolerant species of chronically unproductive habitats). An ordination of these more readily measurable traits then allows the taxa under study to be placed within CSR coordinate space.

A potential solution to the problem in applying standard CSR methods to vegetation complexes containing both woody and herbaceous plants is proposed by Pierce et al. (2013), who employed Principal Components Analysis and a

spreadsheet procedure that returns ternary coordinates and tertiary CSR strategies for target subjects based on leaf area (LA), dry-matter content (LDMC) and specific leaf area (SLA). The method by Pierce et al. (2013) allows classification of target species within a triangular space corresponding to Grime's theoretical CSR triangle and is arguably sufficiently precise to distinguish between different strategies of species within genera and within populations of species. While various authors argue that rapid CSR classification of woody and herbaceous vascular plants is thus possible over landscape scales via ordination procedures, the application has yet to be tested in wide-ranging, complex habitats such as tropical land-use mosaics.

According to Westoby (1998), the CSR triangle defines the axes with reference to concepts, for which there is no simple protocol for positioning species beyond the reference datasets within the scheme; consequently, benefits of worldwide comparison have not materialized. Both theoretical and practical limitations are evident where, under studies of grazing impact and shoreline successional sequences, CSR types cannot be applied readily (Oksanen and Ranta 1992; Ecker and Rydin 2000; Moog et al. 2005). Problems with the CSR format have been noted elsewhere (Austin and Gaywood 1994; Onipchenko et al. 1998; Körner and Jeltsch 2008), although certain studies show promise along environmental gradients including grazing intensity (cf. Cerabolini et al. 2010; Kiliç et al. 2010; Frenette-Dussault et al. 2012; Kelemen et al. 2012; Schmidtlein et al. 2012). Nonetheless, as a scale for environmental assessment, Grime's (1979, 2001) ruderality (R) also has the relatively unsatisfactory feature that some species with high ruderality are mainly associated with perennials that are not ruderal (Hill et al. 2002). Despite improved numerical procedures, the capacity of CSR theory to predict variation in species composition and interaction along environmental gradients remains problematic across differing community and landscape scales.

The Leaf-Height-Seed Size Strategy

The almost infinite array of co-varying plant functional types and traits constrains the search for a 'core' set of orthogonal (functionally independent), parsimonious traits that facilitates the construction of plant strategies in a way that avoids the tyranny of scale. Such an approach, based on specific Leaf area (SLA), mature plant Height (H) and Seed mass (S), i.e. the LHS system of Westoby (1998), represented a significant breakthrough in quantifying plant response to environment, with capacity for generic application worldwide. The LHS system represents a tightly defined functional concept using orthogonal (independently functioning) parsimonious traits and as such indicates a paradigmatic shift towards the understanding and application of plant functional traits. As described by Westoby (1998), the LHS plant ecology strategy scheme employs three axes: SLA (light-capturing area deployed per unit of dry mass allocated), height of the plant's canopy at maturity, and seed mass in which the strategy of a species is described by its position in the volume formed by the three axes. The benefits of the LHS scheme can be understood by comparing it to Grime's CSR scheme over which it has several

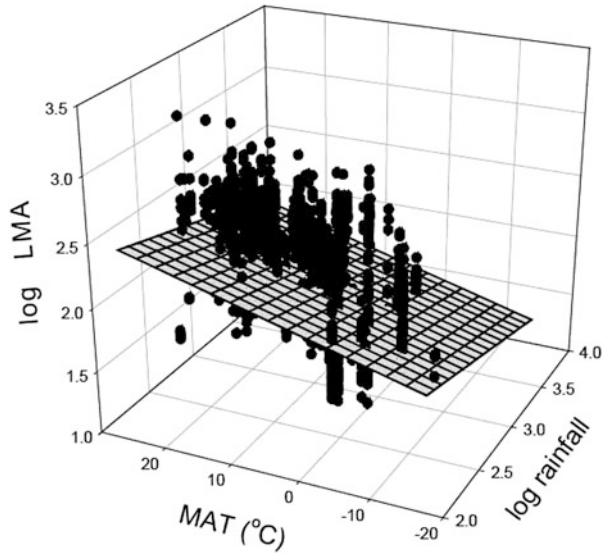
advantages. Whereas certain elements of the CSR scheme (e.g. the C–S dimension) are overtly conceptual, and as such present methodological limitations (Westoby 2007), these limitations are essentially overcome by the more readily quantifiable LHS approach that can be arguably applied at a world scale to any vascular plant species in any terrestrial environment. Apart from these positives, the advantage of the axes defined through a single, readily measured variable needs to be weighed against the disadvantage that single plant traits may not capture as much strategy variation as CSR's multi-trait axes (Westoby 1998).

Apart from its evident application at biome scale, there is evidence that the success of the LHS system is supported at community scale, for example in North American pine forests (Laughlin et al. 2010) and elsewhere, but not necessarily at species level, as described under grazing systems by Golodets et al. (2009). Spatial scale and environmental context clearly influence the utility of LHS where differences in detecting community response can be detected when CSR and LHS strategies are compared in managed grasslands (Moog et al. 2005). Detailed studies in alpine vegetation based on LHS traits (de Bello et al. 2012a, b) emphasized the hierarchical nature of ecological forces in shaping local species assemblage where coarse-scale environmental filters have a primary effect in selecting the pool of species adapted to a site, followed by filters at finer scales that determine species abundances and local species coexistence. According to de Bello et al. (2012a, b), different components of functional community structure respond differentially to environmental change, so that predicting plant community responses will require a hierarchical multi-faceted approach. From a practitioner's viewpoint, and despite established theory, the largely 'laboratory-based' LHS approach constrains the practical acquisition of specific trait data in poorly documented, complex vegetation types. As well, no study so far appears to confirm the utility of LHS as a bioindicator, as illustrated for example in its failure to predict dispersal guilds of birds (Jardim and Batalha 2008) (see section below on bioindicators).

The Leaf Economics Spectrum Strategy

There are evident common trends and functional linkages between the LHS strategy and the LES scheme proposed by Wright et al. (2004) that describes, at global scale, a universal spectrum of leaf economics consisting of key chemical, structural and physiological properties. The spectrum reflects a quick-to-slow return gradient on investments of nutrients and dry mass in leaves that are reflected in six key attributes: LMA (leaf mass per area), photosynthetic assimilation rates (A_{mass}), leaf nitrogen (N), leaf phosphorus (P), dark respiration rate (R_{mass}), and leaf lifespan (LL). Unlike many other strategies, LES is frequently regarded as independent of growth form, plant functional type or biome, a feature not without implications for ecological applications requiring vegetation classification at multiple scales. According to Wright et al. (2004) categories along the spectrum would, in general, describe leaf economic variation at the global scale better than plant functional types, because functional types overlap substantially in their leaf traits.

Fig. 1 Leaf mass per unit area (LMA) (SLA) response to mean annual temperature (MAT) and Log rainfall. Reproduced from Wright et al. (2004) with permission from *Nature*



It is argued by Shipley et al. (2005) that functional linkages between leaf traits and net photosynthetic rate provide a mechanistic explanation for the empirical trends relating leaf form and carbon fixation, and predict that SLA and leaf N must be quantitatively co-ordinated to maximize C fixation, thus lending support to the scale-invariant nature of the LES scheme.

Current evidence suggests nevertheless that the pattern of universality demonstrated by the LES at predominantly global scale (Fig. 1) remains to be confirmed effectively at community or habitat scale. Greenhouse experiments conducted by Wright and Sutton-Grier (2012) on a suite of co-occurring wetland species showed that, apart from significant relationships between specific leaf area and photosynthetic rate under some treatments, there was little support for the relationships predicted by the LES. When examined for their potential connection with ecosystem processes, Jackson et al. (2013) also found that LES traits and litter decomposability were decoupled at infra-specific and whole-community levels in temperate New Zealand forests—a finding that contrasts with studies in a Bolivian lowland forested land-use mosaic by Bakker et al. (2011), in which leaf and litter traits were closely associated. In line with the LES, the Bolivian study also showed a slow-fast continuum over which both individual traits of living leaves and species' position on the LES persisted in litter, indicating that leaves lead influential afterlives, affecting decomposition, nutrient and carbon cycling—a possibility also considered by Freschet et al. (2012).

Other evidence suggests that the biome-invariant LES model may not perform as well as expected across different floras. Differences in leaf-trait allometries among global floristic regions were examined by Heberling and Fridley (2012) who evaluated biogeographic effects on bivariate relationships between LES traits, including relationships of photosynthetic capacity and dark respiration rate

($A_{\text{mass}} - R_{\text{d}_{\text{mass}}}$), leaf lifespan and mass per area ratio (LL–LMA), and photosynthetic capacity and nitrogen content ($A_{\text{mass}} - N_{\text{mass}}$). Their results indicate that evolutionary histories of different floras clearly mediate the scale-invariance implied in the LES model where independent floras can exhibit different tradeoffs in resource-capture strategies.

At the genetic level, Vasseur et al. (2012) tested the evolutionary assumptions of metabolic scaling theory (MST) and the LES using a cross of two genetic variants of *Arabidopsis thaliana*. They found that a small set of pleiotropic genes underlies many plant functional traits and life histories, potentially unifying MST and LES within a common genetic framework. Vasseur et al. (2012) suggest further that observed intermediate size and longevity in natural populations originate from stabilising selection to optimise physiological trade-offs. Despite these findings it remains to be seen whether pleiotropic infraspecific relationships based on a herbaceous winter-annual species can be extended across different life forms to confirm scale-invariance of both MST and LES from species to biome. Although attractive, the prospect of a universal gene-based schema is yet to be demonstrated at the inter-specific and community level among very different trait syndromes involving, for example, woody perennials in forest canopies that exhibit a differential response to habitat filtering and physiological trade-offs along photon flux-density gradients (cf. Posada et al. 2009).

The scale-invariant LHS and LES models are driven primarily by leaf-based traits that ignore significant elements of the world's succulent and semi-succulent vascular flora (~10,000 species, Oldfield 1997), in which the photosynthetic organs and tissues are not readily amenable to quantification of SLA (1/LMA). Further, while SLA is not the only functional trait used in these models, the potentially uncritical application of SLA in plant ecology sounds a note of caution where, for example, SLA values can be similar among otherwise functionally highly dissimilar PFTs, for example the subalpine fir *Abies lasiocarpa* (39.3), the lingonberry *Vaccinium vitis-idaea* (41) and the tropical mangrove *Lumnitzera littorea* (41.2) (SLA values from Wright et al. (2004) and I. J. Wright, pers. comm.).

The Leaf-Life-Form-Root Strategy

Both the LHS and LES strategies are based on parsimonious, arguably independently functioning traits that, although exhibiting a clear case for a biome-invariant pattern, pay only limited attention to other potential trait-interactions or the possibility of a potential 'functional Gestalt' where the totality of functional trait combinations at a 'whole-plant' level represents more than just the apparent sum of the functional parts. Arguments for parsimony assert that orthogonal traits achieve an economy of scale in expressing ecological performance that is otherwise unattainable in "overlapping" or co-varying functional types. Across multiple scales it is yet to be confirmed however, that parsimony is a more effective in predicting response-effect relationships along environmental gradients within and

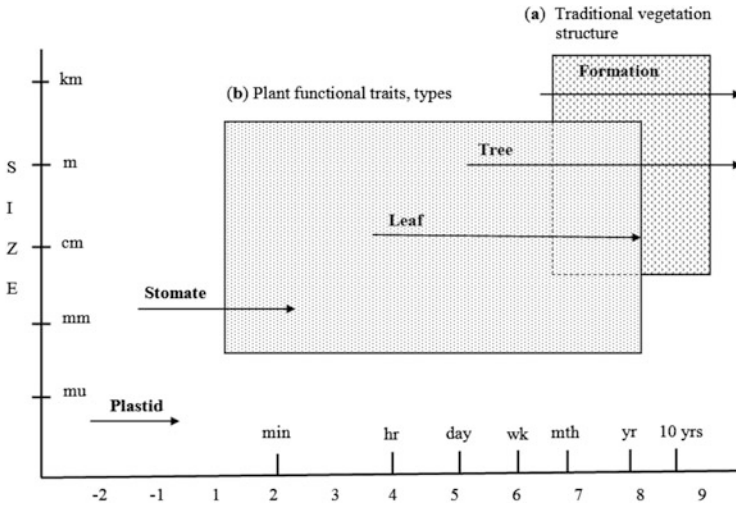


Fig. 2 Approximate log response time (s) of above-ground plant elements including spatio-temporal domains of PFT and individual trait sensitivity. (a) Formation class and (b) Generalized zone of plant functional classifications (adapted from Gillison 2002)

between plant species than functional ‘whole-plant’ syndromes containing co-varying traits. To this extent the LLR approach considers ways in which multiple traits can be used to construct plant functional types (PFTs) or trait syndromes via an assembly system that addresses whole-plant performance rather than economically-acquisitive, single traits such as LMA. This is achieved in part by coupling photosynthetic traits with life form and above-ground rooting structures, and is consistent with observed stem-root interaction (cf. Fortunel et al. 2012). When coupled with additional information that describes vegetation structure, the methodology facilitates comparative analysis across a range of environmental scales (Fig. 2) (Gillison 1981, 2002, 2013). The LLR strategy complements significant gaps in the CSR, LHS and LES systems that otherwise exclude critical photosynthetic traits such as leaf inclination (Falster and Westoby 2003; Posada et al. 2009), leaf phyllotaxis or insertion pattern such as rosettes (Withrow 1932; Lavoire et al. 1998, 1999a, b; Díaz et al. 2007a; Ansquer et al. 2009; Bernhardt-Römermann et al. 2011) and green-stem photosynthesis, all notable plant adaptations to irradiance, nutrition and water availability.

As discussed, one strategy that has stood the test of time is the Raunkiaer life-form system, partly because it is built on a fundamental survival adaptation to cyclic environmental and edaphic (nutritional) extremes and partly because it is simple, with mostly readily observable traits. In its basic form, however, and despite external reference to a table of leaf size classes, the Raunkiaer model excludes photosynthetic traits. In a move to help redress this issue but to retain the essential Raunkiaer format, Gillison (1981) devised a whole-plant classification system based on plant functional attributes in which a plant individual is classified

as a ‘functionally coherent’ unit composed of a photosynthetic ‘envelope’ supported by a modified Raunkiaer life form and an above-ground rooting system presented as the Leaf-Life form-Root’ or LLR spectrum (Gillison 2013).

A fundamental tenet of the LLR is that a single attribute, such as leaf size class, takes on additional functional significance when combined with leaf-inclination and other morphological (e.g. leaf stomatal distribution) and temporal (e.g. deciduous) descriptors of photosynthetic tissue. In this case the photosynthetic attributes describe a ‘functional leaf’ that includes any part of the plant (including the primary stem cortex) capable of photosynthesis. Unlike LHS and LES, this includes succulent vegetation (ca. 10,000 species, Oldfield 1997) that involves significant elements of world flora. For convenience, and to indicate the unique type of PFT, specific LLR combinations are termed functional *modi* (from *modus* Latin SM II, meaning mode or manner of behaviour) (compare also the “modality” of Violle et al. 2007). This initial model (Gillison 1981) appears to be the first coordinated use of plant functional attributes (PFAs) or functional traits to relate whole-plant PFTs to environmental conditions. The method was subsequently formalized (Gillison and Carpenter 1997) using an assembly-rule set and syntactical grammar to construct *modal* PFTs based on 36 generic plant functional elements (PFEs) (Table 2). In this method, a typical PFT *modus* for an individual of *Acer palmatum* might be a mesophyll (*me*) leaf size class with pendulous (*pe*) inclination, dorsiventral (*do*) (hypostomatous), deciduous (*de*) leaves with green-stem (cortex) (*ct*) photosynthesis supported by a phanerophyte (*ph*), the resulting *modal* PFT combination being *me-pe-do-de-ct-ph*.

Within the same species on the same or other site, variation in any one functional element, such as leaf size class, results in a new *modus*, thereby facilitating comparison of intra- as well as inter-specific variability at a described location. This can be especially useful where phenotypic expression within a species may be expressed in different modal combinations along an environmental gradient ranging, for example, from a dry ridge (e.g. small vertically inclined leaves) with skeletal soil to a river margin on alluvium (larger, laterally inclined leaves). With the public-domain VegClass software package (Gillison 2002), quantitative and statistical comparisons within and between species and plots are facilitated via a predetermined ‘costing’ of lexical distances between different PFTs (Gillison and Carpenter 1997). The system comprises a many-to-many mapping whereby more than one modal PFT can be represented within a species and *vice versa*. While ~7.2 million combinations are theoretically possible, a data set compiled using a standard recording proforma (Table 3) from 1100 field sites worldwide covering all major latitudes and climates (Fig. 3) indicates the ‘real’ number of unique modal PFTs approximates 3500 for the world’s approximately 300,000 vascular plant species. For vascular plants, Fig. 4 illustrates whole-plant LLR functional syndromes arranged along two key environmental gradients or axes (irradiance and moisture—see also Lavers and Field 2006).

The distribution of species and PFTs can be seen to vary with latitude (Fig. 5) and, while a strong linear relationship exists between them at global scale (Fig. 6), regression slopes between species and PFT correlations can vary predictably

Table 2 VegClass data variables recorded for each 40 m × 5 m transect

Site feature	Descriptor	Data type
Location reference	Location	Alpha-numeric
	Date (dd-mm-year)	Alpha-numeric
	Plot number (unique)	Alpha-numeric
	Country	Text
Observer/s	Observer/s by name	Text
Physical	Latitude deg. min. sec. or decimal deg. (GPS)	Alpha-numeric
	Longitude deg. min. sec. or decimal deg. (GPS)	Alpha-numeric
	Elevation (m.a.s.l.) (aneroid or GPS)	Numeric
	Aspect (compass. deg.) (perpendicular to plot)	Numeric
	Slope percent (perpendicular to plot)	Numeric
	Soil depth (cm)	Numeric
	Soil type (US Soil taxonomy)	Text
	Parent rock type	Text
	Litter depth (cm)	Numeric
	Terrain position	Text
Site history	General description and land-use/landscape context	Text
Vegetation structure	Vegetation type	Text
	Mean canopy height (m)	Numeric
	Canopy cover percent (total)	Numeric
	Canopy cover percent (woody)	Numeric ^a
	Canopy cover percent (non-woody)	Numeric ^a
	Cover-abundance (Domin)—bryophytes	Numeric
	Cover-abundance woody plants <2 m tall	Numeric
	Cover-abund. lichens (crustose, fruticose, foliose)	Numeric
	Basal area (mean of 3) (m ² ha ⁻¹)	Numeric
	Furcation index (mean and cv % of 20)	Numeric
Plant taxa	Profile sketch of 40 m × 5 m plot (scannable)	Digital
	Family	Text ^b
	Genus	Text ^b
	Species	Text ^b
	Botanical authority	Text ^b
Plant functional type	If exotic (binary, presence-absence) ^a	Numeric
	Plant functional elements (36) combined according to published rule set.	Text
Quadrat listing	Unique taxa and PFTs per quadrat (for each of 8 (5 m × 5 m) or more quadrats) ^a	Numeric
Photograph	Hard copy and digital image ^a	JPEG

^aPreferably a radial view from plot centre and with embedded date and GPS reference^bWhere identified, usually with voucher specimens, used directly in numerical analysis

Table 3 Plant functional attributes and elements

Attribute	Element	Description	
<i>Photosynthetic envelope</i>			
Leaf size	nr	no repeating leaf units	
	pi	picophyll	<2 mm ²
	le	leptophyll	2–25
	na	nanophyll	25–225
	mi	microphyll	225–2025
	no	notophyll	2025–4500
	me	mesophyll	4500–18,200
	pl	platyphyll	18,200–36,400
	ma	macrophyll	36,400–18 × 10 ⁴
	mg	megaphyll	>18 × 10 ⁴
Leaf inclination	ve	vertical	>30° above horizontal
	la	lateral	±30° to horizontal
	pe	pendulous	>30° below horizontal
	co	composite	
Leaf chlorotype	do	dorsiventral	
	is	isobilateral or isocentric	
	de	deciduous	
	ct	cortic	(photosynthetic stem)
	ac	achlorophyllous	(without chlorophyll)
Lf. morphotype	ro	rosulate or rosette	
	so	solid 3-D	
	su	succulent	
	pv	parallel-veined	
	fi	filicoid (fern)	(Pteridophytes)
	ca	carnivorous	(e.g. <i>Nepenthes</i>)
<i>Supporting vascular structure</i>			
Life form	ph	phanerophyte	
	ch	chamaephyte	
	hc	hemicryptophyte	
	cr	cryptophyte	
	th	therophyte	
	li	liane	
Root type	ad	adventitious	
	ae	aerating	(e.g. pneumatophore)
	ep	epiphytic	
	hy	hydrophytic	
	pa	parasitic	

between widely separate biogeographic regions (Fig. 7) as well as at progressively finer scales, for example along gradients of land-use intensity in tropical forested landscape mosaics and in extreme habitats such as arctic tundra (Gillison 2012, 2013). PFT syndromes reflecting position along these gradients together with

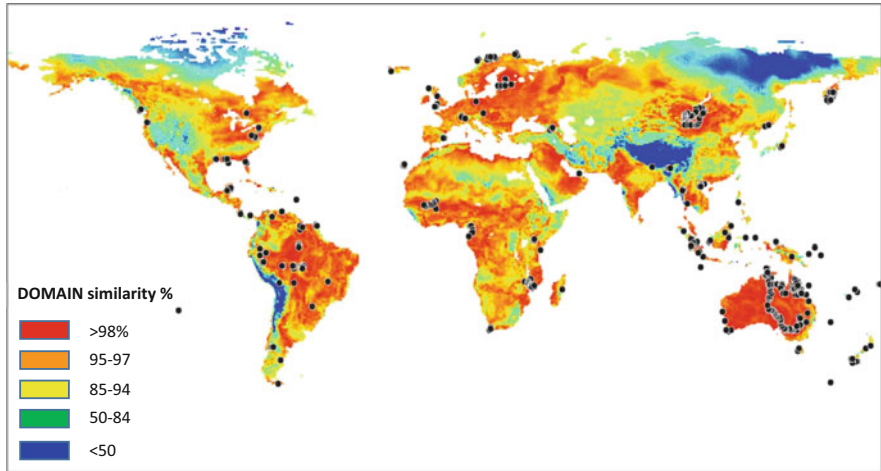


Fig. 3 DOMAIN similarity mapping of key climate variables based on mean annual precipitation (mm), mean annual actual evapotranspiration (mm), mean minimum temperature of coldest month (°C) and elevation (m) above sea level. Legend indicates percentage representation of these environmental domain values derived from 1138 (40 m × 5 m) VegClass transects (*black points*)

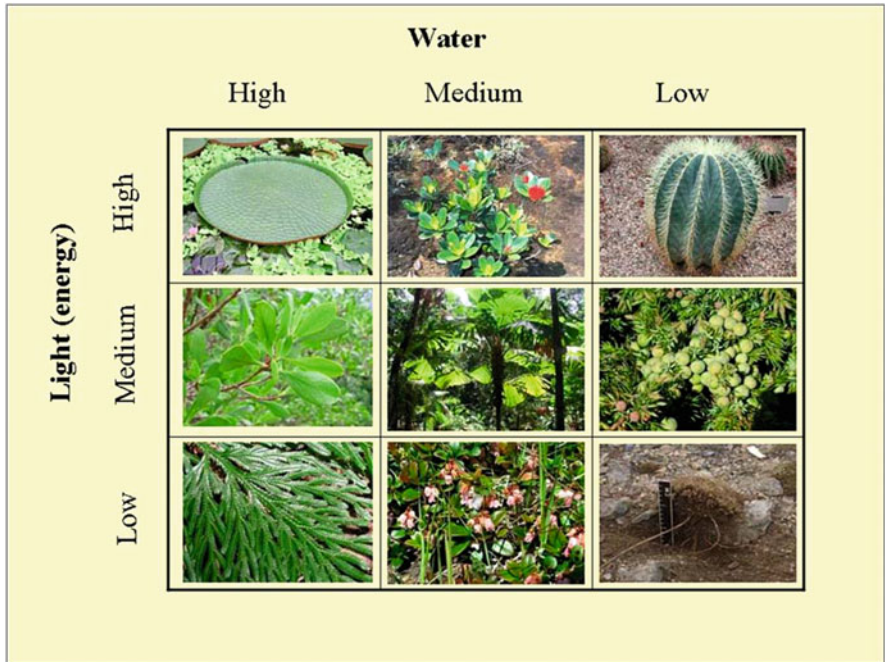


Fig. 4 Different whole-plant PFT syndromes, positioned subjectively along gradients of light (energy) and moisture. L to R: *Victoria regia* (Amazon basin), *Metrosideros* sp. (Philippines), *Echinocactus* sp. (Mexico), mangrove *Lumnitzera littorea* (Indomalesia), phanerophytic swamp fan palm *Licuala ramsayi* (tropical N. Australia), *Juniperus communis* (Fennoscandia), fern *Selaginella* sp. (Indomalesia), *Vaccinium vitis-idaea* (boreal region), and cushion plant *Azorella macquariensis* (subantarctic Macquarie Isl.). Each example can be described as a *modal* PFT according to the VegClass method described under the LLR strategy (after Gillison 2002)

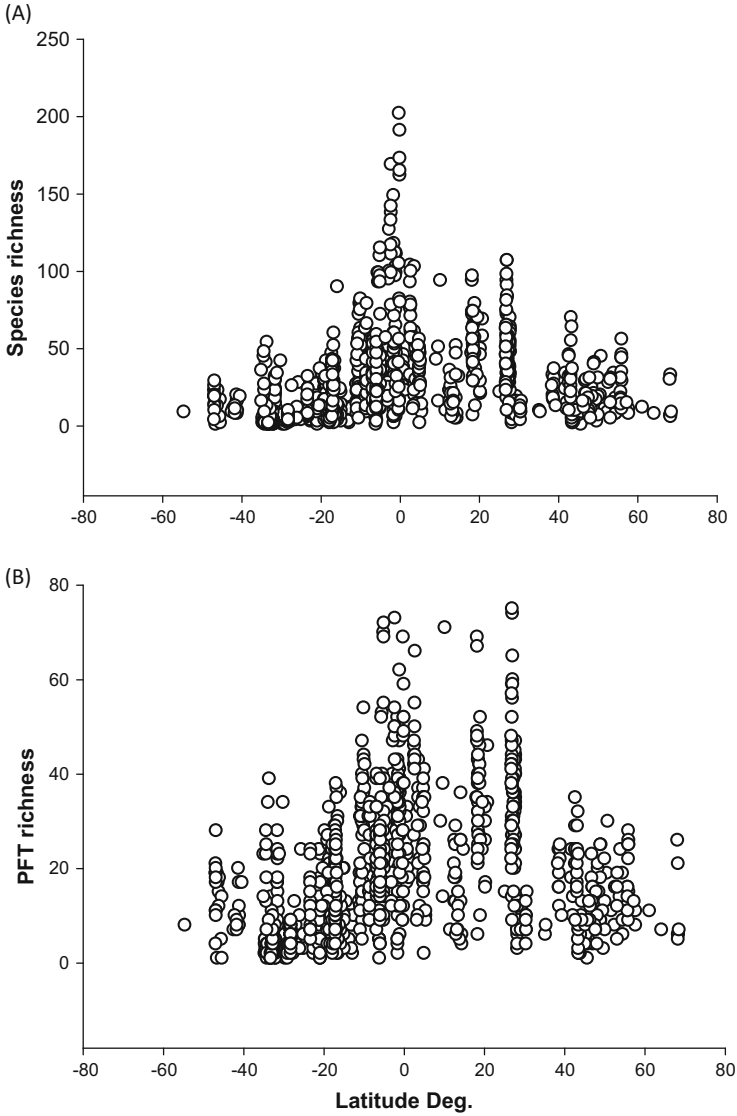


Fig. 5 Variation of vascular plant species and *modal* PFT richness with latitude. Data from 1138 (40 m \times 5 m) transects (see Fig. 3)

disturbance are readily described according to the modal schema and at global scale. Unlike the log-transformed linear relationships indicated in Fig. 1 for LES, untransformed LLR values such as individual PFTs and PFEs can exhibit two-dimensional, mostly non-linear responses to mean minimum temperature of the coldest month (Fig. 8a, b) as well as three-dimensional responses with minimum temperature of the coldest month, mean annual precipitation and mean annual

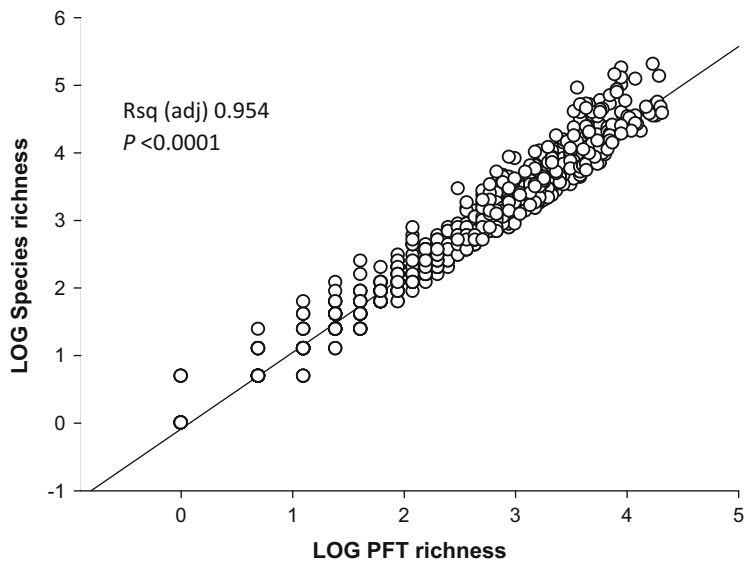


Fig. 6 Counts of vascular plant species regressed against counts of unique (distinct from species) modal PFTs from 1138 (40 m × 5 m) transects as indicated in Fig. 3

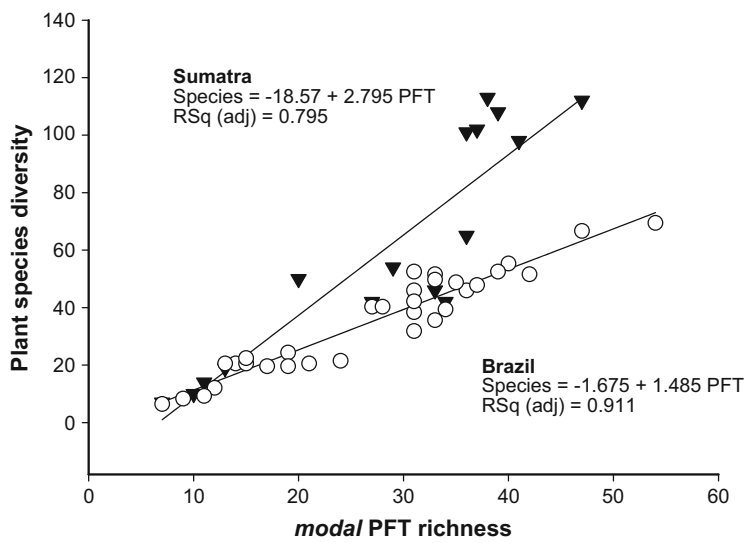
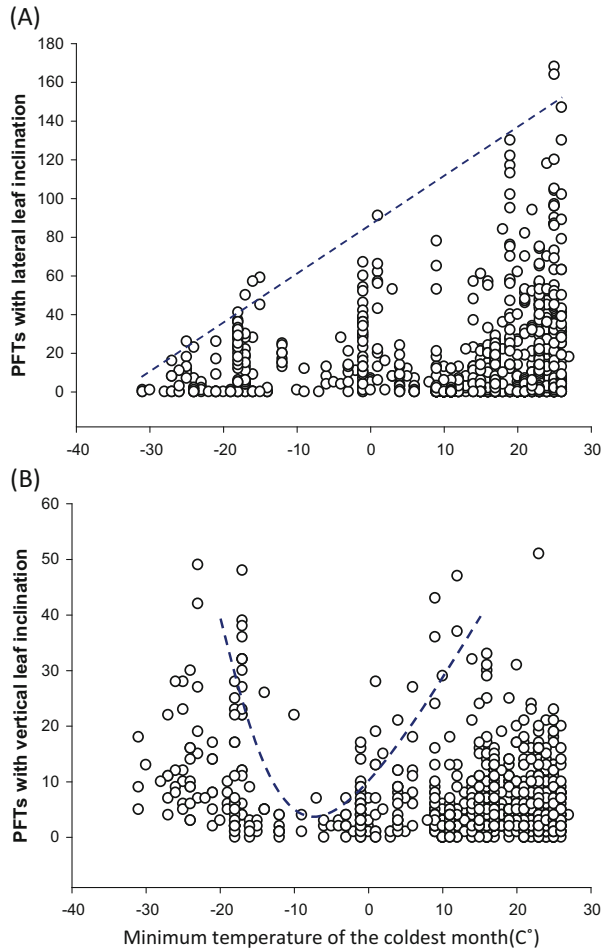


Fig. 7 Different regional ‘signatures’ in species diversity (species richness)-to-modal PFT richness ratios along similar land-use intensity gradients and vegetation mosaics in Sumatra (triangles) and Brazil (circles) may reflect evolutionary separation of floras and functional characteristics. Data points are 40 m × 5 m transects from which species and modal PFT counts were recorded (after Gillison et al. 2013)

Fig. 8 Leaf inclination shows divergent response to minimum temperatures within PFTs in 1138 (40 m × 5 m) transects at global scale (*circles*). (a) Leaf lateral inclination; (b) Leaf vertical inclination (*lines hand-drawn*)



actual evapotranspiration (Figs. 9, 10). Unlike meta-data sets based on community-weighted means of traits, the LLR data used in VegClass are based on original counts.

Functional diversity measures based on the abundance of species per PFT (Shannon H', Simpson's D and Fisher's Alpha) can also be generated on demand in VegClass, with the inverse of the PFT Simpson measure equating to Rao's quadratic entropy (Botta-Dukat 2005; Lepš et al. 2006; Mason et al. 2012; Vandewalle et al. 2014). A separate measure of plant functional complexity (PFC), based on a minimum spanning-tree distance of PFT values within a transect, also provides a useful comparator between sites where the number of PFTs is the same but where their identities differ. The PFC measure has been found useful as a bioindicator, as it is also independent of species—a useful feature where species identification is problematic. An indication of the application of the LLR at global

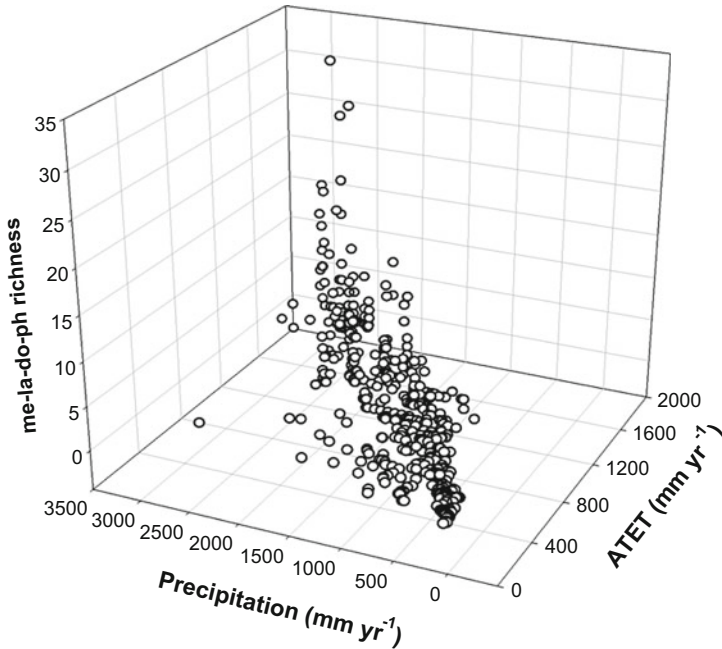


Fig. 9 Example of a *modal* PFT (me-la-do-ph) with mesophyll leaf size class, lateral leaf inclination, dorsi-ventral (hypostomatous) leaf supported by phanerophyte structure, showing distribution against mean annual precipitation (mm) and mean annual actual evapotranspiration (mm). Data points (*circles*) are from 1138 (40 m × 5 m) transects recorded using the VegClass proforma and the LLR strategy

scale is illustrated in Table 4, which includes examples of the most species and PFT-rich, closed forests recorded along latitudinal and altitudinal gradients from the equator to the sub-arctic.

Functional Redundancy

Concept and Evidence

Species designated within a functional group are, by definition, ecologically equivalent and therefore it is argued that they provide some measure of system redundancy (Martinez 1996; Mooney 1997; Blondel 2003; Franks et al. 2009). The ‘functional niche’, defined as the area occupied by a species in an n-dimensional functional space, has also been put forward by Rosenfeld (2002) as a useful conceptual tool for understanding redundancy. A principle that directly supports redundant species as guarantors of reliable ecosystem functioning has been drawn

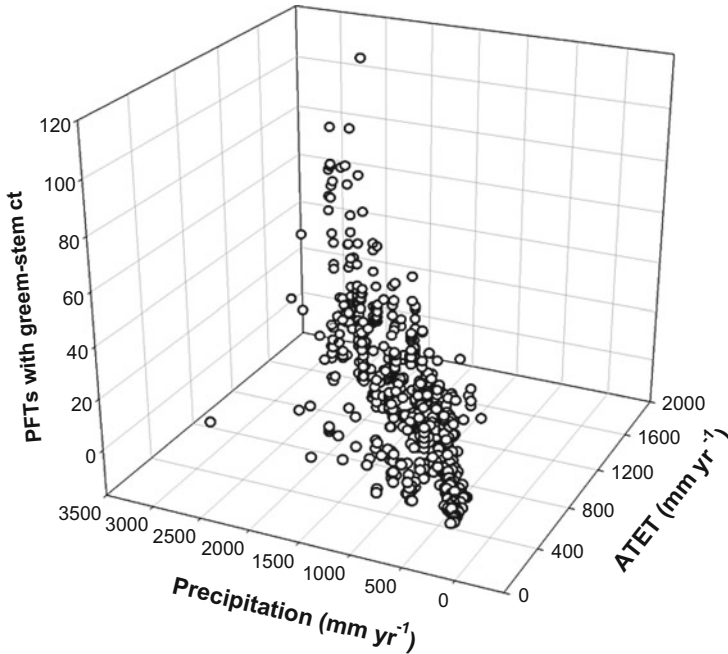


Fig. 10 Counts of *modal* PFTs containing a plant functional trait or element (PFE) ‘ct’ indicating green-stem or corticular photosynthesis, matched against mean annual precipitation (mm) and mean annual actual evapotranspiration (mm). Data points (*circles*) represent counts recorded within 1138 (40 m × 5 m) transects recorded using the VegClass proforma and the LLR strategy

from elementary principles of engineering that indicate reliability always increases as redundant components are added to a system (Naeem 1998). This argument has been applied widely across environmental scales in plant ecology, where it is claimed that ecosystem resilience depends on functional or ‘ecological’ redundancy (the number of species contributing similarly to an ecosystem function) and on response diversity (how functionally similar species respond differently to disturbance) (Laliberté et al. 2010; Mayfield et al. 2010; Messier et al. 2010). On the other hand, where there is limited understanding about the exact form of the species–ecosystem relationship under differing conditions, it is also argued that we should not ignore the ‘insurance value’ of maintaining all species circumstances (Lawton and Brown 1993; Walker 1992; Bolger 2001).

As a concept that is intimately connected with the interpretation and evaluation of plant functional typology, redundancy has attracted broad theoretical support among ecologists based on localised studies or computerised simulations and then often with very limited criteria (Cowling et al. 1994; Pillar and Sosinski 2003; Petchey and Gaston 2002a, b, 2006, 2007; Blondel 2003; Flynn et al. 2009; Laliberté et al. 2010; Mouchet et al. 2010). The essentially intuitive support for the concept is not supported by most empirical observations. To begin with, species

Table 4 Comparative richness in plant species, plant functional types and Plant Functional Complexity (PFC) in closed forest types across an equatorial to sub-arctic latitudinal and altitudinal range in 33 countries

No.	Country	Location	Georeference	Forest type	Species richness	PFT richness	PFC value
1	Indonesia (Sumatra)	Tesso Nilo, Riau Province	0°14'51" S 101°58'16" E	Complex primary forest, logged 1997	202	68	338
2	Indonesia (Sumatra)	Pancuran Gading, Jambi Province	1°10'12" S 102°06'50" E	Lowland forest interplanted with 'jungle' Rubber (<i>Hevea brasiliensis</i>)	112	47	236
3	India	Arunachal Pradesh, Tipi—Pakke Sanctuary	27°2'3" N 92°36'58" E	Complex lowland forest selectively logged	107	74	314
4	Indonesia (Borneo)	Gunung Banalang, Long Puak, Pujungan, E. Kalimantan	2°43'32" N 115°39'46" E	Disturbed complex ridge forest	104	44	232
6	Papua New Guinea	Kuludagi/West New Britain Province	5°38'46" S 150°06'14" E	Complex, primary lowland forest.	99	52	234
7	Bhutan	Near Chasilaka	26°57'15" N 89°33'48" W	Secondary forest <i>Alsinandra</i> dominant tree. Dense Acanthaceae groundlayer	98	72	358
8	Costa Rica	Braulio Carillo, Parque Nacional	10°09'42" N 83°56'18" W	Partially disturbed forest, palm dominated. Many epiphytes.	94	71	336
9	Cameroon	Awae Village	3°36'05" N 11°36'15" E	Late secondary forest. Previously logged.	94	43	232
10	Brazil	Pedro Peixoto, Acre (West Amazon basin)	10°01'13" S 67°09'39" W	Secondary forest (Capoeira) 3–4 years after abandonment	78	43	230
11	Brazil	Alcalinas Canamá N.W. Mato Grosso (West Amazon basin)	10°04'06" S 58°46'00" W	Primary lowland forest on shallow granitic soils.	75	54	298
12	Perú	Jenaro Herrera, Ucayali river (West Amazon basin)	4°58'00" S 73°45'00" W	'High terrace' lowland forest—selective logging	72	39	208

(continued)

Table 4 (continued)

No.	Country	Location	Georeference	Forest type	Species richness	PFT richness	PFC value
13	Russia	Vladivostok, forest adjacent to Botanical Institute	43°13'18" N 131°59'40" E	Tall broadleaf/conifer (<i>Pinus koraiensis</i>) forest with herbaceous groundlayer.	70	29	144
14	Vietnam	Cuc Phuong National Park, Ninh Binh Province	20°48'33" N 105°42'44" E	Lowland forest partly disturbed; on limestone	69	46	256
15	Estonia	Saaremaa	58°14'10" N 22°26'22" E	Oak forest (<i>Quercus robur</i>) with conspicuous forb layer.	68	34	176
16	Perú	Von Humboldt forest reserve, Pucallpa (W. Amazon basin)	8°48'01" S 75°03'54" W	Primary forest selectively logged, 1960	63	31	258
17	Fiji	Bua, Vanua Levu	16°47'36" S 178°36'45" E	Disturbed lowland forest on ridge	60	37	158
18	Thailand	Ban Huay Bong, Mae Chaem watershed	18°30'42" N 98°24'13" E	Humid-seasonal, deciduous dipterocarp forest fallow system	58	44	200
19	Kenya	Shimba Hills near Mombasa	4°11'33" S 39°25'34" E	Semi-deciduous forest in game park area. Disturbed (logged).	56	33	214
20	Malaysia (Borneo)	Danum Valley, Sabah	4°53'03" N 117°57'48" E	Primary forest subject to reduced impact logging, Nov 1993.	54	39	208
21	Guyana	Iwokrama forest reserve	4°35'02" N 58°44'51" W	Primary swamp forest in blackwater system.	52	34	192
22	Georgia	Gezgeti, Mt Kazbegi Central Caucasus Mts	42°40'01" N 44°36'27" E	<i>Betula linwinowii</i> Krummholz	47	35	198
23	Bolivia	Las Trancas (Santa Cruz)	16°31'40" N 61°50'48" W	Semi-evergreen, lowland vine forest, Logged 1996	46	33	302
24	Australia	Atherton tableland, North Queensland	17°18'28" S 145°25'20" E	Upland humid forest managed for sustainable timber extraction	46	25	187

25	Panama	Barro Colorado island	9°09'43" N 79°50'46" W	Semi-evergreen vine forest, ground layer grazed by native animals	43	30	238
26	Brazil	Reserva Biologica da Campiã Km 50 near Manaus (East Amazon basin)	2°35'21" S 60°01'55" W	Moderately disturbed, microphyll, evergreen vine forest on siliceous sands	42	27	276
27	Philippines	Mt Makiling, Luzon	14°08'46" N 131°13'50" E	Regen. forest planted in 1968 with <i>Swietenia</i> , <i>Parashorea</i> , <i>Pterocarpus</i>	42	26	194
28	Outer Mongolia	Bear Cub Pass, Khentii Mountains	48°58'35" N 107°09'18" E	Mixed Larch and Birch forest	40	25	188
29	Norway	Near Tromsø University and Botanical garden	69°40'41" N 18°58'13" E	<i>Betula tortuosa</i> forest with dense forb layer.	38	28	150
30	Vanuatu	Yamet, near Umetch, Aneityum Island	20°12'32" S 169°52'33" E	Coastal primary forest, logged, with <i>Agathis macrophylla</i> (Kauri) overstorey	38	22	217
31	Mexico	Zona Maya, Yucatan peninsula	19°02'26" N 88°03'20" E	Logged secondary lowland forest.	37	26	288
32	Indonesia (Borneo)	Batu Ampar, Central Kalimantan	0°47'48" N 117°06'23" E	Primary forest, heavily logged 1991/1992	35	23	286
33	Russia	Kamchatka, Upper Tupikin Stream	55°54'36" N 158°45'46" E	Stone Birch (<i>Betula ermanii</i>) forest with herbaceous ground layer	35	22	138
34	West Indies (France)	Near Mont Pelée, Martinique	0°47'48" N 117°06'23" E	Humid, lowland forest on volcanic slopes, heavily disturbed.	32	24	279
35	Mozambique	Supita, near Mopeia	17°56'20.6" S 35°43'33.8" E	Semi-deciduous microphyll vine forest. Community reserve	31	24	144

(continued)

Table 4 (continued)

No.	Country	Location	Georeference	Forest type	Species richness	PFT richness	PFC value
36	Argentina	Iguazú Parque Nacional de las Cataratas	25°39'00" S 54°35'00" W	Lowland vine forest, disturbed	28	24	302
37	French Guyana	B.E.C. 16 km from Kourou	14°49'23" N 61°7'37" W	<i>Tierra firme</i> simple evergreen forest on white sand	28	18	146
38	Indonesia (Borneo)	Mandor Nature Reserve, North of Pontianak	0°17'12" N 109°33'00" E	Low microphyll evergreen forest in blackwater system on siliceous sand	25	21	228
39	Austria	Heiligenkreutz	48°03'19" N 16°7'48" E	Disturbed riparian forest	23	16	116
40	England	Newbridge, River Dart NP Devon	50°31'23" N 03°50'7.5" W	Deciduous oak forest	20	19	160
41	Norway	Near Kongsfjord	70°39'36" N 29°11'53" E	<i>Betula tortuosa</i> partially closed forest with herbaceous understorey dominated by <i>Cornus suecica</i> .	13	9	70
42	Spain	Pedro Alvarez Reserve, Tenerife	28°32'4" N 16°19'0" W	'Laurisilva' upland forest	12	9	46

Data summary from 1138 (40 m × 5 m) transects with richest vascular plant species and *modal* Plant Functional Type (PFT) and Plant Functional Complexity (PFC) values in each country listed in descending order, extracted from a series of global, ecoregional surveys and restricted to closed forests. All data collected using a standard 'VegClass' sampling protocol and LLR strategy (Gillison 2002, 2013). Forest conditions range from relatively intact to highly disturbed

Sources: International Centre for Agroforestry Research, Alternatives to Slash and Burn Programme (ICRAF/ASB); Center for International Forestry Research (CIFOR); WWF AREAS project; The World Bank, and CBM (Center for Biodiversity Management)

are evolutionarily and ecologically unique, and grouping into any functional classification will inevitably ignore some biologically relevant information (Fonseca and Ganade 2001), in addition to which, where indications of redundancy appear in trait overlaps, further study usually reveals that each species occupies fairly separate functional space (Sandquist and Cordell 2007). At finer ecological scales, studies of biological soil crust organisms (Bowker et al. 2011) reveal considerable functional singularity between taxa (notably lichens) that may be expressed through both visible and non-visible attributes thus raising the question of phenotypic limitations in functional typology. The general level of imprecision in assessing functional redundancy is well illustrated by an Australian rangeland study (Walker 1992; Walker et al. 1999) in which “functionally equivalent” species were classified mainly according to height, specific leaf area and longevity while excluding potentially critical features in grazing land systems such as life-history traits, rooting system, water use efficiency, fire and drought tolerance and herbivore resistance. In that study functional equivalence was identified through ordination procedures that by themselves are open to significant information loss and a highly arbitrary characterisation of functional differences between species (Fonseca and Ganade 2001; Villéger et al. 2008; Mouchet et al. 2010). Elsewhere, Gitay et al. (1996) and Gillison (2013) argue that the level of knowledge required to implement the method described by Walker et al. (1999) would be very difficult to achieve in practice and, if applied, would run the risk of generating misleading outcomes about ecosystem performance.

Tests for Redundancy

Hard evidence for redundancy and the functional consequences of species loss among terrestrial vascular plant species is singularly lacking, and adequate experimental designs for in situ testing of functional redundancy are yet to be determined. Rather than assuming functional redundancy, Sullivan and Zedler (1999) recommend testing for similarity of group members under varied conditions, e.g. alone and with their common neighbours and under benign and stressful conditions. It is also argued (Rosenfeld 2002) that experiments designed to assess redundancy based on a single functional attribute will be biased towards finding redundancy, because species are more likely to have non-overlapping functional niches in a multi-dimensional functional space. In this respect Gamfeldt et al. (2008) showed that due to multi-functional complementarity among species, overall functioning is more susceptible to effects of species loss than are single functions. The most comprehensive testing for functional redundancy appears to be among soil organisms and related bacterial and fungal microcosms (Yin et al. 2000; Wohl et al. 2004; Bowker et al. 2011), where the high degree of environmental control suggests that similar experimental rigour in studies of vascular plant assemblages would be impractical. Cyclic patterns in highly dynamic community types present clear limitations to redundancy testing if conducted solely at one

specific stage of succession or in vegetation types such as arctic tundra where, because the age of some tundra tussock grasses may exceed 100 years (Bret-Harte et al. 2008), any experimental manipulation to test for redundancy would take a very long time.

Redundancy and Functional Scale

Measures of functional redundancy are closely coupled to varying scales of functional typology from molecule to ecosystem and, by aggregation, to biome. Whereas partitioning functional diversity within and among communities indicates that both trait convergence and divergence co-operate in the formation of assemblages from the local species pool, in spite of changes in species composition, considerable trait convergence at the regional scale implies ecological redundancy among communities at that scale (de Bello et al. 2009). According to Pillar and Sosinski (2003), redundancy at the population level, as indicated by the degree of association between traits based on a matrix of populations by traits, differs from that at the community level, which is the result of redundancy at the population level plus its manifestation in terms of different plant types and quantities in the matrix of populations by communities. The removal of assumed ‘functionally redundant’ species can also influence community dynamics and processes, indicating that there are important functional differences not captured by broad groupings (Cadotte et al. 2009).

The performance of functional traits and syndromes is inevitably influenced by their position along a hierarchy of environmental filters ranging from global climate to local factors such as soil type and land-use history. These filters, in turn, determine the level of functional typology and thus the criteria used to assess redundancy, including differing measures of functional diversity and niche complementarity (Petchey and Gaston 2002b; Mouchet et al. 2010). As illustrated by Laliberté et al. (2010) in a meta-analysis of traits known to influence ecosystem processes, regional land-use intensification can reduce both functional redundancy and response diversity significantly, although specific relationships may vary considerably among the different land-use gradients. In such cases, environmental context can be critical in evaluating niche complementarity and thereby functional redundancy. Similar studies of vegetation response along a land-use intensity gradient in Sumatra, Indonesia (Gillison et al. 2013), revealed a rise in the number of PFTs relative to species at levels of intermediate disturbance that was significantly higher than that recorded in a more species-diverse mature forest. This response pattern is consistent with the intermediate-disturbance hypothesis as well as cyclic patterns of natural disturbance in forest mosaics (e.g. tree-fall gaps), where functional traits and syndromes cycle in situ. In such conditions, where one successional phase may facilitate another in a tropical lowland forest, or where facilitation can be antagonistic between species in alpine herbfields

(Schöb et al. 2013a, b), protocols by which criteria are selected to assess functional redundancy require careful analysis within the context of ecosystem dynamics.

Redundancy and Conservation

Complementarity between functional groups, while playing clearly into links with redundancy, is rarely tested in complex vegetation types and yet may have important consequences for conservation planning at landscape scale. It is frequently argued that, because of the uncertainties surrounding the concept of species redundancy, it is unproductive to apply the concept in conservation where species may be lost needlessly (Lawton and Brown 1993; Collins and Benning 1996; Gitay et al. 1996). It is also axiomatic that, where clear evidence indicates that the number of different functional groups increases with the number of species (Gillison 2013), conserving a large proportion of the functional traits of species will also require conserving a large proportion of all species (Petchey and Gaston 2002a). Based on these principles, conservation planning and management therefore need to employ a conservative approach that maximizes and maintains species diversity at every stage.

Stoichiometric and Metabolic Scaling of Functional Types

Biological stoichiometry theory considers the balance of multiple chemical elements in living systems. Ecological stoichiometry, on the other hand, recognizes that organisms themselves are outcomes of chemical reactions and thus their growth and reproduction can be constrained by supplies of key chemical elements, especially C, N and P (Chapin et al. 1986; Niinemets and Kull 1998; Sterner and Elser 2002; Elser and Hamilton 2007; Ågren 2008; Danger et al. 2008; Elser et al. 2010). In ecology, stoichiometric units are most commonly used as molar ratios in physiological research and in aquatic systems because they reflect the actual stoichiometric relationships, but most literature in terrestrial ecology reports mass ratios (Sterner and Elser 2002; Güsewell 2004). Across environmental scales, natural selection has shaped the form and function of plants so that leaves exhibit a net positive return on resource investment, by which the total mass of carbon assimilated by a leaf over its life span will be greater than the total mass of carbon invested in the leaf (Chabot and Hicks 1982; Williams et al. 1989; Westoby et al. 2002; Blonder et al. 2011)—a relationship consistent with the LHS and LES strategic models. Within this selective process and across multiple scales, the species-specific, stoichiometric constants controlling trait covariation in regulating metabolic processes appear to be largely independent of biome or leaf type (Kikuzawa and Lechowicz 2006; Minden 2010; Blonder et al. 2011). This suggests

that, while genetically pre-determined morphological and physiological characteristics of leaf and other functional traits in terrestrial vascular plants find expression within a realized resource niche (cf. Vasseur et al. 2012), overall ecological performance and fitness will be subject to stoichiometric control, typically operating in a C:N:P type environment. Such control of size-dependent scaling of leaf support investments may also be mediated by life form and climate (Niinemets et al. 2007).

Plant traits related to size and growth rate are particularly important because they determine the productive capacity of vegetation and the rates of decomposition and nitrogen mineralization (Chapin 2003). Metabolic scaling theory considers how size affects metabolic properties from cells to ecosystems. In this context plant stoichiometry exhibits size scaling, as foliar nutrient concentration decreases with increasing plant size, especially for phosphorus. Thus, in line with the LES strategy, small plants, frequently with small leaves, have lower N:P ratios. Foliar nutrient concentration is also reflected in other tissues (root, reproductive, support), permitting the development of empirical models of production that scale from tissue to whole-plant levels (Gordon and Jackson 2000; Elser et al. 2010; Minden 2010). Global trends (see also Reich and Oleksyn 2004; Ballantyne et al. 2008) couple latitude as well as environmental phosphorus concentration with plant stoichiometry. Research thus far suggests that an improved knowledge of the stoichiometric role in the plant size-nutrient-environment nexus can lead to a better understanding of factors such as carbon dioxide, temperature and nitrogen deposition along gradients of environmental change at global scale (Elser et al. 2010; Reich and Oleksyn 2004; cf. Laughlin 2011). At within-community scale, however, stoichiometric control of leaf N may be mediated significantly by a variety of local filters such as photon flux density (PPFD) as observed by Posada et al. (2009), who found tree leaves in a tropical forest canopy optimized photosynthetic use of PPFD rather than N per se. As with biome-invariant scaling exhibited in the LES strategy, response patterns demonstrated at global level in stoichiometric and metabolic scaling may not necessarily hold at ecosystem or community level.

Scale-Related Trait Performance Within and Between Species

The search for traits that reflect plant performance adequately along biophysical gradients has generated a series of scale-invariant models at global dimensions that reveal typically robust linear correlates between functional traits and key physical environmental variables, as illustrated in the LES and LHS strategies. In the majority of these cases species are typically described by functional trait measurements collected from a few individuals from one or few populations and averaged at the population or species level, disregarding the intra-specific functional variability (Albert et al. 2010a). As currently described, plant strategies centred around economic parsimony assume that infra-specific variation in functional traits is of negligible significance compared to individual species or community-weighted means of

inter-specific functional traits. Yet the potential ecological significance of within-species variation in functional traits is rarely subjected to empirical or experimental analysis. Despite the widespread focus on inter-specific variation in trait-based ecology, recent studies across widely differing ecosystems provide increasing evidence that intra-specific trait variability can play a fundamental role in plant community responses to environmental change and community assembly (Gillison 2013; Kichenin et al. 2013). New evidence is also emerging that, using a single trait value to describe a given species can hide large functional variation for this species along environmental gradients and that intra-specific as well as inter-specific functional variability can have significant effects on community dynamics and ecosystem functioning. Such information can be critical to understanding ecological patterns in changing environments (Albert et al. 2010a, b; Gillison 2013).

The detection and analysis of intra-specific trait variation are, to a large extent, context-dependent, with localized observations unlikely to reveal as much within-species variation as in those made along wide-ranging biophysical gradients. Recent recognition of the role of intra-specific traits in ecosystem performance is evident from studies of genotypic variation and phenetic plasticity across a range of spatio-temporal scales. This is apparent at latitudinal scale (de Frenne et al. 2013), in arctic tundra (Soininen et al. 2013), along elevational gradients in alpine and subalpine vegetation (Jung et al. 2013; Kichenin et al. 2013), in temperate herbaceous vegetation (Siefert 2012), in temperate forests (Grady et al. 2013; Jackson et al. 2013) and in tropical forests (Martínez-Garza et al. 2005; Hulshof and Swenson 2010).

The studies referred to above are based on values obtained from differing groups of single functional traits rather than whole-plant (combinatorial) syndromes. The *modal* PFT combinations embodied in the LLR strategy provide a basis for analysing both inter-specific and intra-specific variation in whole-plant variation along environmental gradients as well as unique PFTs (not linked with species) and their component PFEs for individual plants. The latent information embodied in this flexible approach is illustrated in Table 5, in which intra-specific variation in the genus *Betula* is expressed in leaf size class, leaf inclination and presence of green stem photosynthesis in phanerophytes (woody plants > 2 m tall). Numerical analysis of this formalized intra-specific variability is facilitated through quantitative values attached to each PFT and PFE in the LLR system and via the VegClass computer program (Gillison and Carpenter 1997; Gillison 2002).

Functional Types and Traits as Bioindicators Across Multiple Scales

Bioindicators are widely used in assessing and monitoring biophysical environmental conditions, such as acid rain, pollutants, landscape rehabilitation, contamination and environmental impacts on biota. For biodiversity assessment and monitoring at a range of environmental scales, surrogate measures include a wide range of

Table 5 Circumboreal intraspecific variation in the genus *Betula*

Species	modal PFT	Location	Country
<i>B. daurica</i>	mi-co-do-de-ph	Shkotovo	Russia
<i>B. daurica</i>	no-co-do-de-ph	Vladivostok	Russia
<i>B. daurica</i>	no-la-do-de-ch	Vladivostok	Russia
<i>B. ermanii</i>	mi-pe-do-de-ph	Gothenburg (cult.)	Sweden
<i>B. ermanii</i>	no-co-do-de-ph	P. Kiyevka Pass	Russia
<i>B. ermanii</i>	no-la-do-de-ch	Kamchatka	Russia
<i>B. ermanii</i>	no-la-do-de-ct-ph	Kamchatka	Russia
<i>B. ermanii</i>	no-pe-do-de-ct-ph	Kamchatka	Russia
<i>B. ermanii</i>	no-pe-do-de-ph	Kamchatka	Russia
<i>B. litwinowii</i>	mi-la-do-de-ph	Mt Kazbegi	Georgia
<i>B. litwinowii</i>	mi-pe-do-de-ct-ph	Mt Kazbegi	Georgia
<i>B. litwinowii</i>	mi-pe-do-de-ph	Mt Kazbegi	Georgia
<i>B. nana</i>	na-pe-do-de-ph-ad	Abisko	Sweden
<i>B. nana</i>	na-ve-do-de-ch-ad	Båtsfjord	Norway
<i>B. nana</i>	no-ve-do-de-ch	Saaremaa	Estonia
<i>B. pendula</i>	mi-pe-do-de-ph	Ascona	Switzerland
<i>B. pendula</i>	mi-ve-do-de-ch	Tromsø	Norway
<i>B. pendula</i>	mi-pe-do-de-ph	Kuresoo bog	Estonia
<i>B. pendula</i>	mi-pe-do-de-ch	Saaremaa	Estonia
<i>B. pendula</i>	me-la-do-de-ch	Saaremaa	Estonia
<i>B. pendula</i>	mi-la-do-de-ch	L. Peipsi area	Estonia
<i>B. pendula</i>	no-pe-do-de-ph	Raplamaa	Estonia
<i>B. platyphylla</i>	mi-co-do-de-ph	Shkotovo	Russia
<i>B. platyphylla</i>	mi-co-do-de-ph	Khentii Mts	Mongolia
<i>B. platyphylla</i>	mi-pe-do-de-ct-ph	Khentii Mts	Mongolia
<i>B. platyphylla</i>	no-co-do-de-ph	Kamchatka	Russia
<i>B. platyphylla</i>	no-ve-do-de-ph	Kamchatka	Russia
<i>B. platyphylla</i>	mi-pe-do-de-ct-ph	Kamchatka	Russia
<i>B. tortuosa</i>	mi-pe-do-de-ph	Abisko	Sweden
<i>B. tortuosa</i>	mi-co-do-de-ct-ph	Kongsfjord	Norway
<i>B. tortuosa</i>	mi-co-do-de-ch	Helligskogen	Norway
<i>B. tortuosa</i>	mi-la-do-de-ct-ph	Helligskogen	Norway
<i>B. tortuosa</i>	mi-co-do-de-ph	Tromsø	Norway

All data collected using the VegClass recording protocol and the LLR methodology. Variation in PFT combinations reflect differences in regional thermal regimes and in local physiographic (especially aspect and hydrology) and soil property gradients. For PFT coding see Table 2

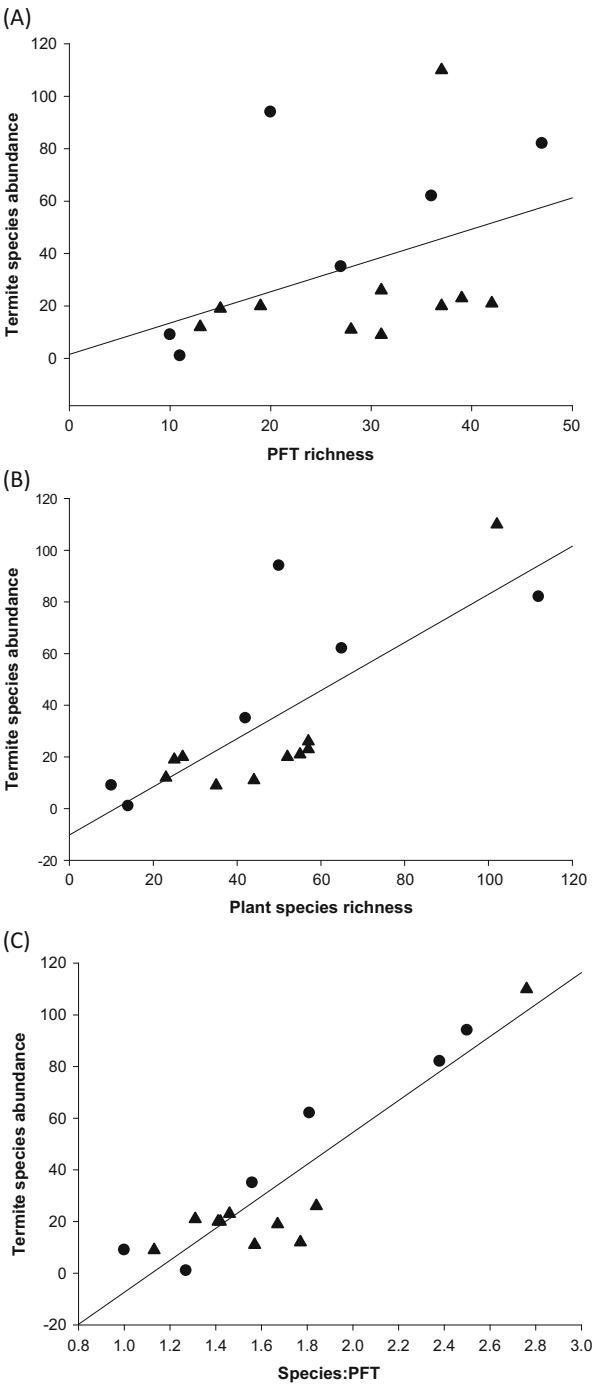
environmental units or arbitrary ecosystem ‘types’ or combinations of both (Oliver et al. 2004; Carmel and Stroller-Cavari 2006; Grantham et al. 2010; Gillison 2013). There is no apparent consensus on how to use bioindicators (Büchs 2003) as they tend to be geared to widely varying scale and purpose. While few examples of generic indicators exist beyond the ecosystem level, for national forest inventories Newton

and Kapos (2002) argue that biodiversity indicators should be appropriate across local and broader scales. For biodiversity at least, plant species are the most widely used of all surrogates, but considerable debate surrounds their efficacy in predicting the distribution of other taxa (Lawton et al. 1998; Lewandowski et al. 2010; Lindenmayer and Likens 2011; Sætersdal and Gjerde 2011). Vandewalle et al. (2010) suggest that the development of indicators using functional traits could complement, rather than replace, existent biodiversity monitoring procedures. In this way, comparison of the effect of land-use changes on biodiversity is facilitated and can be expected to influence conservation management practices positively. While the potential utility of this approach shows promise, field validation is sparse at local and landscape scales (Gillison and Liswanti 2004; Bardgett 2005; Liira et al. 2008; Lavorel et al. 2011) and, with some exceptions in remote sensing (e.g. Kooistra et al. 2007), is seemingly non-existent at broader regional and biome scales.

Data recorded using the LLR strategy along biophysical gradients can exhibit predictable changes in plant species and *modal* PFT combinations as well as vegetation structure. As indicated by Vandewalle et al. (2010), complementary functional traits can be used to characterize biological habitat and thus facilitate predictive modelling of the distribution of taxa. One fundamental measure of habitat characterization namely niche complementarity, is typically expressed for conservation and management purposes through species assemblages and species turnover. When used independently, vascular plant species and PFTs can provide a limited measure of niche complementarity that is subsequently improved when both are expressed as a species:PFT ratio. Across multiple scales the ratio can be shown to vary predictably along resource-availability and disturbance gradients, reflecting quick-slow response strategies contained in LES, LHS and CSR. This is illustrated, for example, in a regional gradient of land-use intensity along which the species:PFT ratio is initially high in an old-growth forest and becomes progressively reduced with increasing disturbance as more ecological niches become available with fewer species available per niche, until the ratio may approximate unity at a disturbance extreme (Gillison et al. 2013). While evident across localized environmental gradients, the pattern can be repeated across biomes; for example, a lowland tropical rain forest in Indomalesia has a species:PFT ratio of 2.97 compared to an exposed Icelandic lava field with a ratio of 0.88.

Apart from serving as an alternative measure of niche complementarity, the species:PFT ratio can be used as a bioindicator for conservation management purposes. Changes in termite species richness along a Sumatran land-use intensity gradient were correlated significantly with plant species richness and modal PFT richness; a correlation that was greatly improved when termite species richness was regressed against the species:PFT ratio (Gillison et al. 2003; Bardgett 2005). The high correlation between relative abundance of termite species and the species:PFT ratio in Sumatra is also repeated in Brazil (Gillison et al. 2013) along a similar land-use intensity gradient. When combined, the data also reveal a constant relationship using the same ratio (Fig. 11), despite there being significant differences in the evolution of biota in these two biogeographically separate regions (cf. Heberling and Fridley 2012).

Fig. 11 Plant functional types as indicators of relative termite abundance across two biogeographic regions. *Solid triangles* are samples from Mato Grosso, Brazil; *Solid circles* are samples from Sumatra, Indonesia: (a) modal PFT richness, (b) plant species richness, (c) species:PFT ratio



Discussion

In the past few decades there has been incremental, albeit rapid progress across three phases of investigation in plant functional ecology. The first of these reflected a change from models based on ‘adaptive’ Raunkiaer life forms to broader, more prescriptive groupings of functional traits within and between communities as well as individual species (Grime 1977; Box 1981, 1996; Gillison 1981; Keddy 1992). This paved the way to a more tightly focused approach leading from ‘noisy’ sets of highly co-varying functional traits towards acquisitive-economic models which sought to identify parsimonious sets of traits that were, on the one hand, recognizably independent in terms of function but, would at the same time, elucidate relationships better between environment and species investment in resource acquisition and return (Westoby 1998; Westoby et al. 2002; Wright et al. 2004). While the spectrum of traits embodied in these biome-invariant models has improved theoretical insights with respect to plant functional and environmental relationships, in practice the methodology is constrained by the need for laboratory-based measurements, thereby limiting field observations. The methodology also excludes, by default, much of the world’s vegetation cover in arid lands, which support extensive areas of succulent or highly seasonal vegetation types with corticular photosynthesis and metabolic pathways that differ from most other vascular plant species.

There is an emerging awareness that the ecological signals generated by parsimonious sets of functional traits may be less clear than previously thought. Current evidence suggests there could be significant information loss where parsimonious, functional criteria exclude co-varying traits that include additional key functional characteristics related to water-use efficiency, photosynthesis and growth. Mechanisms controlling trait convergence and divergence reflected in habitat filtering and niche differentiation may be interacting in tandem within certain trait syndromes, for example along aridity gradients, raising further questions about whole-plant interactive relationships. A realization that whole-plant functional syndromes rather than dispersed functional traits may provide better insights into plant functional response across multiple scales is evident in holistic shoot-root models that scale from tissue to whole-plant levels (Gordon and Jackson 2000; Craine et al. 2005; Elser et al. 2010) to regional scale (Liu et al. 2010; Kang et al. 2013) and above (Fortunel et al. 2012). Evidence for the decoupling of leaf and wood traits as separate functional axes (Kang et al. 2013) supports further the possibility that measures of niche dimensionality across environmental scales will increase as our understanding of whole-plant function improves.

In the majority of cases the successful application of different strategies has much to do with environmental context as well as spatial scale. It is here that new findings about intra-specific variation will be enhanced by studies along extended biophysical gradients, thereby feeding back into models otherwise based on measures of inter-specific response and community-weighted means. The move towards global trait datasets (e.g. Kattge et al. 2011) will facilitate a more comprehensive

synthesis of information and data than exists at present and is a welcome initiative that should lead to improved models of plant-environmental relations across multiple scales. A pervasive problem nonetheless concerns widespread inconsistencies in methods of data recording, storage and access that, if not managed properly, have the potential to generate misleading outcomes in plant ecological research. To this extent and as presented in this chapter, the global data underlying the VegClass LLR system have the advantage of a uniform protocol of field collection, collation and meta-analysis consistent with international standards of data management. Uniformity of this kind greatly enhances the investigation of trait performance across multiple scales and suggests that similar advantages are to be gained through the standardization of methods of data collection and analysis.

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Vegetation Structure and Function at Multiple Spatial,
Temporal and Conceptual Scales

Box, E.O. (Ed.)

2016, XL, 578 p. 168 illus., 111 illus. in color.,

Hardcover

ISBN: 978-3-319-21451-1