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Plant Functional Types and Traits at the Community, Ecosystem and World Level

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12.1 The quest for a functional paradigm

Eugenius Warming's insightful comment (1909) that we are '... yet far distant from the oecological interpretation of various growth-forms' still applies in a world where increased pressure on global resources and rapid environmental change generate questions that remain unsolvable through time-honoured methodologies. It is here that functional ecology can play an important role in helping to better understand ecosystem dynamics through a more detailed analysis of form, function and plant–environment interaction. Criteria for functional classifications vary. Lavorel *et al.* (1997) propose 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; Lavorel *et al.* 2007). Each of these is discussed further in this chapter. Advances in functional ecology show significant gains in the quality of baseline data and readily classifiable functional types where cause and effect relationships can be demonstrated between the biophysical environment and readily measureable, non-phylogenetic, morphological and physiological adaptations of plants. Despite progress, the successful identification, measurement and testing of plant functional characteristics underpin the quest for a functional paradigm where the classification and application of entities such as **plant functional types (PFTs)** and related '**functional traits**' play a central role.

The plethora of definitions (Web Resource 12.4) highlights the uncertainty surrounding the meaning of ‘functional’ type, its component traits and whether functional types actually exist beyond the minds of ecologists. If PFTs and traits are to be useful, we need to know which functional traits are reliable predictors of species abundances, biodiversity or demographic change and whether functional traits can be used, for example, to assess and monitor vegetation change. Related questions concern the genetic basis for functional traits and their connections with phylogeny (Kooyman *et al.* 2011). A key requirement is to establish a robust, scientific basis for the generalization of ecological strategies based on functional traits and to demonstrate their applicability across ecological scales. This chapter addresses the evolution of the concept of plant function, the development of plant functional typology and includes case studies that illustrate the current and potential use of PFTs and functional trait-based approaches at the community, ecosystem and world level.

12.2 Form and function: evolution of the ‘functional’ concept in plant ecology

Early physiognomic-structural classification systems were designed primarily to communicate and compare vegetation physiognomy or appearance rather than function. Until the mid to late 19th century, physiognomic types were the primary descriptive units of a plant community and vegetation of a specific region (Du Rietz 1931). Then, during the late 19th century Eugenius Warming (1895, 1909) first attempted to arrange higher plants into biological groups – the early **epharmonic life-form** (the adaptive form) – a precursor to subsequent classifications of life-forms by others. During this period, Christen Raunkiær (1934) constructed a **life-form** (*‘livsform’*) classification system based on the position of the perennating organ during the most unfavourable season. Following Raunkiær, Fosberg (1967) argued a case for a functional classification based on dynamic rather than static vegetation descriptors – an approach developed by Gillison (1981) who combined modified Raunkiærean life-form criteria with adaptive photosynthetic leaf-stem attributes and above-ground rooting systems as a basis for classifying **whole-plant PFTs**.

12.3 The development of functional typology

There is a clear need to clarify and unify concepts surrounding PFTs (Gitay & Noble 1997; Semenova & van der Maarel 2000). The following sections summarize some key aspects of cross-related terms such as **guilds, growth-forms, life-forms, plant strategies, functional types and functional traits**.

12.3.1 Guilds

The term guild has important connotations for functional typology and emerged as an English translation of *‘Genossenschaften’* applied by Schimper (1903) to

plant types that depend on others for support (lianes, epiphytes, parasites, saprophytes; see also Simberloff & Dayan 1991). When applied to plants the term is frequently equivalent to **functional group** or **functional type** (e.g. Shugart 1997). Boutin & Keddy (1993) define plant guild composition according to functional traits and emphasize that there can be major obstacles when using guild classifications built on broad resource criteria where, for example, an entire community may be included as a single guild (cf. Harper 1977; Grubb 1977). On the other hand, attributes of dispersal, establishment and growth were used to construct a guild hierarchy for the conterminous vegetation of the USA (Johnson 1981). The literature reveals other classificatory diversions such as '**functional guilds**' (Condit *et al.* 1996; Gitay *et al.* 1999) '**structural guilds**' (Gitay *et al.* 1999), '**management guilds**' (Verner (1984) and '**functional cliques**' (Yodzis 1982). Few protocols exist for the objective recognition of guilds. Recent usage in functional typology suggests there is much to support the view of Hawkins & MacMahon (1989) that the guild concept is a useful but artificial construct of the minds of ecologists.

12.3.2 Life-forms and growth-forms

Confusion surrounds the meaning and utility of these two widely used terms. Initial applications of growth-form expressed as physiognomy (appearance) and structure were largely developed for phytogeographical purposes. In functional typology, terminological clarity and ease of interpretation of results are mandatory in today's demand for fast-paced, cost-effective methodology. In this respect Raunkiær's life-form terminology remains a clear winner (see also Floret *et al.* 1987). Attempts to expand Raunkiær's system, for example that of Mueller-Dombois & Ellenberg (1974), failed to capture the interest of practitioners who seek simpler and more readily quantifiable variables with improved return for effort. Unless otherwise indicated, in this chapter '**life-form**' follows Raunkiær (*sensu stricto*) with '**growth-form**' applied as a purely physiognomic descriptor.

12.3.3 Plant functional types and groups

With some exceptions (Vitousek & Hooper 1993; Cramer 1997; Hunt *et al.* 2004) most authors treat **types** and **groups** synonymously (e.g. Gitay & Noble 1997; Reich *et al.* 2003). For the purposes of this chapter, PFTs are considered synonymous with plant functional groups and include closely related entities such as the '**plant functional response type (PRT)**' of Louault *et al.* (2005). Fig. 12.1 provides a spatio-temporal context for measureable PFTs and functional traits above genetic and molecular level. The simplest definition of a PFT is that of Elgene Box (1996) 'PFTs are functionally similar plant types.' PFT definitions can vary according to whether the response to an environment or the effects on an ecosystem, singly or both, are intended. Smith *et al.* (1992) defined PFTs as 'sets of species showing similar responses to the environment and similar effects on ecosystem functioning,' a theme echoed by others (Díaz & Cabido 1997, 2001; Lavorel & Garnier 2002). PFTs are often regarded as trait assemblages or **trait syndromes** (Plate 12.1 shows nine different whole-plant PFT syndromes,

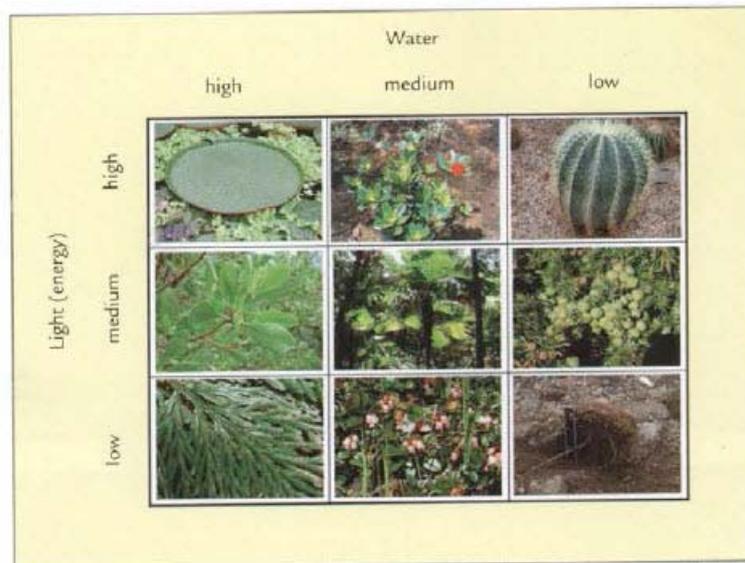


Plate 12.1 Different whole-plant PFT syndromes, subjectively positioned along gradients of light (energy) and moisture. Left to right: *Victoria regia* (Amazon basin); *Metrosideros* sp. (Philippines); *Echinocactus* sp. (Mexico); mangrove *Lumnitzera littorea* (Indomalesia); phanerophytic swamp fan palm, *Licuala ramsayi* (Tropical North Australia); *Juniperus communis* (Fennoscandia); fern *Selaginella* sp. (Indomalesia); *Vaccinium vitis-idaea* (boreal region); cushion plant, *Azorella macquariensis* (subantarctic Macquarie Island). Dominant functional traits are reflected in life-form, chlorophyll distribution, notably leaf size and inclination and green stem.

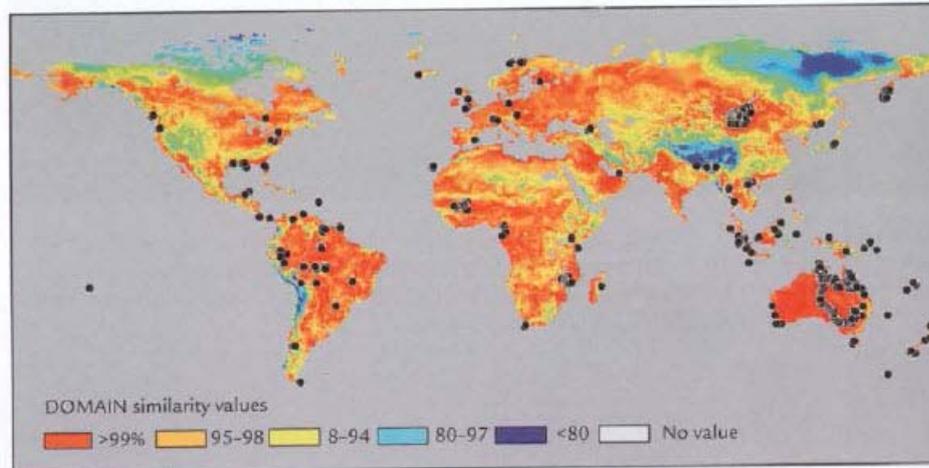


Plate 12.2 Distribution of 1066 VegClass sites (40×5 m transects) used in the recording of *modal* PFTs, taxa and vegetation structure. Degree of environmental coverage by all sites is indicated via a DOMAIN environmental similarity map (Carpenter *et al.* 1993) based on elevation, total annual precipitation, minimum temperature of coldest month and total annual actual evapotranspiration.

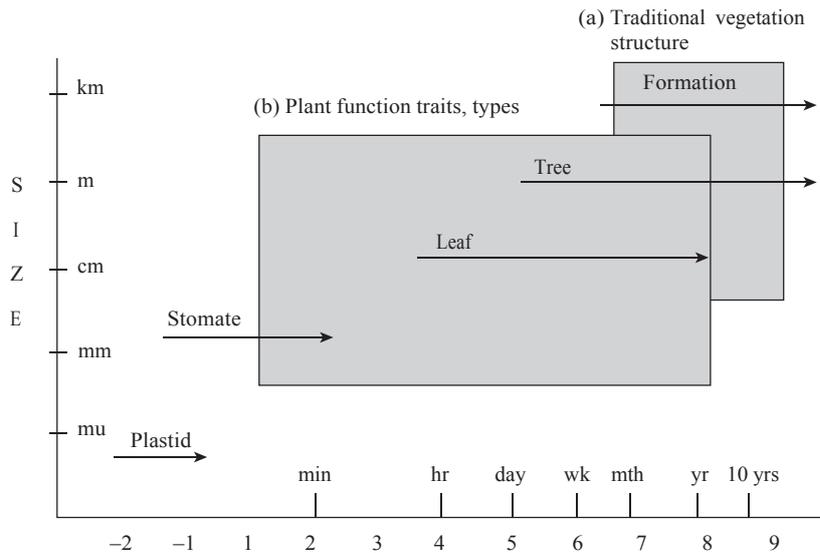


Fig. 12.1 Approximate log response time (s) of above-ground plant elements including spatio-temporal domains of PFT and individual trait sensitivity (a) Formation class and (b) generalized zone of plant functional classifications. (Adapted from Gillison 2002.)

subjectively positioned along gradients of light (energy) and moisture: *Victoria regia* (Amazon basin); *Metrosideros* (Phillipines); *Echinocactus* (Mexico); mangrove *Lumnitzera littorea* (Indomalesia); palm *Licuala ramsayi* (North Australia); *Juniperus communis* (Fennoscandia); *Selaginella* (Indomalesia); *Vaccinium vitis-idaea* (boreal); cushion plant *Azorella macquariensis* (subantarctic).) (Skarpe 1996; McIntyre & Lavorel 2001).

Reich *et al.* (2003) arbitrarily defined four different **functional groupings** expanded in Table 12.1 to include two additional groups. The first and most traditional grouping is based on discrete, typically qualitative individual traits. These include, for example, key ancestral or evolutionary criteria (conifer/angiosperm, monocot/dicot), photosynthetic pathways (C_3/C_4) and seasonality (evergreen/deciduous). The second group is based on taxon position along a continuum of quantitative values for a shared trait such as leaf life-span, seed size, net photosynthetic capacity (A_{max}), or others. The third group is based on suites or syndromes of coordinated quantitative traits (Westoby *et al.* 2002; Wright *et al.* 2004; Hummel *et al.* 2007). The fourth represents a class of traits commonly recorded as ordered or multistate variables such as leaf size class. The fifth uses *post hoc* classification schemes to group plant species based on their responses to specific environmental factors (Gillison 1981; Lavorel *et al.* 1997; Garnier *et al.* 2007). This grouping is based on integrated whole-plant behaviour and outcomes and includes traditional classifications exemplified by shade and drought tolerance as well as plant strategy concepts such as the C-S-R triangle

Table 12.1 Different kinds of functional groupings.^a

<i>Basis</i>	<i>Trait (examples)</i>
1 Qualitative, discrete trait	Dicot/monocot, woody/not, N-fixer/not, C ₃ /C ₄ , conifer/angiosperm, evergreen/deciduous
2 Relative value of quantitative, continuous trait	SLA, A _{max} , leaf life-span, height, seed mass, basal area, hydraulic conductance
3 Quantitative, suite of continuous traits	Leaf-trait syndrome, root-trait syndrome, seed trait syndrome
4 Qualitative suite of ordinal or multistate traits	Leaf (size class, inclination, phenology), plant inclination, canopy structure
5 Qualitative or quantitative; integrated response based mainly on functional strategies	Shade tolerance, drought tolerance, C-S-R scheme, LHS, LES, functional <i>modus</i> , optical spectra, predictive PFTs
6 Qualitative or quantitative; integrated effect of combined traits	Life-form, growth-form, litter structure and chemistry, species richness, herbivore palatability, pathogen defence, flammability, leaf, root and stem leachates

^aModified from Reich *et al.* (2003).

(Grime 1977) and the LHS approach (Westoby 1998). Growing evidence suggests that intraspecific as well as interspecific functional variability can influence community dynamics and ecosystem functioning across a range of ecological scales (Albert *et al.* 2010). The sixth group is therefore based on the concept that additional whole-plant behaviour can influence ecosystem process (see also Table 12.2) and includes life-form and growth-form.

12.3.4 Functional traits

Definitions. According to McGill *et al.* (2006) ‘**trait**’ refers to ‘A well-defined, measurable property of organisms, usually measured at the individual level and used comparatively across species’. A ‘**functional trait**’ on the other hand may be ‘Any measurable feature at the individual level affecting its fitness directly or indirectly’ (Albert *et al.* 2010). Apart from an emphasis on ‘**fitness**’ (Violle *et al.* 2007; Vandewalle *et al.* 2010), functional traits may be characterized additionally by their **adaptive** or **strategic significance** (Semenova & van der Maarel 2000; Ackerly *et al.* 2000; Reich *et al.* 2003; Lavorel *et al.* 2007), growth and/or survival (Lusk *et al.* 2008), their combinatory role in forming a PFT (van der Maarel 2005) or their influence on ‘organismal performance’ (McGill *et al.* 2006). Functional traits can be further described according to ‘biological function’ (Gaucherand & Lavorel 2007; Aubin *et al.* 2009) or their perceived causal connection to ‘**response**’ or ‘**effect**’ in or on ecosystems (Díaz & Cabido 2001; Lavorel & Garnier 2002; Garnier *et al.* 2004, 2007; Violle *et al.* 2007) (see also Web Resource 12.2). For this chapter I define a **functional trait** as ‘any measurable plant trait with potential to influence whole-plant fitness’.

Table 12.2 PFT and trait indicators of terrestrial ecosystem processes and properties.

<i>Ecosystem process, properties</i>	<i>Laboratory^a</i>	<i>Field</i>
Productivity (NEP, NPP, SANPP)	SLA, LAI, LDMC, LNC, mycorrhizal diversity	Life-form, growth-form, canopy height, cover %, basal area all woody plants, root type and depth, bryophyte, lichen cover-abundance of types
Carbon assimilation and investment	Leaf N, P, photosynthetic light response curves, stomatal conductance, SLA, SLW, LAI, optical type, photosynthetic pathway (C ₃ , C ₄ , CAM), RCC	Life-form, growth-form, relative growth rate (RGR), leaf phenology, leaf type (e.g. needle- vs. broad-leaf, hardness, color), green stem, water storage, root diameter, bryophyte, lichen cover-abundance of types
Respiration, decomposition	LDMC, leaf N, P, base content, phenolics, SLA, mycorrhizae, stomatal and stem lenticel conductance	Leaf (size, inclination), phenology, litter depth and type, RGR, RNC, SRL, leaf turnover rate, bryophyte, lichen cover-abundance of types
Water use, evapotranspiration, drought resilience, hydrology	Stomatal conductance, xylem water potential, WUE, SLA	Life-form, growth-form, plant height, basal area, diameter increment, leaf (size, inclination, palisade distribution, phenology, succulence), green stem, root (type, depth, architecture), bryophytes, lichens
Tolerance to flooding, tidal movements, salinization, etc.	SLA, LWC	Adventitious rooting, salt glands, propagule dispersal, lenticels, succulence. Life-form, growth-form, tree height, leaf (succulence, inclination, thickness, palisade distribution) furcation index, green stem, known photosynthetic pathways (e.g. CAM), biocrusts (bryophytes, lichens)
Nutrient stocks, N mineralization, soil fertility	Leaf dry matter content; leaf N, P, mycorrhizal fungi, LDMC, SLA	Trait size, growth rate, litter depth, bryophyte, lichen composition, Mean canopy height, basal area, lichen cover-abundance, functional <i>modi</i>
Stress-tolerance, ruderal pioneers (C-S-R); Disturbance (loss of plant biomass and species)	LCC, LDMC, SLA, Succulence index, Standing biomass, resprouting ability, vegetative spread	Clonality, canopy height, necromass persistence. Stem and canopy structure, basal area, furcation index, life-form, growth-form, seed dormancy, seed dispersal, species: functional <i>modi</i> to richness ratio, bryophytes, lichens

Table 12.2 (Continued)

<i>Ecosystem process, properties</i>	<i>Laboratory^a</i>	<i>Field</i>
Response to grazing, herbivore resistance Response to fire	SLA, palatability, standing biomass. Leaf N, P, phenolics, RTD Flammability	Canopy height, cover %, Vegetation structure, life-form, growth-form, species turnover Life-form, resprouting capacity, seed bank availability and persistence, seedling establishment, bark types, leaf volatiles, fuel load, clonal regeneration
Competition for light	SLA, RGR (seedling)	Plant height, leaf size, type, inclination, diameter, tiller increment, vegetative regeneration, seed size, type
Biodiversity	Functional diversity, functional complexity, mycorrhizal fungi	Functional types (e.g. <i>modi</i> this chapter), species richness, species composition, bryophyte, lichen cover-abundance, composition

^aIncludes instrumentation used to measure gas fluxes, xylem water potential, light dynamics, etc. in the field. Abbreviations: A_{max} , net photosynthetic capacity; PNUE, photosynthetic energy use efficiency; NEP = net ecosystem productivity; SANPP, specific annual net primary productivity; NPP, net primary productivity; LAI, leaf area index; SLA, specific leaf area; LCC, leaf carbon content; LDMC, leaf dry matter content; LNC, leaf nitrogen content; LWC, leaf water content; N, nitrogen; P, phosphorus; C, carbon; RCC, root construction cost; RGR, relative growth rate; RNC, root N concentration; SRL, specific root length; RTD, root tissue density; WUE, water use efficiency. (See Web Resource 12.5 for units used by different authors.)

Attributes and elements. Gillison (1981) applied a systematic approach to trait terminology in which a **plant functional attribute** or PFA is defined as ‘any plant feature that responds in a demonstrable and predictable way with a change in the physical environment’. For PFT classification, Gillison & Carpenter (1997) use a hierarchical system whereby the lowest ranking **plant functional elements** (PFEs) (e.g. microphyll leaf size) are used to quantify PFAs at the next (class) level that, together with other PFAs, are then used to construct **whole-plant PFTs** according to specific assembly rules (Table 12.3, Section 12.4.5, Web Resource 12.7). A similar concept is described by Skarpe (1996), while van der Maarel (2005) considers PFAs to be different expressions of a trait that should rather be called ‘states’. Although many ecologists frequently distinguish between ‘**soft traits**’ (easy to measure) and ‘**hard traits**’ (difficult to measure), I agree with Violle *et al.* (2007) that there is little evidence to support such distinction.

Table 12.3 Plant functional attributes and elements used to construct *modal* PFTs.

<i>Attribute</i>	<i>Element</i>	<i>Description</i>	
[Photosynthetic envelope]			
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	4500–18200
	pl	platyphyll	18200–36400
	ma	macrophyll	36400–18 · 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)
Leaf 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>)
[Supporting vascular structure]			
life-form	ph	phanerophyte	
	ch	chamaephyte	
	hc	hemicytrophyte	
	cr	cryptophyte	
	th	therophyte	
	li	liane	
Root type	ad	adventitious	
	ae	aerating	(e.g. pneumatophore)
	ep	epiphytic	
	hy	hydrophytic	
	pa	parasitic	

12.4 Plant strategies, trade-offs and functional types

12.4.1 On plant strategies

‘Plant strategy’ is usually taken to mean a combination of plant characteristics that best maximize trade-offs 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 & Huston 1989). Strategy differentiation among species contributes to the maintenance of diversity and thus ecosystem performance (Kraft *et al.* 2008) and understanding plant ecological strategies is a fundamental aim of ecological research. 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). According to Craine (2009) all seed-plant diversity can be collapsed onto four central resource **strategy axes** – strategies for low nutrients, low light, low water and low CO₂ – with modifications for increases in resource supply. For practical purposes, the challenge is to identify the most parsimonious factors among whole-plant PFTs and individual traits that best explain causal links with such strategies. The functional significance of leaf traits within the context of the entire plant is highlighted where plant responses to environmental adversity require coordinated responses of both whole plant traits and leaf traits alike (Bonser 2006). 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 involve trade-offs between (1) specific leaf area (SLA) and leaf life-span (LLS), (2) seed mass and fecundity, (3) plant height at maturity (H) and shading, water use and response to disturbance, and (4) leaf size (LS) and twig size (TS). This framework has contributed to two key strategy models (LHS and LES; see Sections 12.4.3, 12.4.4).

Not all trade-offs are above-ground. Investment trade-offs between specific root length (SRL) (ratio of root length to root biomass) and root nitrogen and lignin concentrations indicate covarying plant response (e.g. potential growth rate) along environmentally limiting gradients for overall plant growth (Comas & Eissenstat 2002; Craine & Lee 2003; Craine *et al.*, 2005). Root structural and anatomical traits known to constrain RGR(max) and H(max) have potential links with hydraulic conductance, support and longevity (Hummel *et al.* 2007) and exert a feedforward effect on stomatal conductance. In many circumstances the functional significance of leaf traits can parallel that of root traits (Craine *et al.* 2005).

Among the more significant plant ecological strategies involving PFTs and individual traits is the ‘**resource-ratio**’ model of Tilman (1982, 1985) (see also Clark *et al.* 2007) that views the spatial heterogeneity of resources as a selective force for optimal foraging in chronically unproductive habitats. Tilman’s model requires precise ordering of trade-offs, for example between life history and competitive ability in which data for multiple co-existing species ability may be limiting (Pierce *et al.* 2005). The ‘**vital attribute**’ strategy of Noble & Slatyer (1980) based on the residence time of specific life history traits following

disturbance is theoretically insightful but limited in practice. Rather like the CSR strategy discussed in the next section, the well-known **r-K** model of MacArthur & Wilson (1967), while conceptually useful, also has methodological limitations in complex vegetational successional sequences and in isolated, floristically poor communities such as oceanic islands. Less widely established strategies are reviewed elsewhere (Westoby 1998; Lavorel *et al.* 2007).

Preceding the above and persisting remarkably through time is Raunkiær's (1934) life-form model. Raunkiær defines life-form theoretically as 'The sum of the adaptation of the plant to the climate' (Du Rietz 1931) but practically chooses one of the most fundamental adaptations as a base for his systems of life-forms – the survival of the perennating organ during the most unfavourable season. Although based primarily on sensitivity to winter temperatures, Raunkiær's strategy can be applied equally to 'unfavourableness' under other periodic and even episodic, thermal, light and moisture regimes including flood, fire and strong winds. It can be argued that, as a plant ecological strategy, Raunkiær'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 preponderance of woody phanerophytes in 'optimal' environments with corresponding decreases towards less optimal habitats accompanied by increasing relative percentage of structurally reduced chamaephytes, geophytes and hemicryptophytes. Four strategies described here include leaf-based features and reflect a move beyond the more loosely defined adaptive or 'epharmonic' (cf. van der Maarel 1980, 2005; Floret *et al.* 1987) Raunkiærean descriptors towards more detailed evidence of cause and effect between functional traits and environment.

12.4.2 The C-S-R strategy

Other than Raunkiær's life-form model, the most widely known plant strategy is the C-S-R model of Grime (1977, 1979). CSR theory aims to describe the key mechanisms underlying vegetation processes and 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 (Caccianiga *et al.* 2006). Crucially, the CSR model suggests that stress and sporadic resource availability favour conservative phenotypes (Pierce *et al.* 2005). While theoretical support for CSR is derived from extensive studies in the UK, mainly on herbaceous vegetation, methodological limitations have precluded its application in other countries especially in species-rich, structurally and functionally complex woody vegetation. 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 (leaf dry matter content) can be statistically

coupled with productivity traits that, for example, are relevant to S-type (slow-growing, stress-tolerant species of chronically unproductive habitats). An ordination of these more readily measureable traits then allows the taxa under study to be placed within CSR coordinate space.

The CSR triangle defines the axes with reference to concepts, for which there is no simple protocol for positioning species beyond the reference data sets within the scheme, and consequently benefits of global comparison have not materialized (Westoby 1998). Methodological and theoretical limitations are clearly apparent where, under studies of grazing impact and shoreline successional sequences, CSR types are not readily applicable (Oksanen & Ranta 1992; Ecke & Rydin 2000; Moog *et al.* 2005). Other problems with the CSR format have been noted elsewhere (Austin & Gaywood 1994; Onipchenko *et al.* 1998; Körner & Jeltsch 2008). With some exceptions (e.g. Cerabolini *et al.* 2010; Kiliņ *et al.* 2010) and despite improved numerical procedures, the capacity of CSR theory to predict variation in species composition along environmental gradients worldwide remains problematic.

12.4.3 The Leaf-Height-Seed (LHS) strategy

A more parsimonious approach using a ‘core’ set of more readily measureable functional traits based on specific Leaf area, mature plant Height and Seed mass (the LHS system of Westoby 1998) represents a significant breakthrough in quantifying plant responses to the environment, with a capacity for general application. The LHS system represents a tightly defined functional concept using orthogonal (functionally independent) 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 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 advantages of the LHS scheme can be understood by comparing it to Grime’s CSR scheme, over which it has some significant 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 application to any vascular plant species in any terrestrial environment. Nonetheless, 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).

12.4.4 The Leaf Economics Spectrum (LES) strategy

There are some common trends and linkages between the LHS strategy and the LES scheme proposed by Wright *et al.* (2004) which 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. Unlike several other strategies it is essentially independent of growth-form, plant functional type or biome. Functional linkages between leaf traits and net photosynthetic rate investigated by Shipley *et al.* (2005) provide a mechanistic explanation for the empirical trends relating leaf form and carbon fixation, and predict that SLA and leaf N must be quantitatively coordinated to maximize C fixation thus lending validity to the LES scheme. (See further Section 12.11.)

12.4.5 The Leaf–Life-form–Root (LLR) strategy

The LLR approach considers ways in which multiple traits can be used to construct PFTs via an assembly system that addresses whole-plant performance. This is achieved in part by coupling photosynthetic traits with life-form and readily observable rooting structures. When coupled with additional information that describes stand structure, the LLR methodology facilitates comparative analysis across a range of environmental scales (Fig. 12.1) (Gillison 1981, 2002). The LLR strategy complements significant gaps in the CSR, LHS and LES systems that otherwise exclude important photosynthetic traits such as leaf inclination (Falster & Westoby 2003; Posada *et al.* 2009), leaf phyllotaxis or insertion pattern such as rosettes (Withrow 1932; Lavorel *et al.* 1998, 1999a, 1999b; Díaz *et al.* 2007a; Ansquer *et al.* 2009; Bernhardt-Römermann *et al.* 2011a) and woody green-stem photosynthesis, all of which are noted plant adaptations to irradiance, nutritional and water availability.

As discussed earlier, one strategy that has stood the test of time is the Raunkiærian life-form system, partly because it is built on a fundamental survival adaptation to cyclic environmental and edaphic (nutritional) extremes and because of its sheer simplicity. On the other hand, in its basic form, the life-form model ignores photosynthetic traits. To help redress this issue 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 Raunkiærean life-form and an aboveground rooting system – presented here as the ‘Leaf-Life-form-Root’ or LLR spectrum. The LLR asserts that a single attribute, such as leaf size class, takes on increased functional significance when combined with leaf-inclination and other morphological (e.g. dorsiventral) 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. For convenience, and to indicate the unique type of PFT, specific LLR combinations are termed functional *modi* (from the Latin ‘*modus*’ mode or manner of behaviour) (see also the ‘*modality*’ of Violle *et al.* 2007). This initial model (Gillison 1981) was the first coordinated use of PFAs to relate *modal* PFTs to environmental conditions (Fig. 12.2). The method was later formalized (Gillison & Carpenter 1997) using an assembly rule set and syntactical grammar to construct *modal* PFTs based on 36 plant functional elements (PFEs) (Table 12.3). In this method, a typical PFT *modus* for an individual

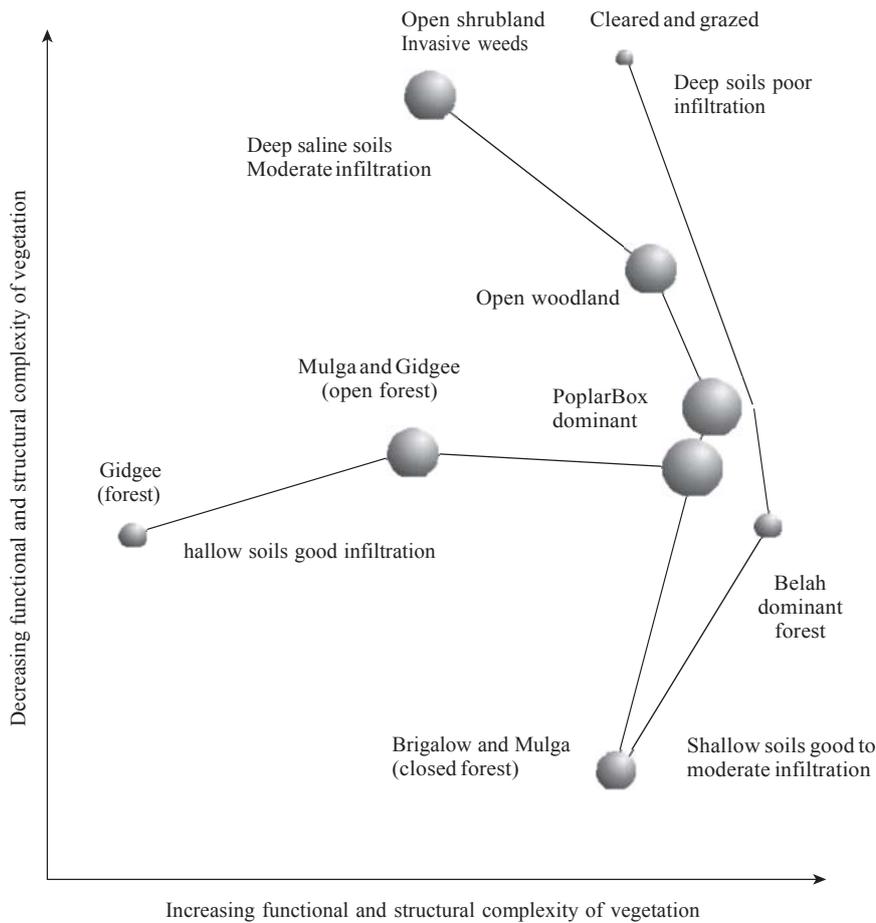


Fig. 12.2 Minimum spanning ordination (Gillison 1978) of plant functional attributes in ten 40 · 5 m transects (globes) mapped against soil depth, infiltration capacity and salinity. The x-axis indicates complexity in leaf size, inclination and phyllodes. The y-axis indicates decreasing functional complexity through decreasing phanerophytes, increasing cryptophytes, and dorsiventral leaves. The z-axis (visualized through decreasing size of the globes) represents mainly a response to vegetation structure (max height, canopy cover %). (Adapted from Gillison 1981.)

of *Acer palmatum* might be a mesophyll (**me**) size class with pendulous (**pe**), dorsiventral (**do**), deciduous (**de**) leaves with green-stem (cortex) (**ct**) photosynthesis attached to 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 (e.g. a leaf size class), results in a new *modus* thereby facilitating further comparison of intraspecific as well interspecific variability within a described habitat. Using the public domain VegClass software package (Gillison 2002), quantitative and statistical comparisons within and

between species and plots are facilitated via predetermined lexical distances between different PFTs (Gillison & Carpenter 1997). The system comprises 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 from 1066 field sites worldwide (Plate 12.2) indicates the ‘real’ number of unique *modal* PFTs approximates 3500 for the world’s estimated 300 000 vascular plant species.

At a global scale, Plate 12.1 illustrates an arrangement of whole-plant LLR functional syndromes arranged along two key environmental gradients or axes (irradiance and moisture; see also Lavers & Field 2006). Syndromes of this kind are readily described according to the *modal* schema. In the same way that the LES LMA varies with rainfall and temperature, preliminary results from a global survey illustrate how both *modal* PFTs and PFEs covary with global environmental gradients of rainfall and total annual actual evapotranspiration (Figs 12.3, 12.4).

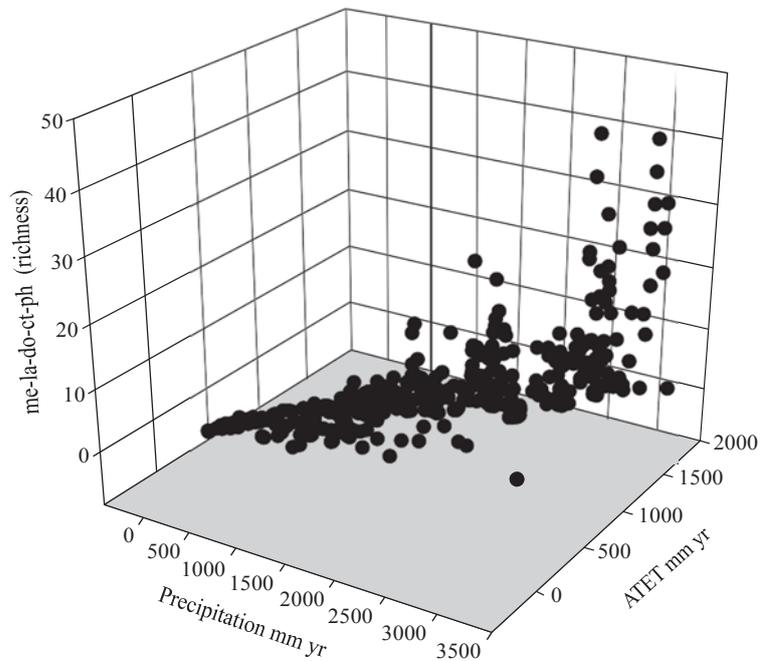


Fig. 12.3 Example of environmentally covarying distribution pattern of plants possessing the *modal* PFT combination me-la-do-ct-ph representing mesophyll (me), laterally inclined (la) dorsiventral (do) (hypostomatous) leaves with a photosynthetic stem cortex (ct), supported by a phanerophyte (ph). Covariates are mean annual rainfall and total annual actual evapotranspiration. Circles are records from 1066 (40 · 5 m) transects.

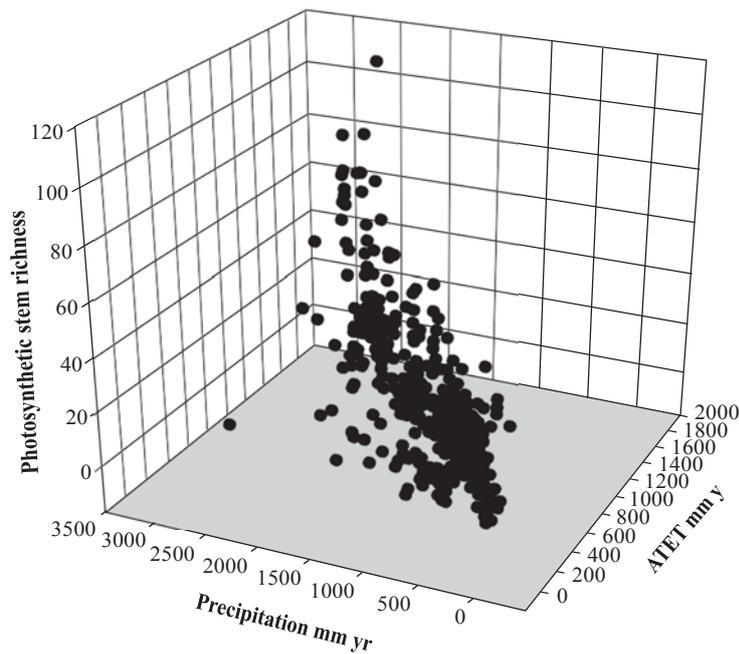


Fig. 12.4 Example of how a single PFE, representing a photosynthetic primary stem cortex (ct) covaries with mean annual rainfall and total annual actual evapotranspiration. Circles are records from 1066 (40 · 5 m) transects.

12.5 The mass ratio hypothesis

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 well supported by empirical evidence (Díaz *et al.* 2007b; Mokany *et al.* 2008) 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 with resource capture, usage and release at the individual and ecosystem levels. Díaz *et al.* (2007c) alluded to overwhelming evidence that the more abundant traits are major drivers of short-term ecosystem processes and their feedbacks onto global change drivers. Garnier *et al.* (2004) found support for the MRH where ecosystem-specific net primary productivity, litter decomposition rate and total soil carbon and nitrogen varied significantly with field age, and with community-weighted functional leaf traits SLA, LDMC and leaf N. On the other hand, McLaren & Turkington (2010) show 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.

12.6 Functional diversity and complexity

Measures of functional equivalence between many traits lack consensus as do measures of functional redundancy (see Web Resource 12.1.1). Similar debate surrounds measures of functional diversity (FD) that comprises the *kind*, *range* and *relative abundance* of functional traits present in a given community. There is, however, increasing evidence that FD can be a better predictor of ecosystem functioning than the number of species or the number of functional groups (Díaz & Cabido 2001; Lepš *et al.* 2006; Petchey & Gaston 2006; Villéger *et al.* 2008). To this end, Mayfield *et al.* (2006) further attach an abundance measure distinguishing ‘**functional composition**’ as the identity and abundance of trait states found from a trait in a community. For rangeland studies in Australia, Walker *et al.* (1999) use two **functional attribute diversity** measures: FAD1: the number of different attribute combinations that occurs in the community that must be equal to or less than the number of species – a feature found to be questionable on ecological grounds (Mayfield *et al.* 2005; Villéger *et al.* 2008).

To counter the problem that a single measure of FD such as Euclidean distance (the FAD2 of Walker *et al.* 1999; Flynn *et al.* 2009) limits ecological interpretation, Mason *et al.* (2005) propose three additional indices: (a) the amount of niche space filled by species in the community (**functional richness**); (b) the evenness of abundance distribution in filled niche space (**functional evenness**); and (c) the degree to which abundance distribution in niche space maximizes divergence in functional characters within the community (**functional divergence**) (but see also Villéger *et al.* 2008; Bernhardt-Römermann *et al.* 2011b). A pervasive problem in estimating FD is the need to take into account multiple traits that can occur within and between species. To this end the Rao quadratic entropy index (The FD_q of Botta-Dukát 2005) fulfils all *a priori* criteria identified by Mason *et al.* (2003, 2005) and according to Botta-Dukát (2005) surpasses other proposed indices, because it includes species abundances and more than one trait (see also de Bello 2012). This is similar to the inverse of Simpson’s D index (1-D) used in the VegClass system (Gillison 2002) where species numbers are measured against counts of *modal* PFTs. Nonetheless difficulties remain in allocating standardized measures of different traits identified by different workers (Villéger *et al.* 2008) and in estimating distance measures between traits and combinations used to describe PFTs.

A very different approach (Gillison 2002; Gillison *et al.* 2012) explores descriptors of functional complexity and diversity based on *modal* PFTs. First, a minimum spanning tree (MST) (cf. Villéger *et al.* 2008) is used to calculate the total ‘*functional distance*’ that represents a potentially useful measure of ‘**plant functional complexity**’ (PFC) as distinct from ‘diversity’ *per se* (see Web resource 12.1.2) Dendrograms (*sensu* Petchey & Gaston 2002) or MST lengths are not, strictly speaking, measures of ecological diversity (Magurran 2004), hence the preferred alternative use of ‘complexity’. As a measure of *modal* PFT

complexity, PFC value can be a useful additional measure of biodiversity in discriminating for example, between two communities that may share the same number of PFTs, but otherwise differ in PFT composition as indicated by a PFC value. Second, whereas the estimation of species diversity relies on individual abundance counts per species, a '**plant functional diversity**' analogue can be estimated using the number of species per PFT instead, to compute three commonly used ecological diversity indices such as Fisher's *alpha* (α), Shannon-Wiener (H_2) and Simpson's (dominance). A summary of different global vegetation types (Table 12.4) illustrates how PFC and FD values derived from *modal* PFTs vary with vegetation type. By implication, the alternative measurement of the number of species per PFT elevates the application (and testing) of the **mass ratio hypothesis** to another level as the focus changes from dominant species to dominant PFTs.

12.7 Moving to a trait-based ecology – response and effect traits

Whole-plant trait combinations or PFT syndromes facilitate a more holistic perspective of plant-environment interaction than their disaggregated, singular traits such as leaf size or plant height. This advantage is offset by difficulties in deciding how and why trait syndromes should be constructed and how and at what scales traits either singly or combined, interact within and between individuals and with the biophysical environment. Recent progress in formulating plant functional strategies through combinations of independently functioning (orthogonal) traits (12.4) is being increasingly complemented by parallel research that focuses on readily quantifiable, core functional traits. While a common functional thread links both trait syndromes and single traits in the study of plant-environment interaction, the following sections focus on how trait-centred aspects of plant functional ecology may complement the study of PFTs.

PFTs have been variously defined according to their response to environmental conditions or their effect on dominant ecosystem processes (cf. Díaz & Cabido 1997; Díaz Barradas *et al.* 1999). In similar vein, functional traits (FTs) may be described according to 'effect' (Díaz & Cabido 2001; Garnier *et al.* 2004; Violle *et al.* 2007) or 'response' (Garnier *et al.* 2007) (Further definitions of traits and trait types can be found in Web Resource 12.4, 12.5). The following subsections discuss these traits.

12.7.1 Response traits

Disturbance. Discrimination between response and effect phenomena in functional types and traits is obscured by complex feedback and feedforward systems. A comprehensive summary of response and effect phenomena by Lavorel *et al.* (2007) cross-links whole-plant and individual leaf, stem and belowground traits as well as regenerative traits based on trait responses to four classes of environmental change or 'environmental filters'; plant competition and plant defense against herbivores and pathogens (biological filters) and plant effects on biogeochemical cycles and disturbance regimes. Plant ecological strategies are inevitably

Table 12.4 Examples of *modal* PFT diversity and complexity indices across a range of global vegetation types.

<i>Vegetation type</i>	<i>Country/region</i>	<i>Site ID</i>	<i>Spp</i>	<i>Modi</i>	<i>Spp/modi</i>	<i>Fisher's alpha</i>	<i>Shannon index</i>	<i>Simpson index</i>	<i>PFC</i>
Rainforest, Broadleaf lowland	Indonesia/Sumatra	Tesso Nilo 2	202	73	2.77	38.49	3.59	3.11	370
Savanna Sub-Saharan, open woodland	Africa/Cameroon	Cameroon 17	45	41	1.10	153.35	0.027	2.91	439
Alpine meadow	Bhutan	Mt Jhomolari 7	34	24	1.42	36.34	3.01	3.33	84
Tundra	Kamchatka (Russia)	Mutrousky pass K01	28	16	1.25	15.51	2.60	3.17	90
Heath – coastal sandy	Australia/temperate/Mediterranean	Hamelin Bay WA08	27	25	1.08	162.09	0.043	3.00	233
Woodland, Miombo	Africa/Malawi	Malawi01	24	20	1.20	56.46	0.056	2.75	159
Desert, hot, dry	United Arab Emirates/desertic	Dubai01	22	15	1.47	20.76	0.095	3.60	91
Pasture 20yr	South America/ Perú/ Amazon Basin	Pucallpa PUC05	21	14	1.50	18.36	0.093	3.04	74
Conifer forest on sand	North America/USA	Ocala Florida Nam02	18	13	1.23	24.03	0.080	3.23	120
Deciduous broad-leaved forest, old growth	South America/ Argentina	Tierra del Fuego 01	10	8	1.25	18.57	0.140	2.57	48
Mangrove, <i>Sonneratia</i>	Indonesia/Sumatra	Jambi AHD05	6	6	1.00	166.75	0.167	3.11	61
Steppe	Outer Mongolia	Baatsaagan Nuur 24	6	4	1.5	1.24	5.24	3.28	30

Spp, species richness; *Modi*, richness of *modal* PFTs; *Sp/modi*, species/*modi* ratio; Fisher's alpha (*modi*) according to the logarithmic series; Shannon, Shannon–Wiener index (*modi*); Simpson dominance index (*modi*); PFC, plant functional complexity Index. For diversity indices see Magurran (2004). All data recorded from 40 · 5 m transects using the uniform VegClass protocol (Gillison 2002). (See also Web Resource 12.6 for an extended list.)

connected with trait response and effect and include a variety of stressor axes among them disturbance and resource availability. Disturbance – *defined here as loss of tissue or taxa* – may result from natural phenomena, land use and other human-related activities. The intermediate disturbance hypothesis (IDH) asserts that along a disturbance gradient, highest species richness and diversity will occur at intermediate rather than extreme levels of disturbance (Connell 1983). Despite some evidence to the contrary, the IDH has general empirical support (Sheil & Burslem 2003; Bongers *et al.* 2009) with emerging implications for functional ecology. Bernhardt-Römermann *et al.* (2011a) for example, show that management treatments with intermediate disturbance regimes maximize biomass yields in temperate environments. Because of the implications for response and effect dynamics and because the IDH has received little attention thus far, Table 12.5 indicates trends in functional response along gradients of both disturbance and resource availability (see also Lavorel *et al.* 2007). Disturbance effects related to recolonization also reflect phylogenetic patterning in tropical and subtropical vegetation when examined using LHS, LES type functional traits (Kooyman *et al.* 2011). Some key elements of disturbance are described here.

Grazing. Investigations into response-based traits concern grazing dynamics are derived mainly from northern (American and European) temperate and Mediterranean grasslands. Differing levels of reporting and conclusions are a consequence of different investigators applying different techniques in different environments. Overall trait response to environmental gradients such as grazing intensity is not necessarily linear (Saatkamp *et al.* 2010) and reports vary as to response to palatability (Jauffret & Lavorel 2003), xeromorphy (Navarro *et al.* 2006) and mediation by climate (de Bello *et al.* 2005). Among the most commonly reported adaptive responses is that of phyllotaxy (arrangement of leaves along a stem) that directly influences the efficiency of light interception in rosette plants – an effect that greatly diminishes when leaves are vertically displaced by elongated internodes (Niklas 1988; Ackerly 1999). Rosettes harvest low-intensity rains and fogs and large succulent leaf rosettes are a characteristic life-form in many arid and semi-arid areas where large numbers of rosette species suggest a close relationship between form and environment (Martorell & Ezcurra 2002). The extent to which climate, soil and grazing individually influence rosette morphology as a functional trade-off to maximize carbon fixing is not clear, although rosette frequency is widely regarded as a common indicator trait of response to grazing (Lavorel *et al.* 1997, 2007; Díaz *et al.* 2007a; Klimešová *et al.* 2008; Ansquer *et al.* 2009; Bernhardt-Römermann *et al.* 2011a, b).

Other characteristics such as species richness and diversity, plant height, vegetative spread, canopy structure, leaf ‘toughness’, leaf mass, life history and seed mass, are linked with community response to grazing across continents (Lavorel *et al.* 1998; Díaz *et al.* 2001; Cingolani *et al.* 2005; Louault *et al.* 2005 and others). Debate centres around the utility of single versus multiple traits. Within temperate European grasslands, although plant height is a significant predictor of management impact, the existence of other important plant traits led Klimešová *et al.* (2008) to conclude that single traits cannot be the only basis for predicting vegetation changes under pasture management and that a functional analysis of

Table 12.5 Functional response trends along resource and disturbance gradients.

<i>Functional scaling</i>	<i>High RA, low disturbance</i>	<i>High RA, high to intermediate disturbance</i>	<i>Low RA, high to intermediate disturbance</i>	<i>Low RA, low disturbance</i>
Whole-plant				
Rosette crown	*	**	***	***
Geophytes	*	**	***	***
Liane form	**	***	**	*
Epiphyte	***	**	**	***
Biomass	***	***	**	*
<i>Modal</i> PFTs				
me-la-do-ph	***	***	**	*
pl-la-do-ct-ph	**	***	**	—
pi-ve-is-ro-ch (see Table 12.3)	—	*	**	***
Stem				
GSP (ct)	*	***	**	**
Height	***	***	**	*
Basal area	***	***	*	*
Specific density	**	*	**	***
Succulence	*	*	**	***
Shoot : root ratio	***	***	**	*
Aerial roots	**	***	*	*
Leaf				
SLA, LMA	**	***	**	*
C:N ratio	**	*	**	***
LDMC	**	*	**	***
CAM pathway	—	*	**	***
N & P content	**	***	**	*
Secondary metabolites	**	***	***	**
Tensile strength	**	*	**	***
life-span	**	**	**	***
Isostomatous	*	*	**	***
Ve or Pe incl.	*	**	**	***
Litter				
Decomposition rate	**	***	*	*
Fungal (mycorrhizal)	**	***	*	*
Below-ground roots				
SRL	***	***	**	*
Regenerative mode				
Clonality	*	**	***	**
Resprouting	*	***	**	*
Seed mass	**	***	**	*
Ecosystem performance				
Species richness	**	***	**	*
<i>Modal</i> PFT richness	**	***	**	*
Species : <i>modal</i> PFT ratio	***	**	**	*
PFC	***	***	**	*

RA, resource availability (light, moisture, nutrients); table excludes response to seasonality and thermal gradients; GSP, green-stem photosynthesis (*modal* element ct); CAM, Crassulacean Acid Metabolism (photosynthetic pathway). Isostomatous, stomata on both sides of leaf; Pe, pendulous inclination; Ve, vertical inclination (Table 12.3); SRL, specific root length; Number of * indicates relative increase in trait response. With the exception of below-ground traits, all or most traits are readily measureable. List is restricted to dry land, non-immersive, terrestrial vascular plants.

the trade-off between multiple key traits is needed. Gradients of grazing intensity are commonly associated with soil properties and functional traits, especially SLA (Ceriani *et al.* 2008; Rusch *et al.* 2009) but at global scale this relationship may be more strongly influenced by climate (Ordoñez *et al.* 2009). Because plant functional type classifications and response rules are frequently specific to regions with different climate and herbivory history, there is a need for more comprehensive studies of ecosystem dynamics at landscape level.

Fire. Regeneration strategies of woody plant species subject to recurrent fire vary between regions (Lloret & Montserrat 2003; Pausas *et al.* 2004; Lavorel *et al.* 2007; Müller *et al.* 2007). Among the primary functional traits that facilitate persistence following crown fire are resprouting capacity and the ability to retain a viable seed bank. Different combinations of these two traits have been preferentially selected in floras with different evolutionary histories. In Australian heathlands for example, the proportion of resprouters and non-resprouters is relatively even, compared with other fire-prone ecosystems, although post-fire obligate resprouters (resprouters without a seed bank) are almost absent. In the Mediterranean basin, most resprouters are obligate, while in California, shrub resprouters are evenly segregated among those having propagules that persist after fire (facultative species) and those without propagule persistence capacity (obligate resprouters). Species with neither persistence mechanism are rare in most fire-prone shrublands (Pausas *et al.* 2004; Lavorel *et al.* 2007), but other significant functional types such as obligate seeders are important components that, together with resprouters, may be adversely affected by short-term alterations to any long-standing fire regime (Regan *et al.* 2010). The highly dynamic nature of fire-prone ecosystems especially towards the lower latitudes, suggests that organization of PFTs and their assemblages is continually mediated by high environmental stochasticity. Limited evidence for deterministic relationships such as between herbivory and fire in savanna (van Langevelde *et al.* 2003) is affected by mainly stochastic phenomena (Jeltsch *et al.* 1996; D'Odorico *et al.* 2006; Keith *et al.* 2007; Regan *et al.* 2010) that typically operate in fire-prone graminoid and heathland ecosystems. In fire-prone wet heathlands of south-eastern Australia, not all species within a PFT follow the predicted direction of change (Keith *et al.* 2007).

Land-use change. Future global change scenarios for terrestrial ecosystems suggest that land-use change will probably have the largest effect, followed by climate change, nitrogen deposition, biotic exchange and elevated carbon dioxide concentration (Sala *et al.* 2000; Bakker *et al.* 2011). Within landscapes, fire, grazing and land-use history are key determinants of vegetation performance. However, discrimination between their differential effects is complex as shown by studies across agricultural landscape mosaics in different countries. An analysis of species data and life history traits across northern temperate forested landscapes (Verheyen *et al.* 2003) showed that different groups of species respond to land-use change according to distinguishable trait syndromes. Simulations of different CSR-type PFT performance under fragmented landscapes (Körner & Jeltsch 2008) suggest that seed-based dispersal traits and PFTs play critical roles in vegetation performance. However, in other areas these can be mediated both by the level of disturbance and resource supply (Kleyer 1999) and land-use

change may be more likely to affect community assembly processes than species *per se* (Mayfield *et al.* 2010). Bernhardt-Römermann *et al.* (2011a) found that vegetation resistance to disturbance within several European landscapes was related to the occurrence of species with traits selected by a history of intensive land use (smaller leaf size, rosette plant form) and local environmental conditions, whereas vegetation resilience was associated with ecosystem properties that facilitate higher growth rates. Liira *et al.* (2008) on the other hand showed that functional group composition and plant species richness are driven mainly by habitat patch availability and habitat quality. These diverse findings indicate that mechanistic responses to disturbance under different drivers (land use or climate) may depend on historical context.

Trait response in tropical forests. Studies in functional ecology are primarily focused in northern temperate regions and then, mostly in grasslands. For this reason, many hypotheses generated in temperate biomes remain to be tested in humid tropical forests where species and functional richness may increase by an order of magnitude. With some exceptions, hypotheses derived from the temperate zone concerning resource-acquisition trade-offs between traits and light, soil nutrients and disturbance tend nonetheless to apply in the tropics. In dipterocarp dominated forests, species distributions and traits show a significant response to soil nutrient gradients, in line with a generally consistent global pattern where rich-soil specialists have larger leaves, higher SLA, leaf N and P, and lower N : P ratios (Paoli 2006). As with some temperate region studies, research in tropical forests (Poorter & Bongers 2006; Markesteijn *et al.* 2007) indicate a similar pattern of correspondence between leaf trait values and growth, survival and light requirements. Compared to temperate regions and despite some exceptions (Gillison 2002), most studies in tropical forests rely on single rather than trait syndromes (Guehl *et al.* 1998; Kariuki *et al.* 2006; Kooyman & Rossetto 2008; Maharjan *et al.* 2011).

Climate. The analysis of plant functional response to climate is confounded by variation in land use, available nutrients, scale of analysis and the nature of the functional types used in the investigation. While a review of literature on plant response to climate is beyond the scope of this chapter (see Chapters 15 and 17), certain inferences can be drawn from studies of trait and whole-plant PFT response at several integrated levels, albeit with some confusing outcomes. At one level, simulated climate change impact on PFTs (Esther *et al.* 2010) suggests that responses are determined by specific trait characteristics and that community patterns can exhibit often complex responses to climate change. For example, while an increase in annual rainfall can cause an increase in the numbers of dispersed seeds for some PFTs, but decreased PFT diversity in the community, a simulated decrease in rainfall can reduce the number of dispersed seeds and diversity of PFTs. It can be concluded that, at this level, PFT interactions and regional processes must be considered when assessing how local community structure will be affected by environmental change (Esther *et al.* 2010). A climatic gradient may dominate and thus confound otherwise predictive functional traits related to grazing in the Mediterranean region (de Bello *et al.* 2005). In

Patagonia, Jobbágy & Sala (2000) demonstrated a differential effect of precipitation on functional type (grass and shrub) ANPP that shifted from precipitation alone to precipitation and temperature when the temporal scale of analysis changed from annual to seasonal. At a subregional level, leaf size class, leaf type, leaf longevity, photosynthetic pathway and rooting depth along a savanna transect in Southern Africa (Skarpe 1996) were strongly associated with total annual precipitation, precipitation of the wettest month, a moisture index and temperature of the coldest month. However, Maharjan *et al.* (2011) found that in West Africa, shade tolerance and drought resistance were the main strategy axes of variation, with wood density and deciduousness emerging as the best predictor traits of species position along the rainfall gradient.

Theoretical models of optimal, adaptive responses of leaf 'shape' size to irradiance also show a divergence in outcomes (Parkhurst & Loucks 1972; Givnish & Vermeij 1976; Shugart 1997). Givnish (1988) demonstrated how effective light compensation points can maximize tree heights as a function of irradiance, and that shade tolerance, in turn, is a consequent function of tree height. In practice however, simple models of this kind may mislead where complex cascade effects in response trade-offs to irradiance need to be considered. Apart from the influence of seasonal irradiance, rainfall seasonality has a profound influence on vegetation and traits associated with trade-offs between carbon investment and water use efficiency. In certain seasonal forest types (Enquist & Enquist 2011), climate may outweigh disturbance as a driver in ecosystem performance.

12.7.2 Effect traits

Effects on ecosystem properties and services. The Millennium Ecosystem Assessment synthesis (2005) covers *provisioning services* such as food, water, timber and fibre; *regulating services* such as the regulation of climate, floods, disease, wastes and water quality; *cultural services* such as recreational, aesthetic and spiritual benefits; and *supporting services* such as soil formation, photosynthesis and nutrient cycling. While these services are strongly affected by abiotic drivers and direct land-use effects, they are also modulated by community FD (Lloret & Montserrat 2003; Díaz *et al.* 2007a, b). Analyses of ecosystem services using plant functional variation across landscapes offer a powerful approach to understanding fundamental ecological mechanisms underlying ecosystem service provision, and trade-offs or synergies among services (Lavorel *et al.* 2011). On the negative side, univariate investigations of the response–effect relationships between functional traits and ecosystem performance show no coherent solution as yet to the search for a generic methodology or a unified syndrome of traits that can be applied worldwide. A significant contribution to solving this problem is a framework proposed by Díaz *et al.* (2007b) based on the way in which FD response to land-use change alters the provision of ecosystem services important to local stakeholders. Other workers (e.g. Quetier *et al.* 2007), argue that because PFTs relate to universal plant functions of growth (e.g., light and nutrient acquisition, water-use efficiency) and persistence (e.g. recruitment, dispersal, defence against herbivores, and other disturbances), they have the potential to

couple community structure to ecosystem functions. These authors also show that, at least for subalpine European grasslands, plant traits and PFTs are effective predictors of relevant ecosystem attributes for a range of ecosystem services including provisioning (fodder), cultural (land stewardship), regulating (landslide and avalanche risk), and supporting services (plant diversity). Leaf traits such as leaf nitrogen content (LNC) for example, are markers of plant nutrient economy (Wright *et al.* 2004) and are associated with faster nutrient cycling at the ecosystem level (see also Sierra 2009).

Single versus multiple trait effects. Emergent properties of vegetation are affected by interacting plant traits and trait syndromes but as yet, little is known about their degree of influence. Reduction of covarying traits to a minimum set of key predictors can suffice for monitoring effects of land-use change on ecosystem behaviour (cf. Ansquer *et al.* 2009; Falster *et al.* 2011). A novel theoretical framework, the **functional matrix** (Eviner & Chapin 2003; Eviner 2004) describes the relationship between ecosystem processes and multiple traits, treating traits as continuous variables, and determining if the effects of these multiple traits are additive or interactive. PFT assemblages or ‘trait syndromes’ thus described, provide a means of moving forward from individual to composite sets of traits. In this context, PFTs based on morphology have the potential to link ecophysiological traits with ecosystem processes relevant at large scales (Chapin *et al.* 1993) and to offer alternatives to species representing ecosystem structure (Smith *et al.* 1997). Supporting evidence from Aguiar *et al.* (1996) suggests that changes in PFT composition (diversity) – especially growth-form – independent of changes in biomass, affect ecosystem functioning.

12.8 Plant functional types and traits as bioindicators

Bioindicators are a well-established feature of modern ecology and are commonly used to assess and monitor the status of the biophysical environment with regard to acid rain, pollutants, landscape rehabilitation, contamination and the like. For assessing and monitoring biodiversity, surrogate measures include a wide range of environmental units or arbitrary ecosystem ‘types’ or combinations of both (Oliver *et al.* 2004; Carmel & Stroller-Cavari 2006; Grantham *et al.* 2010). Because most definitions of biodiversity are impractical for operational purposes, I propose an operational definition of biodiversity as ‘*The number and composition of all recordable species and functional types and traits in any given area*’. This definition provides for the extension beyond the species as the most common currency of biodiversity, to include traits and trait syndromes that, as with Linnean species, are gene-based.

12.8.1 Species versus PFTs and functional traits as bioindicators

Taxon-based bioindicators are common surrogates for other taxa and more often an expression of taxonomic richness in biodiversity conservation; however, their application is not without debate (Lawton *et al.* 1998; Lewandowski *et al.* 2010; Lindenmayer & Likens 2011). Recent findings (Sætersdal & Gjerde 2011) point

to a general failure of surrogate species or other taxonomic levels in conservation planning – an outcome that suggests functional rather than species-based measures of complementarity may be more appropriate for such purposes. Vandewalle *et al.* (2010) propose standard procedures to integrate different components of species-based functional traits into biodiversity monitoring schemes across trophic levels and disciplines where the development of indicators using functional traits could complement, rather than replace, existing biodiversity monitoring. The frequent use of confamilial or congeneric ‘means’ or species data, often from wide-ranging locations (Jackson *et al.* 1996; Duru *et al.* 2010; Moles *et al.* 2011; Ordoñez *et al.* 2010), runs the risk of misleading matches as illustrated, for example, by phenotypic plasticity within certain species of arctic or boreal *Salix* (Argus 2004) or tropical Rubiaceae (e.g. *Psychotria*, A.N. Gillison pers. obs.).

Despite the potential utility of traits and trait syndromes in biodiversity conservation, field-validated research is surprisingly sparse. The few examples available suggest only that at broad scale there is predictive potential between plant functional group composition and species richness and landscape ‘patch’ habitat availability and quality (e.g. Liira *et al.* 2008; Lavorel *et al.* 2011). A general review of PFTs and traits as biodiversity indicators is beyond the scope of this chapter. Three case studies below summarize outcomes from rapid biodiversity and land-use surveys in Sumatra, Indonesia and Mato Grosso, Brazil, using trait syndromes recorded as *modal* PFTs via the VegClass field recording protocol (Gillison 2002).

12.8.2 Regional biodiversity signatures and predictive functional traits

Functional ‘signatures’ can describe a quantitative profile of community–environment interaction. They can be derived by a variety of means such as a spreadsheet tool for calculating functional signatures for herbaceous vegetation within the context of the C-S-R system of plant functional types (Hunt *et al.* 2004), or spectral signatures for functional types from satellite imagery (Kooistra *et al.* 2007). *Modal* PFTs can be used as reliable indicators for plant species richness in different countries (Fig. 12.5) where, once baseline surveys have been conducted, plant species richness can be estimated from species-independent counts of unique *modal* PFTs, usually with a high degree of confidence. This can be useful where species richness is required for conservation purposes and especially so where species identification is difficult – as can be the case in poorly known areas. In Fig. 12.5, differences in the regression slope between Sumatra and Brazil may represent evolutionary and other historical differences in the species pool, suggesting differential species : PFT ‘signatures’. The ratio of species to *modal* PFTs can vary predictably along resource availability and disturbance gradients (Gillison 2002) reflecting strategies such as LES and LHS. Certain faunal groups also exhibit a close relationship with the species : PFT ratio; changes in termite species richness along a Sumatran land-use intensity gradient are significantly correlated with plant species richness and *modal* PFT richness (Fig. 12.6a,b). However, the correlation becomes appreciably linear when termite species richness is regressed against the species : PFT ratio (Fig. 12.6c). As discussed in the foregoing, functional complexity (PFC) provides an additional measure of biodiversity. In Sumatra, PFC values were significantly related to the

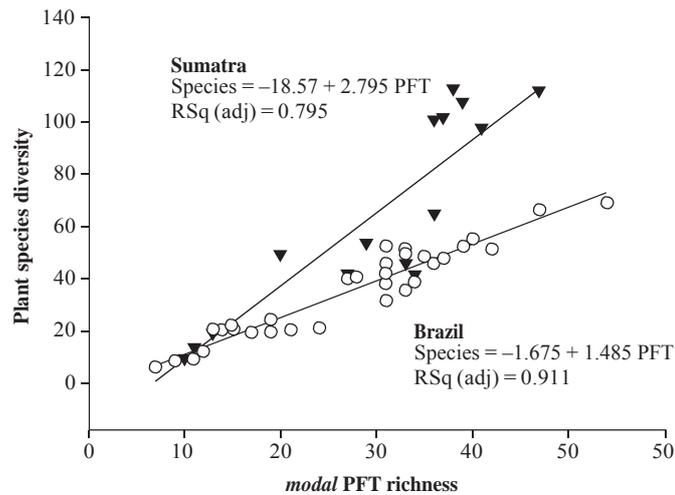


Fig. 12.5 Different regional ‘signatures’ in species to *modal* PFT ratios along land use intensity gradients and vegetation mosaics in Sumatra, Indonesia (triangles) and Brazil (circles) may reflect evolutionary separation of floras and functional characteristics. Data points are 40 · 5 m transects.

distribution of certain invertebrate and vertebrate fauna (see Fig. 12.7 for mammals) and, as with termites, reflects variation in habitat as indicated by vegetation and land use and indirectly, availability of food and shelter resources (Gillison *et al.* in press).

12.9 Environmental monitoring

Research outcomes from the past two decades identify potential PFT and trait-based indicators for monitoring the effects of environmental change on biophysical resources, although very few are actually taken up by management. A method proposed by Hodgson *et al.* (1999; see also Cerabolini *et al.* 2010) for assessing and monitoring change in CSR characteristics is based on long-term monitoring (1958 to date) of permanent plots in Northern England. Most potential indicators, such as CSR types, are based on herbaceous communities (Lavorel *et al.* 1998, 1999a, b; Díaz *et al.* 2007a; Jauffret & Lavorel 2003; Lavorel *et al.* 1997, 2007; Ansquer *et al.* 2009; Bernhardt-Römermann *et al.* 2011a, b) and are unlikely to apply as readily in non-herbaceous biomes. For monitoring purposes, criteria and indicators should target key ecosystem drivers with a focus on the most parsimonious sets of indicators that can be readily measured in a repeatable way by different observers. A move away from species to complementary, functional trait-based indicators is advocated by Vandewalle *et al.* (2010). Detailed studies in different environments suggest minimal indicator groups can be selected from trait syndromes where convergence between plant traits simplifies their monitoring (Ansquer *et al.* 2009).

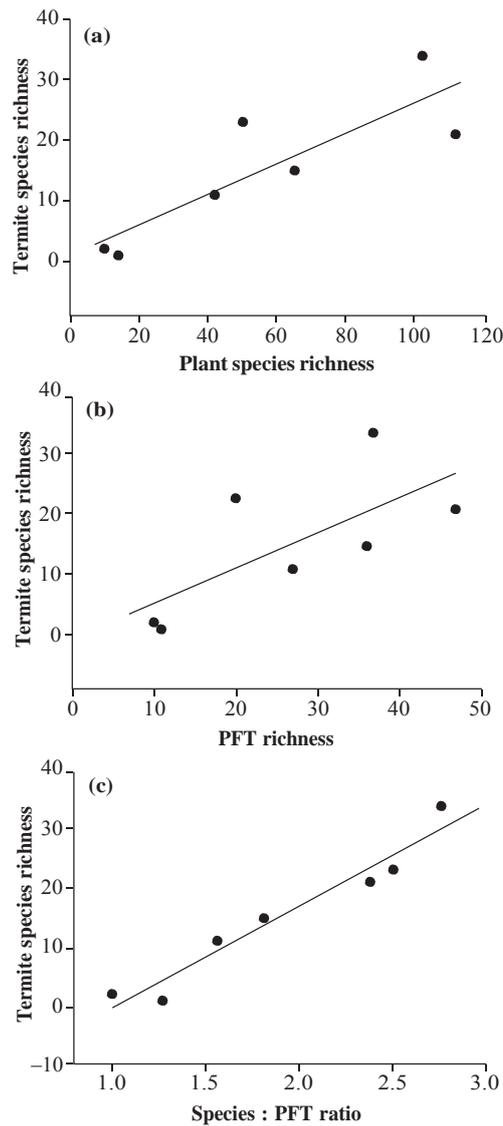


Fig. 12.6 Improved prediction of termite species richness along a land use intensity gradient in Sumatra when ratio of plant species richness to *modal* PFT richness is applied: (a) plant species richness; (b) *modal* PFT richness; (c) plant species richness:*modal* PFT richness. (Adapted from Gillison *et al.* 2003; Bardgett 2005.)

Rapid, repeatable, cost-effective assessment and monitoring methods are a central goal for environmental monitoring. Community-aggregated (i.e. weighted according to the relative abundance of species) functional traits (Garnier *et al.* 2004), while potentially useful in herbaceous assemblages are unlikely to be effective in botanically poorly known, structurally complex vegetation. As also pointed out by Gaucherand & Lavorel (2007), a standardized population-centred

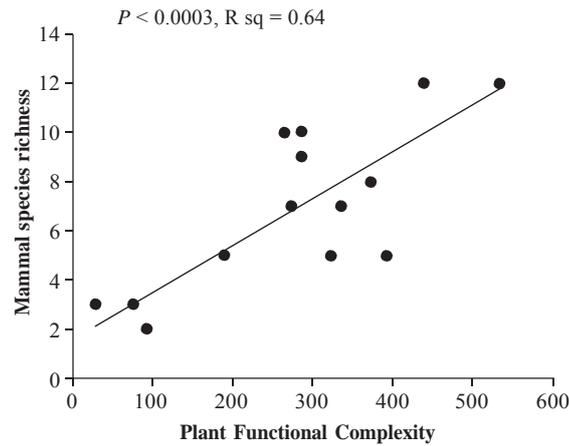


Fig. 12.7 Plant functional complexity (PFC) and mammal species richness in Jambi Sumatra, Indonesia. Dots are 40 · 5 m transects recorded along a land use intensity gradient. (Adapted from Gillison 2000.)

method for measuring species traits already exists (Cornelissen *et al.* 2003), but requires substantial labour and reliable botanical knowledge. An alternative low-cost approach using a rapid **trait-transect** combined with a minimal readily measurable set of traits (Gaucherand & Lavorel 2007) was found to be just as effective for the rapid assessment of functional composition in herbaceous communities. When combined with baseline ground data using rapid survey techniques, recent developments in satellite and airborne imagery are already delivering the next generation of environmental monitoring tools (White *et al.* 2000; Asner *et al.* 2005) that may be usefully combined with dynamic vegetation modelling (Kooistra *et al.* 2007).

In the lower Zambezi valley of Mozambique, Gillison *et al.* (2011) combined an LLR strategy with gradient-based rapid-survey using remote-sensing technology to explore linkages between biodiversity and agricultural productivity along multiple biophysical gradients. Baseline ground data were obtained using gradsects and the VegClass system to sample vascular plant species, *modal* PFTs and their PFEs, vegetation structure, soil properties and land-use characteristics along an inland-to-coast 450-km corridor. Landsat 7 satellite imagery was used to map photosynthetic and non-photosynthetic vegetation and bare substrate along each gradsect. Highly significant correlations between single and combined sets of plant, soil and remotely sensed variables permitted spatial extrapolation of biodiversity and soil fertility throughout a regional land-use mosaic (Plate 12.3) that at 30-m grid resolution, provides a rich source of spatially co-referenced data for management purposes.

12.10 Trait-based climate modelling

A wide range of models is now available for modelling vegetation response to climate change (Chapter 15) across biomes. In the absence of any global

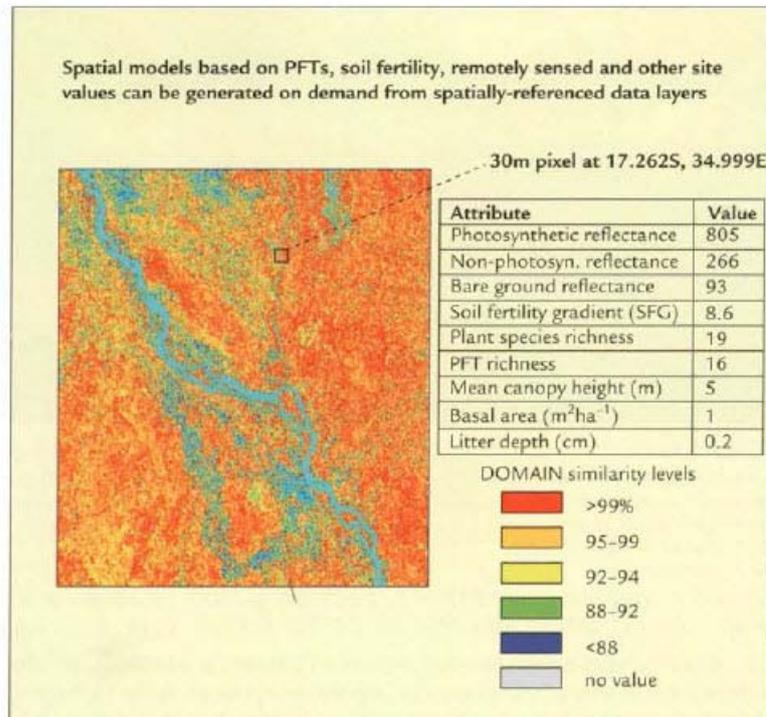


Plate 12.3 DOMAIN spatial model of landscape similarity values in the lower Zambezi river basin, Mozambique, at 30-m pixel resolution using ordinated values of Landsat satellite imagery, *modal* PFT and plant species richness, PFT complexity, soil properties and vegetation structure. (From Gillison *et al.* 2012.).

‘functional’ (i.e. physiological) plant types, many of these are based on ecophysiological growth-form such as ‘Evergreen broad-leaved laurophyll tree’ (Box 1981, 1996; Box & Fujiwara 2005). To simulate vegetation responses to past and future climate change, well-known mechanistic vegetation models (see Chapters 15 and 17) are BIOME4 (Kaplan *et al.* 2003) and LPJ (Lund-Potsdam-Jena; Sitch *et al.* 2003). These models simulate the distribution of plant functional types (e.g. grass, evergreen needle-leaved trees), which can be combined to represent biomes and habitat types (Hickler *et al.* 2004; Broennimann *et al.* 2006; USGS 2010). Harrison & Prentice (2003) used similar growth-form in conjunction with BIOME4 to simulate climate and CO₂ controls on global palaeovegetation distribution at the last glacial maximum. They concluded that more realistic simulations of glacial vegetation and climate will need to take into account the feedback effects of these structural and physiological changes on the climate. Peppe *et al.* (2011) have since shown that, compared to ecophysiological growth-form, the inclusion of leaf traits that are functionally linked to climate improves palaeoclimate reconstructions.

A fundamental difficulty with ‘biome’ models is that they are rarely structurally monotypic (i.e. pure grass or pure trees) representing instead, a mix of many growth-forms or PFTs. To address this problem Oleson *et al.* (2010) describe a Community Land Model (CLM), a land surface parameterization of two other models – the Community Atmosphere Model (CAM4.0) and the Community Climate System Model (CCSM4.0). In the CLM, vegetation is not represented as biomes (e.g. savanna) but rather as patches of PFTs (e.g. grasses, trees) (Bonan *et al.* 2002). The PFT (broadly defined for example, as ‘*broad-leaved evergreen tree*’) determines plant physiology while community composition (i.e. the PFTs and their areal extent) and vegetation structure (e.g. height, leaf area index) constitutes direct input to each grid cell for each PFT. This allows the model to interface with models of ecosystem processes and vegetation dynamics where each PFT is defined by a variety of optical (reflectance, transmittance), morphological (e.g. leaf habit, stem type) and physiological (photosynthetic) parameters. In the same context Laurent *et al.* (2004) refined vegetation simulation models in order to apply global scale modelling to regional scale. From a bioclimatic analysis of 320 taxa they produced a series of **Bioclimatic Affinity Groups** (BAGs) based on growth-form that could be shown to correspond with different geographical ranges and climatic tolerances.

The question of which level of PFT sensitivity is most appropriate for modelling climate change impact has engendered much discussion where there is now a tendency to argue a case for finer scale interactive levels (Esther *et al.* 2010; Peppe *et al.* 2011). Here the use of spatially continuous distributions of coexisting PFTs may be a necessary step to link climate and ecosystem models (Bonan *et al.* 2002). Studies of functional traits such as phenology (Arora & Boer 2005), LLS, LMA, photosynthetic capacity, dark respiration and leaf N and P concentrations, as well as leaf K, photosynthetic N-use efficiency (PNUE), and leaf N : P ratio (Wright *et al.* 2005) show that at the global-scale, quantification of relationships between plant traits may be fundamental for parameterizing vegetation-climate models. Imaging spectroscopy is now capable of delivering full optical spectra (400–2500 nm) of the global land surface on a monthly time step and can be used to estimate (i) fractional cover of biological materials, (ii) canopy

water content, (iii) vegetation pigments and light-use efficiency, (iv) plant functional types, (v) fire fuel load and fuel moisture content, and (vi) disturbance occurrence, type and intensity (Asner *et al.* 2005).

12.11 Scaling across community, ecosystem and world level

Here, ‘scaling’ refers to (1) dependent variation of an organism’s form or function (e.g. body mass) in which the most commonly used scaling equation is the power function, and (2) the use of empirical models of trait-based, response–effect interactions that can be scaled up from local to global scale. In the former case, metabolic scaling theory is proposed by Enquist *et al.* (2007) as a basis for constructing a general quantitative framework to incorporate additional leaf-level trait scaling relationships such as LES, and hence integrate functional trait spectra with theories of relative growth rate.

Scales can range from biome, landscape and forest canopy, to leaves and their components (Fig. 12.1). The LES has helped defuse some of the earlier pessimism (He *et al.* 1994) that the effect of scaling on measures of biological diversity is non-linear and that heterogeneity increases with the size of the sampling units so that fine-scale information is lost at a broad scale. By itself, LES describes biome-invariant scaling functions for leaf functional traits that relate to global primary productivity and nutrient cycling. Similar scaling analogues have been proposed for wood (Chave *et al.* 2009) and leaf venation (Blonder *et al.* 2011). Although each of these strategies reveals scaling trends along global environmental gradients, all are concerned primarily with bivariate rather than multivariate relationships and as such may oversimplify significant plant–environment interaction at a variety of environmental scales (see also Shipley 2004; Grueters 2009). Serial dependency (where trait A depends on B for its existence but not *vice versa*) is also an issue when generating biologically realistic models (Shipley 2004) and in ensuring parsimony when selecting functional traits for generalizable scaling purposes. Both the LHS and LES avoid this issue by selecting traits with independent (orthogonal) functional axes, a feature demonstrated to a lesser extent by LLR, although the combinatory nature of the functional traits used in the LLR encapsulates vegetation features from leaf to structural formation level (Fig. 12.1).

Leaves represent a common starting point for upscaling to whole-plant properties that, according to Wardle *et al.* (1998), have the potential to manifest themselves over much larger scales (see also Read *et al.* 2006). The use of plant functional traits, rather than species and other taxa, to generalize complex community dynamics and predict the effects of environmental changes has been referred to as a ‘Holy Grail’ in ecology (Lavorel & Garnier 2002; Lavorel *et al.* 2007; Suding & Goldstein 2008). In this context, Kooistra *et al.* (2007) argue that PFTs should be adopted for global-scale modelling. An approach devised by Falster *et al.* (2011) uses a structured trait, size and patch model of vegetation dynamics based on four key traits (leaf economic strategy, height at maturation, wood density and seed size) that allows scaling up from individual-level growth processes and probabilistic disturbances to landscape-level predictions. Varying

suites of traits have been suggested for scaling up from organ to ecosystem such as the ‘functional markers’ of Garnier *et al.* (2004) using three leaf traits, SLA, LDMC and N concentration. Again, field-testing of these and other scaling-up approaches at global scale (Körner 1994; Hodgson *et al.* 1999; Niinemets *et al.* 2007) remains a challenge as does common agreement on sampling protocols (Kattge *et al.* 2011) (see Web Resource 12.2).

12.12 Discussion

Despite a lack of consensus regarding the theory and practice of identifying appropriate PFTs and functional traits, it would be wrong to say that plant functional ecology is in a state of undisciplined chaos. Particularly in the past two decades, much has been achieved in the way of new insights and technology. Nonetheless, the search for a functional paradigm and the recent explosion of literature surrounding trait-based ecology reflects as much the multi-faceted interests of investigators as that of the entire research agenda of ecology itself (cf. Westoby 1998). In the move towards a more synthetic and more predictive science of ecology, the search for a single, comprehensive yet relatively parsimonious, plant functional classification remains as yet, an elusive Holy Grail (cf. Lavorel & Garnier 2002; Lavorel *et al.* 2007; Suding & Goldstein 2008). While quantification and synthesis remain a central focus, emerging theory related to the stoichiometry and metabolic scaling of functional traits and types (Web Resource 12.3) is also assisting in the move towards an improved understanding of plant functional interaction with global change.

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