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## Plant functional classifications: from general groups to specific groups based on response to disturbance

The history of research in community ecology has often been compared to a pendulum oscillating between holistic, generalizing, and reductionist, specific views. From that perspective, the renewed interest in classifying species into groups that relate directly to function through shared biological characteristics, rather than phylogeny, is not surprising. Recently published approaches involving the analysis of sets of biological attributes fall into four main types of functional classifications of plant species. In order of increasing specificity of objective, these are: (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 by responding in similar ways to multiple environmental factors; and (4) specific response groups – contain species which respond in similar ways to specific environmental factors. The two latter categories, however, represent substantial recent conceptual advances stimulated by research aimed at predicting the effects of global change on vegetation dynamics<sup>1,2</sup>. The goals are twofold: to build models that simulate shifts of vegetation types with changing climate<sup>3</sup>; and to provide land managers with models that can be used in a variety of situations, including cases where detailed

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**Predicting the effects of anthropogenic changes in climate, atmospheric composition and land use on vegetation patterns has been a central concern of recent ecological research. This aim has revived the search for classification schemes that can be used to group plant species according to their response to specified environmental factors. One way forward is to adopt a hierarchical classification, where different sets of traits are examined depending on growth form. Also, at the level of interpretation, the environmental context and purpose of functional classifications need to be specified explicitly, so that global generalizations can be made by comparing across environments functional classifications derived from similar methodologies.**

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information is limited. More specifically, recognition of land use change as one of the main drivers of global change has raised the need to identify specific groups based on disturbance response. This activity builds on knowledge acquired from the development of the more general classifications (1–3 above).

### **Emergent groups – classifications based on correlations of biological attributes**

Emergent groups reflect the combination of adaptive responses and of evolutionary constraints appearing as sets of correlated traits. They are identified in an inductive manner, using multivariate analyses of usually large sets of traits – covering life history, morphology, physiology, phenology and regeneration biology – expected to determine species behaviour in the ecosystem. Such classifications tend to not address any ecosystem function explicitly or, when they attempt to, lack relationship to particular mechanisms<sup>4</sup>. They tend to produce sets of traits essentially corresponding to main life forms (trees, shrubs, grasses and forbs), although the degree of detailed subdivision depends on the breadth of the spectrum taken from global<sup>4,5</sup>, to regional<sup>6,7</sup> and to a particular vegetation type<sup>8–10</sup>. Yet classifications into emergent groups have been useful to identify broad correlation patterns, such as relationships between plant size or seed mass and

important functional traits such as growth rate<sup>11,12</sup>. A major debate about this approach has arisen concerning the risk that phylogenetic correlations – the fact that phylogenetically related species can inherit common groups of attributes regardless of function – may obscure functional correlation patterns. However, appropriate methods of analyses, using pairs of phylogenetically independent taxa, are available if these effects need to be alleviated<sup>13</sup>.

Trait correlation analyses have also pointed out that adult and regeneration traits can show incongruent patterns of correlation<sup>8</sup>, as highlighted by the recognition of distinct 'regeneration strategies'<sup>14,15</sup> to describe community dynamics. This discrepancy is highly pertinent to the construction of functional classifications because it implies that in the analysis of traits relating to specific functions, adult and juvenile traits need to be considered independently.

### Strategies – adaptive patterns relating to resource use and availability

The identification of adaptive strategies is a more directed exercise in linking species traits to variation in resource availability in habitats, and their consequences for plant growth and reproduction. Strategies are identified as 'major recurring axes of adaptive specialization in life history and in the physiology of the adult (established) organism [which] appear to be associated with variation in the duration and quality of the opportunities which habitats provide for resource capture, growth and reproduction'<sup>16</sup>.

The best known and most debated example is the plant strategy (or CSR) scheme<sup>17</sup> where species are classified according to their abilities to cope with disturbance (R), abiotic stress (S) and competition (C). That scheme has been successfully applied in studies of the distribution and dynamics of many communities. However, authors have tended to focus on the environmental classification as an interpretative tool rather than actually testing the strategy scheme by identifying attributes that are correlated to the same end of an environmental gradient. Such a test was carried out for European wetlands, where the *a priori* determined C-strategy was explicitly correlated with species traits describing competitive ability<sup>18</sup>. A difficulty of using predetermined syndromes of plant attributes is that they may be meaningful only in vegetation for which they were developed. For example, competitive ability has been related to seed weight in old-field plants<sup>19</sup> and sand dune annuals<sup>20</sup>, while in perennial herbaceous communities, competitive ability was related to root and shoot traits determining foraging for patchy resources<sup>21</sup>. Therefore, the search for adaptive strategies relevant to particular vegetation types needs to incorporate methods for identifying the contribution of individual traits.

It may be possible to modify strategy schemes for specific purposes or locations. For example, the axis describing disturbance has been subjected to much criticism because it potentially incorporates different types (e.g. soil disturbance, grazing, fire) and variation in intensity and frequency. In response to this problem, a redesigned CSR scheme for the inclusion of grazing can account for disturbances of different frequency and intensity. Specific attributes of grazing tolerance incorporate elements of either S or R strategies (e.g. low stature, tough and narrow leaves, low shoot/root ratio)<sup>22</sup>. But it is also important to recognize strategy classifications for what they are – general schemes. Their value is to provide a broad framework and to identify traits that may be used as a starting point in more explicitly targeted studies.

### Functional groups – species with similar ecological roles

Plant functional types (PFTs) are defined as non-phylogenetic groupings of species which perform similarly in an ecosystem based on a set of common biological attributes<sup>23</sup>. They can be defined in relation to either the contribution of species to ecosystem processes (such as carbon or water cycling) or the response of species to changes in environmental variables (such as climatic variables or disturbance)<sup>24,25</sup>. The search for functional groups usable in models of global vegetation dynamics needs to provide for species groupings that may differ according to the function or group of functions considered. For example, PFTs associated with climatic factors differ from those relevant to species migration<sup>25</sup>. Classifications using *a priori* selected traits under present factor combinations (e.g. present climate) will also not necessarily hold under changing conditions, such as new combinations of temperature and precipitation regimes<sup>24,25</sup>. These two concerns can be addressed by explicitly linking function to response mechanisms<sup>1</sup>. This is possible for functions for which adaptive syndromes are established from direct structural manifestations, but ultimately functionality of any attribute should be assessed experimentally<sup>26</sup>. For example, drought tolerance can be related to patterns of allocation to leaves versus roots, leaf characteristics and metabolic adjustments (e.g. C<sub>3</sub>, C<sub>4</sub>, CAM). In other cases however, the relationship between form and function is known only from correlation patterns, as is the case for plant size and relative growth rate<sup>11</sup>. Some essential functional attributes (e.g. photosynthetic pathway) do not translate to morphology<sup>26</sup>. Finally, classifications cannot be expected to be universal, yet their development should aim at reaching greater generality by addressing mechanisms.

In practice, construction of PFTs has involved a combination of subjective preselection of traits based on expert knowledge and correlation analyses applied to environmental gradients and experimental manipulations. Subjective growth form classifications have been repeatedly found to reflect broad ecosystem functions along regional environmental gradients<sup>25,27</sup>. However, refined analyses of vegetation structure and dynamics at landscape or community scales require different sets of traits that explore the details of interactions between the plant and its abiotic and biotic environment<sup>28</sup>.

### Specific groups for response to disturbance

Individual studies may combine emergent and function-oriented classifications, although not always explicitly. For example, classifications used to model global or regional vegetation shifts associated with climatic change are based on growth form<sup>3,5,29</sup>. That decision reflects both the outcome of emergent classifications at large scales and the relevance of growth form to primary ecosystem functions such as carbon assimilation. To make classificatory schemes applicable to smaller regional or landscape scales, where the effects of natural and human disturbance regimes are of primary interest, specific response groups relating to the effects of different disturbance types need to be identified. Many results relevant to this aim pre-date the functional classification literature and need to be synthesized for further elaboration of these response groups. This task is particularly pressing for herbaceous dominated vegetation (e.g. old-fields, grasslands, herbaceous stratum of shrublands and woodlands) where ongoing land use changes affect disturbance regimes. Disturbance is taken here in its broad definition of any event that destroys biomass and thus frees up space for colonization.

In the CSR scheme, the strategy relating to disturbance has been unequivocally related to a group of attributes

### Box 1. Methods used to relate grazing tolerance to the attributes of grazed species

Recent interest in developing plant functional classifications has stimulated advances in the methods used to link species ecological responses and their biological attributes. The case of response to grazing illustrates how progress has been made, starting with inference of adaptive significance from ecological patterns, and moving to direct tests on sets of species attributes.

(1) Classically, the dynamics of communities under varying grazing pressures has been described in terms of changing abundances of three response groups: increaser, decreaser and neutral species<sup>32</sup>. An examination of component species of those groups in Israeli mediterranean grasslands led to the inference that grazing favours short-statured prostrate plants which can escape the herbivore's teeth, and that grazing decreases competition from taller erect species<sup>32</sup>. Alternatively, biological characteristics of the three response groups can be identified through analysis of correlations with selected sets of attributes. In Australian arid rangelands, response groups were thus characterized by life form (forbs, grasses and shrubs) and a subdivision based on palatability within life forms<sup>35</sup>.

(2) Pattern analysis over species distributions along grazing gradients reveals that, for a wide selection of traits, there are patterns of correlation of attributes with grazing. It differs from the previous *a posteriori* characterization in that species are not pre-classified into response groups. This method firstly identifies sets of correlated attributes represented in grazing tolerant versus grazing intolerant species. In Spanish mediterranean annual grasslands, suppression of grazing resulted in a decline of cover by annuals and an increase in the cover of taller species<sup>42</sup>. Secondly, multivariate methods also provide a ranking of importance of contribution of different traits, which can be used to generate hypotheses about the mechanisms of response. In Argentinian montane grasslands, plant morphological attributes were related to grazing intensity<sup>43</sup>. In the light of these patterns, hypotheses about the role of response to light, response to herbivory, and within-species morphological variation were generated. For example, attribute syndromes associated with decreasing grazing intensity (increased life span, plant height and verticality, and leaf size) were hypothesized to be mechanisms for sustained occupation of above ground space by plants.

(3) Hypotheses resulting from interpretations of distribution (1) and correlation (2) patterns have been tested directly by analyzing the frequency distribution of particular attributes across grazing intensities. In Australian temperate grasslands, increasing grazing intensity favoured species with an annual life history, rosette morphology or wind dispersed seeds while eliminating species with perennial life histories and leafy stems<sup>34</sup>. While providing direct tests of hypotheses regarding specific attributes, such individual testing does not provide insights into correlation patterns amongst traits, or the relative importance of potential mechanisms.

(4) Hierarchical analyses identifying particular biological profiles within broader groups such as life forms appears to be a useful approach, as it provides the means to bridge broad correlation patterns, such as those identified by multivariate pattern analyses (2), and specifically tested responses of particular traits (3). Explicit hierarchical approaches have not yet been well developed in the search for functional groups describing grazing response.

designated as 'ruderalness' (short life span, small stature, abundant and widely dispersed seeds, dormant seed bank)<sup>9,17</sup>. Individual studies have supplemented this list by progressing towards more specific approaches to identify disturbance-related attributes (Box 1). These attributes fall into three biological categories:

- Life history – annuals or short-lived perennials are usually favoured by disturbances that open gaps in the usually grassy and mainly perennial-dominated matrix<sup>30,31</sup>.
- Plant morphology – tends to be well correlated with response to disturbance. Morphological types have been described *a posteriori* from species lists of increaser, decreaser and neutral species<sup>30,32</sup> or inferred from changes in vegetation structure<sup>33</sup>. In direct analyses of simultaneous changes of community composition and species morphological attributes, plant size or height has often been found to decrease with increasing disturbance intensity<sup>33</sup>. Presumably, this pattern results from the correlation between plant size and several physiological attributes<sup>11</sup> that provide adaptation to open environments, and from the direct relationship between plant size and accessibility to grazers<sup>32</sup>. Alternatively, synthetic descriptors like Raunkiaer's life form classification<sup>34</sup>, or growth form<sup>27</sup>, can be used to analyse morphological changes along gradients of increasing disturbance intensity. Morphology can also be analysed by seeking clusters of traits (e.g. height, lateral spread, leaf morphology) correlated with disturbance gradients<sup>31,35</sup>. The patterns obtained ultimately reflect growth form, as it captures correlation patterns among morphological traits.
- Regeneration traits – although generally inferred to be key factors, are often not investigated in great detail, possibly because of the effort involved in their measurement. Synthetic classifications designed under the schemes of Grime's regeneration strategies<sup>15</sup> and the Vital Attributes<sup>36</sup> have attempted to capture species persistence mechanism (seed bank, dispersal or vegetative regeneration) and

the spatio-temporal distribution of recruitment. Indeed, cluster classification of regeneration traits of dry limestone grassland has suggested that seed persistence contributes to species ability to respond to gaps and hence will be a predictor of the effects of changes in disturbance regimes<sup>28</sup>. When dealing with specific floras, the list of relevant traits needs to be adapted according to dominant life forms. For example, in vegetation with a large annual component, germination biology has been used to classify species according to post-disturbance dynamics<sup>37</sup>. When conversely perennials dominate, resprouting ability<sup>36</sup> and clonal spread<sup>15,34</sup> need to be considered. Disturbance of increasing intensity tends to favour seeders over sprouters<sup>38</sup>. Finally, although its re-

lationship to timing of disturbance is essential, species phenology is often neglected when analysing response to disturbance<sup>37,39</sup>.

### A hierarchical approach to the analysis of trait sets

Although various studies have addressed the response of species to disturbance according to their biological attributes, results keep confirming a few very general trends (disturbance favours annuals, small stature) and have not progressed through refinement of biological traits. Regardless of the approach, analyses invariably converge on a growth-form-based classification: annuals and short-lived perennials, perennial forbs, perennial grasses, with possibly subdivisions within grasses, and shrubs if present. In further refinements, response-specific attributes have been used to split these groups for particular disturbances, for example using palatability for response to grazing<sup>32,35</sup>. To characterize responses to specific disturbances in a given vegetation type, classification should explicitly operate in a hierarchical manner within growth forms. While the relevance of growth form remains primary, and its effects should be accounted for as a first step, further analyses within each growth form are needed to examine how other traits contribute. In addition, different sets of traits can be examined for each growth form. For instance, arctic tundra species have been classified hierarchically by using trait subsets relevant only to particular life forms<sup>25</sup>. Another example of a hierarchical classification is found in an analysis of the response of Kansas tall-grass prairie to prescribed burning<sup>40</sup>. The degree of splitting within each life form and within life histories depended on number of species within each group. Life history (annual versus perennial) and photosynthetic group ( $C_3$  versus  $C_4$ ) were regarded as secondary classifications within life forms. Within  $C_4$  perennial grasses, a further subdivision was made according to stature.

To characterize the response of herbaceous-dominated vegetation to grazing and soil disturbance, the two most common disturbances in many grassland areas, the hierarchical scheme is based on the recognition of the primary division of species into four growth forms: shrubs, forbs and grasses/sedges, and a subdivision of grasses into annual and perennial. The first step of an analysis of community response to disturbance will consist in a univariate analysis of the distribution of growth forms among disturbance regimes. The hierarchy is based on (1) the need for different sets of traits depending on growth form, particularly acute in the case of grazing response, and (2) the need to analyse groups of traits independently (e.g. morphology and regeneration strategy). Thus, within each growth form, traits are distributed into four categories that are designed and analysed independently: life history, morphology, grazing response and regeneration. The choice of specific traits within each category is typically deductive, with a particular concern for parsimony and accessibility of traits *in situ*. Studies in a given floristic and environmental context may involve removing and adding specific traits to a core list defined for a particular disturbance type. Within each trait group a multivariate method is used to analyse how biological attributes of species explain the response of community composition to disturbances<sup>41</sup>. This method, which reconciles inductive and deductive approaches to functional classification, takes into account natural correlations among traits to draw profiles of species characteristic of different disturbance regimes. By offering the means of accessing detail at finer levels, such a hierarchical approach might ensure that the interpretation of specific patterns of diversity remains possible.

## Conclusions

Approaches to the identification of functional groups to date have tended to be *ad hoc*, with little articulation of philosophy and methods. Recent work on trait correlation patterns, plant strategies and plant functional types has made a valuable contribution in identifying broad patterns of distribution of plant species along environmental gradients. However, plant functional types identified at broad scales may conceal the more subtle mechanisms that underlie the response of species with different growth forms to a specified disturbance.

Hierarchies of traits need to be devised to further the synthesis and exploration of formal or empirical knowledge on attributes. The primary hierarchical level recognizes the obvious difference between growth forms which, in the literature, has been responsible for concealing relevant traits within each growth form. Adequate sets of traits describing morphology, regeneration, and other traits relevant to specific disturbances within life forms are then identified and analysed independently.

The utility of the approach will depend on setting a contextual framework, along with the standardized methodology, for comparing studies across regions with different climates, evolutionary histories and management. This is necessary to explain variation between sites in the traits identified as being relevant to disturbance response, and in specific attribute profiles associated with particular disturbance regimes. In particular, the broader context of evolutionary history and more recent management is necessary to explain results, and to account for ecological variation occurring across the globe. The aim of this task should not be a universal classification of response groups to various disturbances but rather to identify a hierarchy of generality in functional attributes ranging from global to regional. Developing a global scheme

of plant functional types based on major disturbances (e.g. fire, grazing) specific to different biomes and regions is crucial for further developments of models of global vegetation dynamics.

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# The role of experimental microcosms in ecological research

Lauchlan H. Fraser and Paul Keddy

**M**icrocosms are small ecosystems in containers. They can range from simple experimentally sown mixtures of two species of plants (for example, de Wit's<sup>1</sup> replacement series) to sophisticated controlled environments housing entire terrestrial ecosystems such as the Ecotron<sup>2</sup>. Microcosms also vary in size from test-tube studies<sup>3</sup> to the vast multi-ecosystem complex constructed in Arizona (Biosphere 2)<sup>4</sup>. The main role of microcosms, also called model systems, is to act as a bridge between theory and nature – they can increase our understanding of natural processes by simplifying the complexities of our natural environment<sup>5</sup>. Gause's<sup>6</sup> pioneering work on competitive exclusion, Huffaker's<sup>7</sup> spatial predator–prey models and Park's<sup>8</sup>

**A number of recent and important developments in community ecology have been derived from experiments conducted in microcosms. Studies with microcosms have addressed a broad range of phenomena, including climate change, biodiversity, assembly rules, habitat restoration, trophic dynamics and mycorrhizal associations. The common factor linking these studies is that they manipulate an individual environmental axis and explore the role that axis plays in structuring communities. We discuss six recent studies to illustrate the use and design of microcosms for community ecology research.**

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trol from carnivores and its effect on plant community composition<sup>9</sup>; and (6) the effects of mycorrhizae on plant community composition<sup>11</sup>. The early studies explored population ecology principles, while the later studies explored community and ecosystem ecology.

Advantages of using microcosms include ease of replication, precise control over environmental variables, and the power to manipulate the parameters and treatments under investigation<sup>15,16</sup>. Limitations and disadvantages are restricted space and over-simplification<sup>17,18</sup>.

Limnologists, toxicologists and microbiologists<sup>19</sup> have used microcosms as a powerful research tool, but they have been relatively neglected by terrestrial community ecologists (Table 1).

flour beetle competition experiments are classic examples of microcosm use. A number of recent studies that use microcosms include: (1) the effects of elevated CO<sub>2</sub> on a plant community<sup>9</sup>; (2) biodiversity effects on community factors<sup>10</sup>; (3) assembly rules for a wetland plant community<sup>11</sup>; (4) effects of microtopographic heterogeneity and seed propagule source on floristic diversity<sup>12</sup>; (5) top-down con-

The total number of published microcosm/mesocosm experiments has doubled in the past seven years and this has been reflected in the large increase in review papers. To illustrate the application of microcosms as an important research tool in terrestrial community ecology we will explore six studies, and highlight some common threads among them.