SPECIAL FEATURE

Plant functional types and disturbance dynamics

Editors

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Based on contributions presented at the GCTE-Workshop on Functional analysis of vegetation response to disturbance held in Montpellier, France, in March 1998, and, in part, the Session on Plant Functional Types and Plant Strategy Types held at the 41st Symposium of the International Association for Vegetation Science in Uppsala, Sweden, in July 1998.

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Plant functional types and disturbance dynamics – Introduction

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Abstract. Plant functional traits and types are useful concepts in relation to disturbance responses of natural and managed ecosystems. To explore their applicability in greater depth, a set of 12 papers presents a broad range of issues from methodologies to the results of particular trait studies in the field, and modelling approaches. So far, empirical studies have only allowed us to identify a few functional traits that are consistently associated with disturbance. To determine the trait variations associated with climate, disturbance history and current disturbance regime as well as the interactions between these factors, global-scale comparisons of numerous individual studies are required. Significant advances toward this ambitious goal are presented in these papers, and include: (1) the articulation of experimental and analytical methodologies for individual studies that could usefully contribute to a global comparison; (2) the identification of core traits that can be used in the further search for disturbance-related traits common to a range of environments; (3) further information on vegetation response to disturbance in terms of trait representation, and the identification of attribute syndromes; (4) the identification of issues for modelling disturbance dynamics using functional types.

Keywords: Functional trait; Disturbance; Plant community.

Introduction

The search for plant functional types is the response to a long-standing desire of ecologists to seek simplified patterns in the richness of plants and the complexity of ecosystems (e.g. Raunkiær 1907). The search is being carried out for a range of purposes, e.g. for the systematic analysis of ecosystem function, or for the improved assessment of ecosystem sensitivity against changes in the environment. However, the sets of traits or types necessarily differ among those applications (Woodward & Cramer 1996). Disturbance dynamics in natural and managed ecosystems have recently received increased attention in empirical, as well as theoretical, studies. It has been recognized that diversity (or complexity) is closely related to disturbance at several levels of scale. Our ability to address critical issues of diversity therefore depends on our ability to understand disturbance. Investigating disturbance from a generic point of view (i.e. for more than one ecosystem) requires the identification of plant functional types that are directly related to the disturbance regime.

To advance research with respect to this goal, and to come closer to a global synthesis, a workshop was held in Montpellier, France, in March 1998, under the auspices of the International Geosphere Biosphere Programme (IGBP) and its core project Global Change and Terrestrial Ecosystems (GCTE). All key papers from this workshop, as well as related presentations from a session on Plant Functional Types and Plant Strategy Types held during the 41st Symposium of the International Association for Vegetation Science (IAVS) in Uppsala, Sweden, in July 1998, are assembled in this special issue.

While it is relatively easy to reach agreement on the general aim of defining functional types for disturbance assessments, the diversity of approaches that are possible is bewildering, even within groups of scientists with a tightly defined philosophy. The research process involves a counterpoint between the creativity of individual efforts and the need for a unified, disciplined approach between individuals, over time. The twelve papers presented in this issue represent this counterpoint well. The ideal of testing a unified set of traits (Westoby 1998; *Weiher et al.* 1999) and using a uniform methodology (*McIntyre et al.* 1999) is immediately challenged by the myriad of choices, restrictions and interesting avenues for discussion that faces each researcher involved in collection and presentation of data.

The authors in this issue present material that can be described under the three topics with which the papers are primarily concerned: methodologies (*Pillar* 1999; *Gitay et al.* 1999; *McIntyre et al.* 1999; *Weiher et al.* 1999), results of trait studies (*Díaz et al.* 1999; *Díaz Barradas*

et al. 1999; *Hadar et al.* 1999; *Kleyer* 1999; *Landsberg et al.* 1999; *Lavorel et al.* 1999) and modelling (*Campbell et al.* 1999; *Pausas* 1999). Under these same headings we discuss conclusions in common, issues raised and finally, the implications of these writings for future directions.

Methodologies

Trait selection and measurement

Functional trait studies need to consider the choice of traits to measure, how they are measured and how the results are reported. *Weiher et al.* (1999) propose a list of core traits that could conceivably be tested over a range of environments, while *McIntyre et al.* (1999) outline how such a list could be developed in relation to a specific function (grazing response) including the need to tailor a final trait list to the assemblage under study. Both papers, and *Díaz et al.* (1999), advocate the use of easily-measured traits (e.g. the structural traits described by Box 1996) over those that may be more closely linked to ecosystem function but are less likely to be used, or to be measured in large numbers of species (e.g. chemical composition, decomposition rate, seed persistence in the soil). It seems that a comparative approach to trait analysis will continue to depend on easily-measured traits that are surrogates for function. However, the need to ultimately establish the links between traits and function will also need to be addressed. *Díaz Barradas et al.* (1999) measured traits relating to response to water stress and were able to link these with the distribution of species along a gradient of water table depth. A possible way forward would be to calibrate easily-measured traits, which can be assessed in a high number of species, against more quantitative traits, whose measurement is much more demanding, but whose ecosystem meaning is more direct or better known. Examples are the calibration of leaf toughness against litter decomposition rate, or specific leaf area or leaf water content against relative growth rate.

Comparing functional analyses across different sites and studies

McIntyre et al. (1999) argue that meaningful interpretations of functional traits will only result from the synthesis of many studies. The use of common traits across studies as proposed by various authors (e.g. Hendry & Grime 1993; Westoby 1998; *Weiher et al.* 1999) will go part way to achieving this. Even when the same traits are reported in different studies, the measurement and definition of attributes becomes important to

the reader trying to compare studies. For example the 'medium' and 'large' seed weight classes in *Landsberg et al.* (1999) were both less than 1 mg and most species would have been classified as 'light' using the *Lavorel et al.* (1999) scheme. However, the fact that the attributes are defined in both papers makes this difference apparent to the reader. For the same reasons it is important that authors report the entire profile of their study system, including the overall attribute make-up, the composition in terms major life forms (not all of which may have been analysed in detail) and traits that did not vary in the assemblage (*McIntyre et al.* 1999). Also, *Díaz et al.* (1999) stress that trait variation between different populations within the same species growing under different grazing regimes may be substantial. This makes it difficult to extrapolate information on individual taxa between regions, or even sites.

There are further problems for the reader trying to compare and interpret published results from different sites. Milchunas et al. (1988) eloquently argued for the importance of considering disturbance history in the interpretation of present-day disturbance response in vegetation. More recently Balmford (1996) and *Díaz et al.* (1999) have reinforced this point. In most cases relevant disturbance history can only be provided by the author and is not freely available to the reader. Therefore unless the disturbance history is appropriately described in published studies, the author forfeits the chance to contribute to the global picture of disturbance-related traits.

However, there are barriers to authors including the above-mentioned information in publications. It is most relevant to inter-site comparisons, and not to the individual, immediate study being reported. Therefore there is both a self-imposed and journal-imposed tendency to leave out basic descriptive information in manuscripts. This limits the potential use of published studies in later syntheses which compare many published studies. New ways of exchange of scientific information, such as the electronic networks established through programmes such as IGBP-GCTE, provide alternative routes to more complete documentation, but they clearly also leave questions open, such as the long time archive availability of electronically disseminated information.

Comparing different functional classifications of the same plant assemblage

We have discussed the role of uniform methods and reporting in the comparison of data sets across different sites. A less daunting, but still important task is to examine the robustness of functional classifications relating to a particular plant assemblage. Formal approaches to this have been described in Gitay & Noble (1997). In

this issue, *Gitay et al.* (1999) exemplify one of these formal approaches by examining different classifications of the same rainforest vegetation with respect to gap dynamics. Congruency occurs when species in the assemblage are classified similarly using different character sets. The authors concluded that a morphological classification, which was strongly related to phylogeny, was not relevant to dynamic behaviour. Instead, a deductive classification based on an *a priori* theoretical view of the factors important in controlling gap dynamics was more successful.

Comparisons need to address not only classification philosophies and trait sets but also classification methods *per se*. *Pillar* (1999) carried out a quantitative assessment of the relative performance of different subsets of traits from a full trait list. A new approach based on fuzzy set theory made it also possible to compare classical classification with classifications introducing varying degrees of fuzziness. Such optimization methods open new avenues to address the spiny problem of trait selection and to perform quantitative comparisons across classifications.

Less formal comparisons of *a priori* classifications and response-related classifications are also reported in *Lavorel et al.* (1999) and *Hadar et al.* (1999). In these studies, individual attributes were associated with disturbance response. Using the same data describing vegetation response to disturbance, *a priori* functional types were also tested for disturbance response. Again, the deductive approach was useful for data interpretation and the identification of trait syndromes. When traits are analysed on an individual basis, the challenge is to identify combinations of significant attributes that actually occur in the flora (syndromes). The testing and comparison of both individual attributes and *a priori* functional types assisted in the identification of syndromes.

Results of trait studies

Five papers in this issue present data in which response to disturbance is analysed in terms of plant attribute response. Although the general philosophies behind them were similar, they represent a diversity of approaches and traits sets over a range of systems. Traits relating to grazing response were examined in four papers (*Díaz et al.* 1999, *Hadar et al.* 1999, *Landsberg et al.* 1999, *Lavorel et al.* 1999) with the focus being on the herbaceous or understorey component of the vegetation in most cases. A fifth paper addressed the identification of traits relevant to disturbance in agricultural landscapes (*Kleyer* 1999).

These studies consistently identify the broad, al-ready well-documented traits (e.g. prostrate growth forms with protected buds increase under heavy grazing), but further details and syndromes tend to differ across regions, even within a comparable climate. For example, in Israel the main grazing increaser groups in the herbaceous vegetation of cleared shrublands were legumes and perennial geophytes (*Hadar et al.* 1999). On the other hand, in Portugal grasslands dominated by annuals, receiving similar annual precipitation, small forb species with leafy stems were the only group favoured by grazing (*Lavorel et al.* 1999). Major differences across sites were interpreted as resulting from differential availability of propagules at the landscape scale (a lack of perennial propagules in the Portuguese landscape), as well as from differences in grazing regimes (seasonal in Israel vs. continuous in Portugal).

Authors of the five papers agreed that plant functional classifications should search for syndromes (defined here as repeated attribute combinations that actually occur in the flora), rather than identifying a list of isolated traits. This is because a group of individual functional attributes identified in a data set may identify 'ideal' functional combinations which may not actually exist in the vegetation. The description of syndromes has been possible in most cases (*Díaz et al.* 1999; *Hadar et al.* 1999; *Lavorel et al.* 1999). The exception was *Landsberg et al.* (1999) who identified a number of traits negatively or positively associated with grazing pressure, but failed to find strong recurrent patterns of association among them that would match associations in the local flora. An alternative approach is followed by *Kleyer* (1999) who first identified syndromes represented in the flora and then assigned functionality to these syndromes through an analysis of their distributions along disturbance and productivity gradients.

Modelling

At some level, functional type classifications will be incorporated into theoretical frameworks that allow the use of a predictive mode, in other words, numerical simulation models (Cramer 1997). Two papers describe very different modelling approaches which demonstrated applications for functional classifications based on disturbance and climate response. *Pausas* (1999) used four functional types based on regeneration and growth attributes to predict response to fire in Mediterranean shrublands using two simulation models. To the extent that the predictions could be verified (which is limited), the modelled results were accurate, and consistent between models. *Campbell et al.* (1999) described the conceptual stages of model development for a wider range of vegetation types, climates and land uses.

In general, moderately simple classifications with few attributes seem desirable for modelling applications. Simple models based on these seem to have moderate success, supporting the premise that functional types are useful for modelling. This at least is compatible with progress in functional type identification so far. At a global scale, it has been possible to identify only very few traits that are consistently associated with disturbance (Lavorel et al. 1997). *Campbell et al.* (1999) concur with *Lavorel et al.* (1997) on the need for functional types to be tailored to a specific purpose or function e.g. response to climate or response to disturbance. There is also a need for further developments in process-based modelling of plant functional types in different environments.

Several issues were found to be in common with both field-based studies and modelling. First, is the need to further understand which attributes are linked with specific climate and disturbance regimes. Second is the question of how to relate a set of individual functional attributes to actual vegetation (i.e. what syndromes are functionally significant and therefore what are the plant functional types). This problem is intensified by the lack of congruency between regeneration traits and traits of the established phase within the same plant assemblage (e.g. Leishman & Westoby 1992; Díaz & Cabido 1997). Both types of traits are useful for modelling applications. Finally, modellers need assembly rules to describe the coexistence of different plant functional types in vegetation, a problem which field-based researchers are tackling from the bottom up. Field work provides essential information to formulate 'sensible' assembly rules that are constrained by what actually happens in nature.

Some unanswered questions

The fact that most findings connecting plant traits and specific disturbances so far appear to be 'trivial' or 'expected' does not invalidate the search for functional types relating to climate or disturbance response. There is still a need for formal comparison of many studies at a global scale, something which still appears to be lacking. Also, climate and disturbance history are factors that operate at higher organizational levels in biotic systems (*sensu* Allen & Starr 1982) and interact with present-day disturbance regimes in complex ways. The vast majority of the literature linking disturbance with plant traits to date involve individual case studies. In those cases, climate and disturbance history are assumed as fixed, and therefore hardly addressed. In global cross-comparisons, however, these two sources of variation have to be formally incorporated.

The following list of questions are some issues that are relevant to the global cross-comparison of trait studies. To propose formal methods for the comparison of classifications across sites is beyond the scope of this summary. However, the following questions may serve to sharpen thinking and assist the development of such a comparison:

1. *Which traits are consistently associated with particular disturbances across a wide range of climates and disturbance histories?* Only a small number of traits have been identified to date, but have enough traits been tested at enough sites to accept this result? The core traits identified by Hendry & Grime (1993), Westoby (1998) and *Weiher et al.* (1999) provide a starting point for this question. These are traits identified as likely to be linked to vegetation dynamics in a general sense. Those that are relevant to most vegetation, easy to measure, and that have well-articulated methodologies producing consistent measurements, are most likely to be widely tested in a range of environments.

2. *How do climate or disturbance histories affect vegetation composition in terms of major life forms?* The long-terms effects of climate and disturbance regime are primary determinants ('filters', cf. Díaz et al. 1999) of vegetation composition, and account for major differences in form and structure. Major life forms (e.g. trees, shrubs, grasses, annual forbs) are a simple way to account for variation, and identifying vegetation that is comparable at finer levels of detail e.g. there may be few relevant traits in common between tree-dominated vegetation and annual grasslands.

3. *How does vegetation of comparable life forms, climate and disturbance history respond to current disturbance?* When comparable data sets are identified, a more detailed analysis of trait response data will be possible. Responses to different disturbance types should be considered separately. A sub-question, touched upon by *Pillar* (1999), is: What is the minimum number of traits we need to predict responses to disturbance history/ climate/ current disturbance combinations?

4. *Does climate act more strongly on physiological traits and disturbance history act more strongly on regeneration traits?* The apparent lack of correlation between vegetative and regeneration traits may relate to the long-term selection pressures of climate and disturbance, acting separately.

Attempting to address these and related questions may assist our progress towards finding some generalisations linking plant traits and disturbance at a worldwide scale. The challenge here is in providing knowledge that represents a substantial advance with respect to tradi-

tional and well known life-form classifications. This must be balanced with efforts to keep the whole approach as simple, parsimonious, and realistic as possible.

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