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Trait convergence and trait divergence in herbaceous plant communities: Mechanisms and consequences

Grime, J. Philip

Unit of Comparative Plant Ecology, Department of Animal and Plant Sciences, University of Sheffield,
Sheffield S10 2TN, UK; E-mail j.p.grime@sheffield.ac.uk

Abstract

In landscapes subject to intensive agriculture, both soil fertility and vegetation disturbance are capable of impacting strongly, evenly and simultaneously on the herbaceous plant cover and each tends to impose uniformity on the traits of constituent species. In more natural and ancient grasslands greater spatial and temporal variation in both productivity and disturbance occurs and both factors have been implicated in the maintenance of species-richness in herbaceous communities. However, empirical data suggest that disturbance is the more potent driver of trait differentiation and species co-existence at a local scale. This may arise from the great diversity in opportunities for establishment, growth or reproduction that arise when the intensity of competition is reduced by damage to the vegetation.

In contrast to the diversifying effects of local disturbances, productivity-related plant traits (growth rate, leaf longevity, leaf chemistry, leaf toughness, decomposition rate) appear to be less variable on a local scale. This difference in the effects of the productivity and disturbance filters arises from the relative constancy of productivity within the community and the diversity in agency and in spatial and temporal scales exhibited by disturbance events. Also, evolutionary responses to disturbances involve minor adaptive shifts in phenological and regenerative traits and are more likely to occur as micro-evolutionary steps than the shifts in linked traits in the core physiology associated with the capacity to exploit productive and unproductive habitats.

During the assembly of a community and over its subsequent lifespan filters with diversifying and convergent effects may operate simultaneously on recruitment from the local species pool and impose contrasted effects on the similarity of the trait values exhibited by co-existing species. Moreover, as a consequence of the frequent association of productivity with the convergence filter, an additional difference is predicted in terms of the effects of the two filters on ecosystem functioning. Convergence in traits selected by the productivity filter will exert effects on both the plant community and the ecosystem while divergent effects of the disturbance filter will be restricted to the plant community.

Keywords: Disturbance; Ecological filter; Ecosystem functioning; Productivity.

Introduction

Over the last three decades there has been a gradual increase in the number of published investigations in which traits suspected to be of predictive value with respect to the ecology of plant species have been measured. The scale and momentum of this research is now such (Knevel et al. 2003; Díaz et al. 2004; Wright et al. 2004; Grime et al. 2006) that we can predict that in some areas of the world it will be possible soon to consult standardized databases in which trait profiles will be available for most native species. For this development to be of use in the study and management of vegetation it will be necessary to elucidate the role of particular traits and of trait variation in the assembly of plant communities and the functioning of ecosystems. At present it is necessary to exercise caution in the search to recognise patterns and ecological explanations for trait variation. This is because some potentially important traits have not yet been investigated on a sufficient number of species. Even more important, there is continuing uncertainty about the mechanisms controlling trait variation within sets of coexisting plant populations and its role in the functioning of communities and ecosystems. Researchers in this field have inherited insights that are strongly affected by the fact that they have originated from two research schools with diametrically opposed philosophies. One school, traceable to Darwin (1859) and implemented by Diamond (1975), has emphasized coexistence between organisms with differing traits or trait values as the key to the coherence and predictable composition of both animal and plant communities. In marked contrast, the second school with roots extending back to the pioneers of plant geography, sociology and physiology, has drawn attention to the extent to which members of the same plant community often tend to exhibit similarity in plant traits.

This paper seeks to reconcile these two philosophies. During the assembly of a plant community from the

local species pool and over its subsequent life span many filters may operate to admit or exclude species and traits. It is important therefore to distinguish between filters that have a diversifying effect on the traits that are recruited and maintained in the community and those that lead to trait convergence. How do the two types of filter and traits differ and what are their effects on the community and the ecosystem? How are unifying and diversifying filters distributed across landscapes and biomes? Do the two types of filter operate in all communities? Are trait similarity and trait dissimilarity in the community consistently associated with different aspects of plant life history or physiology and what is their significance in relation to community and ecosystem functioning?

The main purpose of this paper is to recognize the dominant factors responsible for trait convergence and divergence and to explore their implications for community structure and ecosystem functioning.

Trait convergence

Plant species co-existing in communities usually exhibit some conspicuous similarities in life history, morphology and physiology (Tansley 1939; Ellenberg 1963; Box 1981; Chabot & Mooney 1985; Rodwell 1992) but, as observed by Keddy (1992), this evidence of trait similarity within the community has been slow to impact upon theories of community assembly. An exception to this general pattern has been the early and widespread acceptance of a controlling effect of soil fertility on trait similarity within communities. Pearsall (1950) observed that within both productive and unproductive grasslands in northern Britain coexisting species were similar with respect to the concentrations of mineral nutrients in their leaves and Parsons (1968), working in Australia, noted that the potential growth rates of sets of species coexisting in plant communities appeared to be similar and positively correlated with the fertility of the soils of their natural habitats. These relationships were later confirmed by investigations that involved many more species and by comparative experiments in which species from contrasted communities were examined under controlled laboratory conditions (Higgs & James 1969; Grime & Hunt 1975; Field & Mooney 1986; Lambers & Poorter 1992; Thompson et al. 1996b).

Co-incidentally, the perspective widened beyond leaf nutrient concentrations and plant growth rates to include other traits that vary in relation to vegetation productivity: these included leaf longevity, defence against generalist herbivores and rate of leaf litter decomposition (Reich et al. 1992; Sydes 1984; Rogers & Clifford 1993; Grime et al. 1996; Cornelissen et al. 1996, 1999). From these surveys it is apparent that, as foreshadowed in the reviews of Grime (1977) and Chapin (1980), the transition from productive to unproductive vegetation is associated with parallel shifts in a set of traits that are deeply embedded in the core physiology of plants, the structure and dynamics of the community and the functioning of the ecosystem. The consistency with which these predictable and parallel changes in the trait values of component species occur across the productivity gradient is apparent in three recent studies (Grime et al. 1997; Díaz et al. 2004; Wright et al. 2004) in each of which it is concluded that they represent a shift that simultaneously imposes upon plant individuals, plant communities and ecosystems a transition in resource dynamics from the acquisitive ('fast and leaky') to the retentive ('slow and tight'). Further support for the hypothesis that productivity acts as a filter selecting predictable sets of traits is available from experiments in which plant communities have been allowed to assemble from a large and functionally diverse pool of candidate species under contrasted conditions of soil fertility (Fraser & Grime 1999; Buckland & Grime 2000).

Although trait convergence within the community is most fully documented with respect to the impact of productivity; examples can also be found with respect to other variables. For example, in circumstances where vegetation on fertile soils is completely destroyed at least once every year (e.g. arable fields) there is a strong tendency for communities to consist exclusively of ephemerals with early allocation to seed production.

Trait divergence

The idea that co-existing species within a plant community may be expected to have different biologies whereby resources are captured and exploited in different ways had an auspicious beginning:

"The truth of the principle, that the greatest amount of life can be supported by great diversification of structure, is seen under many natural circumstances. In an extremely small area especially if freely open to immigration, and where the contest between individual and individual must be severe, we always find great diversity in its inhabitants. For instance, I found that a piece of turf, three feet by four in size, which had been exposed for many years to exactly the same conditions, supported twenty species of plants, and these belonged to eighteen genera and to eight orders, which shows how much these plants differed from each other..... the advantages of diversification of structure, with the accompanying differences of habit and constitution, determine that the inhabitants, which thus jostle each other most closely shall, as a general rule, belong to what we call different genera and orders."

Charles Darwin, 1859

This idea that competition for resources has resulted in trait divergence and encouraged stable coexistence between organisms has been formalized as 'limiting similarity' (Diamond 1975; Pacala & Tilman 1994). According to this line of reasoning, past competition for the same resources between organisms has resulted in trait divergences that, now, as a legacy or 'ghost of competition past' (Connell 1980) reduce competition and permit coexistence often leading to more exhaustive use of resources and enhanced productivity.

It is, to say the least, unfashionable to question the conclusions of Charles Darwin but there can be little doubt that the Darwin-Diamond model of competition as the mainspring of trait variation within communities is not supported by empirical study of plant communities. Further, one may suspect that it is this hypothesis and the unresolved debates that it has provoked (Weiher & Keddy 1999) that provide an explanation for what Lewontin (1974) has graphically described as 'the agony of community ecology'. As explained later in this paper, there is a large body of evidence implicating vegetation disturbance rather than competition as the most potent mechanism creating and sustaining trait variation in plant communities. Before developing this subject further it is necessary to visit one of the most enduring of the philosophical and semantic discontinuities currently preventing the unification of ecological theory.

Competition and trait divergence: Botanical and zoological perspectives

Field observations and experiments (e.g. Tansley & Adamson 1925; Donald 1958; Mahmoud & Grime 1965; Kadmon & Shmida 1990; Janssens et al. 1999) confirm that trait variation and species richness are suppressed by competition and promoted by natural disturbance events, animal activities and forms of vegetation management that reduce the vigour and competitive ability of potentially dominant species. Although there is no supporting documentation, there can be little doubt that the diversity Darwin observed in his 'piece of turf' originated and persisted because exposure "for many years to exactly the same conditions" had involved management that prevented the incursion of plant species of high competitive ability.

In studies of trait divergence in animal communities the role of competition and of adaptations reducing competitive interactions have often been inferred rather than measured. In comparison with plants it is often extremely difficult to distinguish between effects of competition and differences in fitness that are imposed on co-existing animals by direct effects of the environment or differential predation. This has resulted in a very unsatisfactory situation in which, as pointed out by Milne (1961) and Holt (1977) most zoological field workers and modellers and some plant ecologists have equated competition (the effort of neighbours to capture the same unit of resource) with 'the Darwinian struggle for existence' (the effort through a wide diversity of mechanisms to sustain and expand populations). Clearly such broadening of criteria prevents cross-reference to the stricter, mechanistic definitions of competitive ability now achieving wide application in functional classifications of plants (Grime et al. 1997; Wright et al. 2004). This paper will not attempt to resolve this unfortunate divide. It is important, however, to emphasize the advantages that follow from a trait-based analysis of coexistence mechanisms in plants. Only if we know in some detail how plant functional types and particular species persist in the community can we devise adequate procedures for vegetation management and conservation and understand how different types of plants confer different properties on communities and ecosystems.

Mechanisms responsible for trait convergence and divergence

Large databases of plant traits are now available; it is inevitable that in their current state of development these will provide incomplete coverage due to uneven sampling of floras, communities and traits. There have been several pioneering studies (e.g. Cunningham et al. 1999; Stubbs & Wilson 2004) but there remains an acute shortage of standardized data on the responses of plants to specific climatic and edaphic factors and this contrasts strongly with the wealth of information with respect to seeds, germination and leaf characteristics. Despite this patchiness in the supply of reliable comparative data some clues are now available in the quest to distinguish between the circumstances conducive to trait convergence and those responsible for trait divergence within plant communities. In particular, insights can be obtained by examining the causes of the relative uniformity within the community of productivity-related traits and comparing this with the diversity often observed in regenerative traits. The value of such a comparison is underlined by the investigation of Thompson et al. (1996a) where screening of many traits in the same community at one particular site revealed that trait convergence in the established phase of the life cycle coincided with trait divergence in the regenerative phase.

In seeking an explanation for convergent and divergent patterns of trait variation within the community it is informative to recognize a difference in the spatial and temporal scales at which productivity

and disturbance impact on the plant community. With some well-defined exceptions such as the dissected communities of limestone pavement and rock outcrops, most semi-natural plant communities are relatively homogeneous and constant with respect to productivity. In the case of disturbance it is also possible to find circumstances (e.g. river margins, mudflats, arable fields) in which the phenomenon operates uniformly over large areas.

However, it is much more common for vegetation to experience a complex array of disturbance mechanisms. A great variety of phenomena are capable of inflicting disturbance and there are wide ranges in the temporal and spatial scales at which particular forms of disturbance may operate. Thus it is possible, even within the same small area and over the passage of only a few years for vegetation to be exposed to many contrasted types of disturbance. As explained by Grubb (1977), vegetation disturbance has acted as a powerful evolutionary force, restricting the competitive effects of established plants and promoting the development of a rich variety of regenerative mechanisms capable of exploiting different opportunities for recruitment of juveniles. The traits involved include the size, shape, dispersal mechanism and dormancy of seeds (Grime & Jeffrey 1965; Thompson et al. 1993; Moles et al. 2000) and the physiological characteristics that influence the time and place of germination (Grime et al. 1981; Baskin & Baskin 1998).

Examples of the extent to which variation in the agency, scale and timing of disturbance can bring together a diversity of regenerative traits within the same community are apparent in investigations such as those of Thompson & Grime (1979), Peart (1984), Masuda & Washitani (1990), Gigon & Leutert (1996) and Thompson et al. (1996), in which plant species with contrasted regenerative mechanisms were found to be coexisting in communities.

The scope for trait diversification as a consequence of disturbance extends beyond the regenerative phase. Variation in the intensity and spatial distribution of disturbance may permit coexistence between ephemeral and perennial life histories (Crawley & May 1987). There is experimental evidence (Campbell et al. 1992; Grime & Mackey 2003) that occasional grazing and mowing events are sufficient to allow coexistence between potential dominants and smaller subordinates in pastures and meadows. It is also suspected that variation in the seasonal distribution of grazing, mowing and burning events over a number of years promotes trait and species diversity in grassland communities by sustaining differences in the phenology of leaf growth, photosynthesis, flowering and seed production (Al-Mufti et al. 1977; Grime et al. 1985; Bakker 1989; Kahlert et al. 2005).

In this comparison of trait convergence and divergence strong emphasis has been placed on the relative constancy of productivity in space and time over the area occupied by a community and this has been contrasted with the capacity of disturbance to generate spatial and temporal heterogeneity within the community and to allow regeneration and persistence of a diversity of traits, trait values and species. It may be a mistake, however, to seek to explain the mechanisms responsible for trait convergence and divergence exclusively in terms of the greater spatial and temporal diversity of disturbance events.

Two additional factors deserve consideration:

1. Many spatial patterns in vegetation are strongly determined by productivity-related and visually-apparent plant traits. Either deliberately or as result of formal procedures, ecologists have frequently used them to classify communities and to map their spatial distribution in the field. On this basis it might be argued that homogeneity in community productivity is merely a human construct arising from the visual clues most readily available to field ecologists. After careful consideration, I reject this interpretation. It is more parsimonious to conclude that productivity has emerged as a widespread, coarse-scale determinant of plant community structure and functioning because it is strongly correlated with soil fertility, topography and agriculture, three correlated variables that are themselves varying at a coarse spatial scale.

2. It seems necessary also to recognise differences in the severity of the physiological and genetic constraints that operate in different stages of the life cycle and in different components of the plant's biology. The scope for inter- and intra-specific variation in evolutionary responses to disturbance, through minor evolutionary changes in germination biology (Baskin & Baskin 1998) or shoot architecture and phenology (Bakker 1989) is likely to be considerably greater than that associated with responses to productivity which appear to involve relatively intractable, multigenic linkages and trade-offs between different aspects of the core physiology of the plant (Grime 1977; Chapin 1980; Wright et al. 2004).

Consequences for communities and ecosystems

Following the initiative of Schulze & Mooney (1993), many plant ecologists have been prompted to investigate the impacts of declining plant diversity upon the functioning of ecosystems. In a recent paper (Grime 2002) it has been argued that the random deletions of species often applied in diversity/ecosystem functioning experiments do not resemble the functional shifts in

species composition and ecosystem properties that are the main processes by which the biosphere is changing under the impact of human activities. This criticism about the unsatisfactory nature of 'diversity' as an experimental variable connects with a more general unease about the way in which its use has sometimes diverted attention away from the primary and difficult task of elucidating the mechanisms by which specific plant traits, individually or as sets, influence the development and functioning of communities and ecosystems. Until recently, the proliferation of theoretical models to explain the coexistence of species in plant communities has been relatively unconstrained due to the shortage of empirical data. The advent of extensive screening of plant traits now promises to redress this situation by introducing a more rigorous mechanistic approach.

This contribution resonates strongly in its intentions with the experimental analysis of Fukami et al. (2005) in the extent to which it attempts to distinguish between the species compositions and the trait compositions of communities. For further progress to be achieved, however, it will be necessary to identify which plant traits drive ecosystem functioning and which are merely concerned with the contest between functionally-equivalent species or populations to enter and persist in the community. From the arguments developed earlier in this paper it can be predicted that the productivity filter will exert a profound effect on both the community and the ecosystem by admitting or excluding traits, trait values and species that are directly implicated in dry matter production, carbon storage, nutrient cycling, anti-herbivore defence and litter decomposition. In contrast, the influence of the disturbance filter will be a divergence in traits that are mainly confined to the local Darwinian struggle for entry, persistence and relative abundance in the plant community. This low impact of the local disturbance filter on ecosystem functioning is predicted on the basis that it mainly selects between regenerative and phenological traits that have a lesser influence on the physical and chemical processes that drive ecosystems.

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