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Perspectives on the scientific legacy of J. Philip Grime

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REVIEW

Grime Review: Phil Grime's Impact on the Present and Future of Plant Ecology

Perspectives on the scientific legacy of J. Philip Grime

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Abstract

1. Perhaps as much as any other scientist in the 20th century, J.P. Grime transformed the study of plant ecology and helped shepherd the field toward international prominence as a nexus of ideas related to global environmental change. Editors at the *Journal of Ecology* asked a group of senior plant ecologists to comment on Grime's scientific legacy.
2. This commentary piece includes individual responses of 14 scientists from around the world attesting to Grime's foundational role in plant functional ecology, including his knack for sparking controversy, his unique approach to theory formulation involving clever experiments and standardized trait measurements of large numbers of species, and the continued impact of his work on ecological science and policy.

KEYWORDS

grasslands, Grime's triangle, history of ecology, plant functional traits, plant strategy theory

1 | INTRODUCTION

When John Philip ('Phil') Grime died in 2021 at the age of 85, the field of plant ecology lost one of its most accomplished, innovative and, at times, polarizing figures. Today, a half century after Grime

published his first ground-breaking papers on plant strategy theory (Grime, 1973, 1974), his work is both canonical in the discipline (Pierce & Fridley, 2021) and subsumed into mainstream British natural history (Wilkinson, 2021). Since 2020, the *Journal of Ecology* has honoured Grime's contributions with the *Grime Reviews* series,

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involving commissions of a set of Essay Review papers on a selected theme that changes annually. This year, the theme involves Grime's own scientific contributions and how they shape the present and future of plant ecology in its myriad forms. As part of this series, three members of the Editorial Board (Fridley, Liu, Pérez-Harguindeguy) asked a group of senior plant ecologists to describe the impact of Grime's research on the development of the field, the trajectory of their own work, and potential future discoveries.

This commentary paper is unusual: it is not a consensus piece but a compilation of individual reflections on Grime's scholarship. Our intent was to record for posterity Grime's intellectual standing at the time of his death by those contemporaries that have thought deeply about his ideas. We offered guidance in the way of four questions: (1) How will history judge Grime's work and lasting impact on ecological and evolutionary science? (2) What was novel or unique about his scientific approach? (3) What do you see as likely future directions of one or more of Grime's achievements? (4) In what ways do you feel his ideas have contributed to environmental policy or conservation? We asked for honest evaluations rather than mere praise, and gave contributors a 1000-word limit, which means that many pertinent details had to be left out. Those wanting a comprehensive review of Grime's research achievements are referred to his Royal Society Memoir (Pierce & Fridley, 2021), as well as other scientific obituaries (Fridley & Pierce, 2021; Thompson & Díaz, 2021).

Grime's scientific contributions were extensive and often controversial. In response to our first prompt about how history will judge Grime's work, the perspectives below suggest some of his most popular conceptual innovations, such as the CSR triangle of 'competitive', 'stress-tolerant' and 'ruderal' plant strategies, or the humped-back model (HBM) relating plant diversity and productivity, are far from what are typically considered precise, falsifiable theories. And yet there is strong consensus that Grime changed the practice of plant ecology as much as anyone since Humboldt, particularly as one of the key innovators of trait-based functional ecology. Many regard part of Grime's genius as the ability to see the forest for the trees (or perhaps, the sward for the grasses) and distill complex and contingent natural patterns into easily digestible rules of thumb. To some, this approach lacked scientific and mathematical rigour; to others, it was an alternative to population-level modelling that nonetheless made real predictions about how communities work. Several commentators specifically reference Grime's prescient ideas about plant functional traits and global change factors, which long predate the origin of global change ecology. In response to our second prompt concerning the novelty of Grime's scientific approach, many commentators view Grime's lasting legacy as the uncanny ability to weave together detailed field observations with the results of clever experiments (often done on a shoestring) in defence of new theory. Indeed more than one commentator suggests the popularity of Grime's works stems from his embrace of both natural history and general theory, which have always had an uneasy coexistence in the minds of many field biologists.

Commentators expressed a range of views on the impact of Grime's work on conservation and policy, as well as how his ideas

are likely to inform future work. Given his lifelong association with managed grasslands, it is no surprise that Grime's theories have informed grassland management practices (mowing, grazing, fertilization) for decades. However, commentators also noted general application of plant strategy theory to ecosystem restoration (e.g. choosing species of appropriate trait values) and predicting community stability under climate change (e.g. greater resistance of species of conservative traits to perturbations). Further, linkages between climate, vegetation and traits of dominant plant species—particularly in terms of carbon and nutrient dynamics—play an increasingly large role in Earth System Models that inform global environmental policy (Bonan & Doney, 2018), and more than one commentator attributes the origin of this perspective to Grime's early work on relationships between functional traits and ecosystem processes. Indeed, the success of the functional trait approach in understanding biogeochemical processes has motivated an array of new methods that are expanding Grime's framework in myriad ways, including spatial upscaling (e.g. remote sensing of plant traits), greater integration of plant functional strategies above- and below-ground, and extensions of ecological strategy theory to plant and soil microbiomes (Treseder, 2023). As the perspectives below make clear, much of Grime's legacy depends on the continued development of ecology as a predictive science and whether his generalizations continue to be useful constructs at a time when accurate ecological forecasts are increasingly crucial to society at large.

Reflections are presented alphabetically.

2 | F. STUART CHAPIN III: SEARCHING FOR UNIVERSAL PATTERNS IN THE FOOTSTEPS OF HUMBOLDT

Grime's conceptual contributions have had a monumental impact on modern ecological thought, theory and practice. His work played a leading role in transforming ecology from a largely descriptive science into one that is grounded in empirical observations of nature and process-based hypotheses that are amenable to experimental tests. His conceptual frameworks were based on his own local observations and the literature but were intended to explain vegetation patterns and their changes at landscape to global scales—he wanted to understand universal patterns. He tested these frameworks with large experimental arrays involving massive numbers of species. His research was reminiscent of that of Alexander von Humboldt, who first documented the relationship of global vegetation patterns with climate, geology and culture more than 150 years earlier (Wulf, 2015). No wonder Grime was the inaugural recipient of the Humboldt Prize from the International Association of Vegetation Science.

Grime's strategy theory focused on the response of individual species to disturbance and environmental stress, which he viewed as the two independent variables that most profoundly affected species performance and community composition (Grime, 1977). He categorized the main species types as stress tolerators, competitors

(species that grew rapidly in the absence of stress) and ruderals (species that readily colonized disturbances), with a spectrum of intermediate types. He wanted to understand how functional differences among these types influenced vegetation structure and functioning.

Since Grime's early work, global change research has shown that human impacts on these same variables (climate, pollution, increase or loss of water and nutrients, and disturbance) are the primary causes of changes in Earth's ecosystems and their effects on society (IPCC, 2018). In other words, Grime's research provided a mechanistic framework for understanding some of the most profound changes that are now occurring in the Earth System.

Grime, his collaborators and others have applied and extended Grime's strategy theory to global scales, identifying a suite of traits that are easily measured or which have easily measured correlates (e.g. leaf nitrogen as a correlate of photosynthetic capacity; Reich et al., 2006). The resulting global databases confirm the broad application of the patterns that Grime originally identified (Kattge et al., 2020). They also demonstrate the functional importance of biodiversity (maintaining a suite of traits that govern species interactions and influence key ecosystem processes; Díaz et al., 2019). This link between species traits and biodiversity provides a pragmatic rationale for conserving biodiversity at local to global scales. Key traits of dominant species have become essential components of most biogeochemical models that are used to understand and project changes in Earth's climate and the benefits that ecosystems provide to society. In other words, the impact of Grime's research framework extends far beyond the realm of science.

Grime's plant-strategy research was inherently integrative, drawing on a wide range of plant traits to explain the general circumstances in which functionally distinct species performed well (Grime, 1977). These traits included leaf and root properties, growth rate, palatability to herbivores and reproductive traits. This was radically different than the approaches of most physiological ecologists at the time, which typically considered one or a few closely related traits (e.g. photosynthesis and water relations). When I first met Grime in 1979, I had become dissatisfied with the limited context of my own ecophysiological research (response of phosphorus absorption by roots to temperature and phosphorus concentration) because I had learned that root-microbial interactions were the primary control over phosphorus delivery to roots, and that growth rate and storage determined plant demand for phosphorus. Discussions with Grime inspired me to focus on multi-trait plant stress responses (Chapin III, 1980, 1991) and the functional role of plants in ecosystem processes and eventually social processes. Although I was only a budding scientist at the time, Grime listened to my ideas and did not hesitate to debate how these ideas related to his own conceptual frameworks. This was typical of his interactions with many scientists. My debates and arguments with Grime convinced me of the value of dialogue with colleagues who have very different perspectives than my own. This experience motivated me to develop a much more interdisciplinary and less reductionist approach to science than I had previously pursued. This shift toward interdisciplinarity now broadly characterizes many branches of ecology and global-change science.

Although it is impossible to tease out the impact of any one individual's work, I suspect that Grime's research and his interactions with other scientists have had long-lasting positive impacts on the way science is done as well as on our current understanding of how the world works.

3 | MICK CRAWLEY: THE BIG THREE OF BRITISH PLANT ECOLOGY

A central part of the narrative has to be the triangle: not the CSR triangle, of course, but the relationship between the three giants of British plant ecology in the late 20th century: Grime, Peter Grubb and John Harper. Grime the working class pragmatist, Grubb the posh well-travelled polymath and Harper the analytical one who had the nerve to emerge from an agricultural background (the cheek of it). In fact, their contributions were complementary: Grime with his emphasis on a knowledge of the traits of real plant species in the field and in the growth chamber; Grubb with his encyclopaedic knowledge of world ecosystems; and Harper with his emphasis on population dynamics and natural selection.

As we all know, the original Goldilocks Principle applied to porridge: too hot, too cold, just right. Grime saw Goldilocks Curves wherever he looked. For example, he believed passionately that the principle applied to plant diversity as a function of productivity. If there are no resources then there will be no plants, so it is zero at the left-hand end of the axis. If resources are unlimited, there will be one species that outcompetes all the others, so there will be a monoculture (i.e. there is one species at the right-hand end). If the graph is so low at both ends, then there must be a hump in the middle.

The trouble is that that is not what the data show. Importantly, there are two different kinds of data on this: observational data from latitudinal gradients of productivity (e.g. from the pole to the equator) that show plant species richness increasing with productivity. On the other hand, experiments carried out at one place, like Park Grass at Rothamsted, where productivity is increased by adding nutrients like nitrogen and phosphorus, show the opposite: species richness declines steeply with increasing productivity. In fact, there is no general pattern, and very few examples of a clearly humped relationship.

John Harper never tired of making fun of Grime's CSR triangle in his public utterances. His fundamental criticism was that you cannot illustrate a three-dimensional object with axes for competition, stress and intrinsic rate of increase (R) on a two-dimensional page. More seriously, he argued that Grime's vision of stress was completely wrong-headed. Harper argued that all plants suffer stress all the time from competitors, natural enemies and lack of mutualists, as well as from challenging abiotic conditions (like highs and lows of light, water, temperature or soil nutrients). Harper joked that 'stress was what I wouldn't like if I was a plant'.

From conversations with Grime over many years, it is clear that he wasn't envious of any of John Harper's ideas. He was, however, distinctly cheesed off that he had not conceived of Peter Grubb's

regeneration niche, which Grime recognized as a seminal contribution to the theory of plant ecology.

Pre-Grimean plant ecology had inherited ideas from the extreme determinism of Clements' view of primary succession and the extreme stochasticity of Gleason's take on secondary succession. By explicitly broadening the definition of disturbance (destruction of plant biomass) Grime highlighted the role of herbivores and pathogens in plant community dynamics, where previously disturbance had been thought of in terms of physical abiotic processes (natural ones like land-slides or lava flows, or human like cultivation or clear-felling). Perhaps the crucial insight, however, came not from America but from Germany, where Ellenberg's beautifully simple experiments laid the foundation for Ellenberg's Principle: plants are not found where conditions are best for them, but rather where their competitors and natural enemies allow them to grow. Grime took these ideas about disturbance, competition and herbivory and asked how the suite of traits exhibited by an individual plant species equipped it to deal with the interaction of these processes.

I think Grime's long-term legacy will be his insistence that the entire suite of plant traits, morphological, physiological, reproductive and genetical, both above- and below-ground, need to be considered if its ecology is to be properly understood. I suspect that Grime will come to be seen as the natural successor to Ellenberg. Grime understood perfectly well that a plant's trait space was multi-dimensional (harking back to Hutchinson's definition of niche as an n -dimensional hypervolume) but Grime was way too much of a plain-speaking pragmatist to fall into the arms of jargon (especially if the jargon involved mathematical modelling). It would be wrong to think that Grime believed that there were only three axes (competitive ability, stress tolerance and intrinsic rate of increase): The triangle kept it simple in order that others might see the light.

4 | GERLINDE DE DEYN: DISCOVERIES THROUGH INTEGRATION OF OBSERVATION, EXPERIMENT AND THEORY

The ambition of Grime to find generality in complexity and make ecology a more predictive science will leave a lasting imprint. Anyone studying ecology should know the plant strategy theory of CSR, and upon extension to other organisms as universal adaptive strategy theory, which place organisms in their eco-evolutionary environment based on organismal traits and trade-offs (Grime, 1977; Grime & Pierce, 2012). By considering the axis of resources and axis of disturbance CSR will remain an important extension of the r/K strategy view of species adaptation to their environment. Furthermore, Grime's view that plant functional traits not only reflect adaptations to the abiotic environment but also affect this environment during and after the plants lifetime has been of major influence in community and ecosystem ecology, for example in understanding plant–soil feedbacks (Cortois et al., 2016), above–below-ground interactions (De Deyn, 2017), and potential implications of climate and land use change on ecosystem functioning (van der Putten et al., 2016).

The Grime approach to me means an integrative and comparative approach of field observations, field and lab experiments, and theory to uncover generalities in ecology. The large screenings of plant functional traits of many plant species using standardized methodology to discover trait trade-offs and their link to field observations was unique and visionary. This comparative functional trait-based approach is still inspiring researchers to date in developing and using trait databases, ranging from terrestrial plants (Kattge et al., 2020), to microorganisms (Cébron et al., 2021) and fauna (Herberstein et al., 2022). Also the strong visual representation of the CSR strategy theory as the CSR triangle which depicts viable plant strategies given prevailing conditions has been instrumental to its resonance in ecology as conceptual and didactic tool.

The urge for generalities in ecology by Grime provided theory and conceptual tools to build-on in decades to come. While helpful in large scale comparisons, the CSR strategy theory and associated trait collections have their limitations in mechanistic understanding of how plants respond to their environment and how they affect biological interactions and ecosystem processes. In response, those using trait-based approaches will further explore the ultimate and proximate traits of plants and their associated organisms, notably below-ground (Freschet et al., 2021; Williams et al., 2022). This endeavour will be helped by methodological advances and integrated above–below-ground approaches that enable non-destructive in situ and in silico studies at relevant spatial and temporal scales of the organisms, their environment, and the ecosystem processes at stake. This will require inter- and transdisciplinary research in which, for example, remote sensing tools are co-developed and integrated with in situ and lab data and mechanistic modelling (Cavender-Bares et al., 2022; De Deyn & Kooistra, 2021).

The debate over biodiversity's relationship to ecosystem functioning relations remains highly relevant given global issues of biodiversity decline, land use and climate change. In this context the mass ratio hypothesis of Grime stating that ecosystem functioning is chiefly determined by trait values of the dominant contributors to plant biomass remains relevant. However, the extent to which community weighted mean (CWM) trait values explain one or multiple ecosystem processes depends on the process under consideration and the roles of keystone species and species complementarity. Consequently, next to CWM traits the analysis of additional parameters that capture diversity components of the community can provide important insights to enhance mechanistic understanding of biodiversity-ecosystem functioning relations (Barry et al., 2019; Díaz et al., 2007; Gross et al., 2017). Furthermore, when considering soil-based ecosystem processes, the legacy of preceding plant communities can be more important than that of the current community, stressing the need to consider temporal dynamics (De Deyn & Kooistra, 2021). Theories of Grime and adaptations thereof will remain inspirational for the conservation and restoration of natural ecosystems, redesign of agro-ecosystems (MacLaren et al., 2020) and design of novel ecosystems (e.g. urban areas, solar parks, etc.).

The ideas of Grime on plant species strategies, the unimodal relationship between species richness and site productivity, and the

intermediate disturbance hypothesis have all been instrumental in understanding why species disappear or thrive in plant communities. These insights provided management tools for conservation and restoration efforts of species-rich ecosystems, for example by counteracting eutrophication and adjusted mowing or grazing regimes. The role of soils in plant community restoration was for a long time considered solely from an abiotic perspective, notably pH and nutrient availability. However, in his experimental approach Grime already demonstrated in the 1980s how mycorrhizal fungi in the soil promote plant diversity (Grime et al., 1987). This notion inspired generations of soil ecologists to elucidate the role of soil biodiversity, spanning a range of functions and levels of specialism (root mutualists, herbivores, pathogens and decomposers) in ecosystem restoration (De Deyn & Kooistra, 2021). In practice these insights resulted in soil inoculation of appropriate donor sites into restoration sites as tool to speed up restoration after excavation of eutrophic soil (Wubs et al., 2016).

5 | SANDRA DÍAZ: TOWARD SIMPLICITY AND PREDICTABILITY IN ECOLOGICAL THEORY

History will likely judge Grime's work as one of the most influential in the field of ecology of the 20th century, particularly in plant terrestrial ecology, but reaching beyond it. His work was a rare combination between very general theory and detailed empirical work, which one finds in very few ecologists. His strategy theory (Grime, 1974) is one of the most general theories not based on mathematics that we have in plant ecology. Plant ecology evolved mainly from natural history and therefore carries a legacy of relishing in the unique way in which each organism is different from other organisms. Grime broke with this and produced a very general, highly stylized theory that could explain at least to a large degree many phenomena, like local coexistence, succession, and plant species richness patterns, and provided a way to compare taxonomically very different species and communities. This generality without losing biological content (like it happens, e.g. in strongly mathematically based theories and models) made his ideas extremely appealing to many, both in the area of fundamental ecology and also in management. Precisely because of their simplicity, these ideas also attracted the largest criticisms but the fact they are still applied and refined in many parts of the world after 50 years is a testimony of their robustness and appeal.

There is another aspect to his scientific approach, probably less well known: his experimental testing of many aspects of plant ecology, not necessarily related to CSR theory. He and his team produced pioneering articles on, for example, carbon sharing in plant communities via mycorrhizal networks (Grime, Mackey, et al., 1988), top-down versus bottom-up control in local trophic networks (Buckland & Grime, 2000; Fraser & Grime, 1998), community- and ecosystem-level effects of elevated carbon dioxide (Díaz et al., 1993, 1998), the role of intraspecific genetic diversity in plant communities (Fridley & Grime, 2010), mechanisms of ecosystem invasion

(Burke & Grime, 1996; Davis et al., 2000) and competition (Campbell et al., 1991, 1992), and community resilience and resistance (Grime et al., 2000), often based on ingenious, small-scale experimental setups, putting forward ideas that later on were developed into large-scale research programs by other research groups around the world.

Always going for fundamental mechanisms and testing them with surprisingly simple methods, his design of experiments in which the lack of a dedicated budget was compensated with immense ingenuity is a very strong inspiration to younger generations of ecologists, even if they do not find CSR theory convincing or directly applicable to their work. He also was arguably the founding father of comparative plant ecology and the now widespread functional trait research programme, through the founding of the Integrated Screening Programme (Grime et al., 1997; MacGillivray et al., 1995), and the books *Comparative Plant Ecology* (Grime, Hodgson, et al., 1988) and *Methods in Comparative Plant Ecology* (Hendry & Grime, 1993).

Given fast global environmental change, and the advent of big data and large-scale scientific collaborations across the world, I highlight two of his achievements with large potential projections into the future. First, the idea of a simple set of recurrent patterns of plant evolutionary specialization, which in the last years of his career he extended to other organisms, has found a continuation and expansion in the recent global stylized phenospaces identified, e.g. for vascular plants, birds and other animals. Second, his idea of the 'twin filters' (Grime, 2006; Grime & Pierce, 2012) is also very powerful, linking drivers at different scales in the shaping of local plant communities. The advent of big data provides a way to empirically test it at the worldwide scale.

6 | JAMES GRACE: ECOLOGICAL GENERALIZATIONS AND THE HUMPED-BACK MODEL

I started graduate school right when Grime was in his most creative phase during the 1970s. It was clear to me at the time that he was a classical theoretician working at the conceptual level who wanted to extract general principles from the complexities of plant communities. It was also clear that he had a solid knowledge of plant biology to inform his ideas, examples and illustrations. As a plant scientist myself, I very much appreciated both his general ideas and his biological insights. What soon caught my attention, however, was the abundance of debate that accompanied the models that he and other theoreticians promoted during that era. This quickly led to my career-long dual interest in ecological generalization and the associated elements of the scientific method.

In Grime's initial attempt to generalize about the controls of species richness (Grime, 1973), he proposed separate but parallel models to explain the distinct influences of environmental stress and disturbance gradients on species richness patterns. For both types of gradients, he proposed that under the most favourable conditions (low stress or low disturbance), species richness will be low because

of high rates of competitive exclusion. At high levels of stress (and thus low potential productivity) or high disturbance rates, diversity was predicted to be low because conditions would be too severe for most species. Sites with intermediate levels of stress or disturbance were therefore predicted to have the highest species richness. In his 1979 book, he expanded on his initial ideas to propose the 'HBM' for herbaceous species richness. Here, he considered a larger number of mechanisms for diversity regulation while condensing the prediction to one about how diversity changes along a combined gradient of stress and disturbance. To simplify empirical expectations, he proposed that standing crop biomass (including litter) could serve as a measure of the combined effects of stress and disturbance on biomass production. This led to a single model representing his expectations for species diversity along a variety of gradients.

In the same time period other theoreticians proposed alternative models designed to explain patterns of species diversity along gradients of habitat favorability/productivity. This confluence fueled a multi-decades-long discussion of the various models, as well as a great stimulation of empirical work on the topic. It was not until the mid-1990s before interest in the additional process of biodiversity leading to enhanced productivity became part of the conversation. Consideration of this process led to entirely new models and none of the diversity models developed in the 1970s and 1980s included it as a major component, including Grime's.

In my view, Grime's HBM model has two main sources of appeal. First, it is a model for the controls of diversity in herbaceous plant communities, not making claims for all community types. This allows for a more detailed and specific consideration of the mechanisms controlling diversity than is possible with more abstract models. Second, his model involved the interplay of five major processes, (1) competitive dominance, (2) abiotic stress, (3) disturbance, (4) niche differentiation and (5) supply of suitable species. As a result, his model attempted to summarize a great deal of what was known about the processes operating in herbaceous plant communities.

As theoreticians often do, Grime vigorously championed his model, published additional explanations, sought confirming evidence and defended it against numerous challenges, as did virtually all the authors of competing models. While the process of judging the different models was challenging, what most attracted my attention was the fact that all competing models, as different as they were, drew support from a common set of empirical examples. These examples were represented in the form of bivariate correlation plots of richness on the y-axis and various things on the x-axis that relate in some way to habitat productivity. Soon, many saw the need for more and better data to advance the topic, which stimulated a large number of literature reviews and meta-analyses, ultimately helping to motivate the development of a globally distributed network using common field methods (Borer et al., 2017).

Surprisingly, by itself it seemed that standardized data did not lead to resolution of opinion. What was conspicuous was that at that time ecologists were not using statistical methods that could test competing multi-process models against data. That absence meant that multi-process models could neither be properly evaluated nor

compared to each other, producing a stalemate that blocked progress and prolonged profitless debate. Fortunately, the global database produced by the Nutrient Network (Borer et al., 2017) included a large complement of measurements sufficient to allow for an integrative quantitative test of the processes proposed to be important in the ensemble of models being debated (Grace et al., 2016). Interestingly, the results showed that virtually all the processes being promoted as important by Grime and others (including a feedback from diversity to productivity, which he disavowed) operate together simultaneously. This means that Grime's humped-backed model can be seen as a useful conceptual model of the many of the factors regulating herbaceous plant richness, though not a sufficient model for understanding the full set of interconnections between productivity and diversity. I believe this reframing of the HBM as one summarizing many of the factors influencing diversity can preserve much of the historical legacy that Grime's model represents.

For me, the challenge of objectively evaluating Grime's humped-back model leads us to an awareness that integrative models and the ability to test them contributes importantly to the advancement of our understanding of ecological systems. Grime's inventiveness and tenacity helped fuel the push toward this awareness, which represents an even broader contribution to the science of ecology.

7 | PETER GRUBB: LARGE SPECIES COMPARISONS, CLEVER EXPERIMENTS AND MISSED OPPORTUNITIES

Grime's work on the comparative ecology of large numbers of species growing in one geographical area was undoubtedly novel. Comparative ecology on a smaller scale, say five to six species in one family in one geographical area, was introduced by Tony Bradshaw and his associates in papers of 1958–64. Bradshaw et al. also got people thinking about inherent differences between species in relative growth rate. However, the paper of Grime and Hunt (1975) took the approach to a new level of ambition and promise, and introduced comparisons of species under controlled conditions.

There were arguably two major faults in Grime's analysis. I was one of the three editors of *Journal of Ecology* at the time, and I was in charge of Grime's paper. I failed to spot the faults, so I must share the blame. First, the irradiance in the growth cabinets was low, and so low that the plants would not respond to an increased nutrient supply when given it; as a result the relative growth rates (RGRs) measured were not maximum RGRs as claimed—RGRs under certain standardized conditions but not the maximum attainable. Secondly, the published account did not report any correlation between the measured RGR and seed mass, even though it was clear if functional groups were considered separately. All comparisons of seedling RGR between different functional groups should be made allowing for seed size. Fenner (1983) brought the RGR-seed mass correlation to peoples' attention more than any of the previous authors who had shown the relationship and were quoted by Fenner. The two faults should be recognized, but the paper by Grime and Hunt was still a

major advance, was very stimulating to the rest of us, and will surely continue to be seen as that.

In a similar way Grime's successive studies on 2c DNA values, sensitivity to Red/Far Red light ratio, impact of being mycorrhizal and so forth were ground-breaking because they involved so many species, and were based on laboratory experiments and field observations as appropriate.

Grime also initiated impressive experiments on plant communities outdoors, notably on the controls limiting invasion by species not naturally present (Thompson et al., 2001) and the extent to which variation within species might contribute to the maintenance of species mixtures (Booth & Grime, 2003).

I do not think Grime impacted on my career or indeed any research I did or supervised. It did take my time to set out the major objections to his CSR system (as in my review of the 1979 book; Grubb, 1980) and at greater length (as nobody else could bring themselves to do it), in my chapter in White (1985). By the time I wrote my paper on three basic and strikingly different strategies of plants which cope with shortages of resources (Grubb, 1998), I related my three types to Grime's one because readers were familiar with his system, but I was no longer primarily directing my comments against the CSR scheme, and had a lot more positive new things to say.

I think my writing impacted in at least one way on Grime's. He immediately saw that there was some value in my 'regeneration niche' review (Grubb, 1977), and presented his own perspective on 'regenerative strategies' in chapter 3 of his 1979 book. He did not write about regeneration before then.

I think it will strike some thoughtful writers in the future that it is remarkable that Grime 'presumed' to come up with very generalized ideas about functional types of plant or primary strategies (and especially their key characters) while not having any personal experience of distinctive and very extensive vegetation types or any feel for them (most notably tropical rain forests and dry forests, and semi-deserts and deserts). However, it has to be said in Grime's defence that other leading ecologists have done the same, notably T. A. Rabotnov in the USSR, and R. H. Whittaker in the USA, among others. It has to be remembered that the literature is often wrong or at least misleading and personal experience is vital.

Grime defended his ideas fiercely, and I fear that this trait could have been an impediment to his making new discoveries. One possibility that comes to mind arises from the conversations he and I had on the last two occasions when we met. He was very keen to tell me how wrong I was to think E. J. Salisbury was right to think of species or populations or individuals competing with each other at the seed stage, for example by a plant making more seeds, seeds over a longer period, larger seeds, smaller seeds, seeds less eaten, inherently longer-lived seeds, more dispersible seeds, etc. He was provoked by what I had written in my brief commentary on Salisbury's Presidential Address to the BES (p. 27 in Grubb & Whittaker, 2013). If Grime had accepted the point, his imagination could have exploited the near-vacuum in the literature and offered some new perspectives and/or generalizations.

8 | SUSAN HARRISON: EARLY INSIGHTS INTO GLOBAL CHANGE ECOLOGY

It seems inarguable to me that history will judge Grime as a visionary among plant community ecologists, who brought greater cohesion and generality to the field through a set of insights that have proven prescient under modern global change. His core insights were, of course, that plants can be characterized by alternative ecological strategies that reflect different environments and different pathways of life history evolution, that these strategies can be quantified using functional traits, and that these strategies and traits can be used to predict the responses of species and communities to environmental change. Modern trait-based plant community ecology is founded on these premises. While there is now an emphasis on exploring a broad range of variation in continuous traits, rather than invoking the three functional categories defined by Grime, it is remarkable to me how well some of his fundamental conclusions have held up even since the advent of Big Data. For example: unproductive environments select for traits such as short stature, low RGR, evergreenness and sclerophylly, and these traits in turn have a reliable set of ecological consequences that can be summarized as high resistance to perturbation. Results of the climate change experiment by Grime and colleagues (Fridley et al., 2011; Grime et al., 2000, 2008; Ravenscroft et al., 2014) are to me a strong affirmation of the soundness and lasting relevance of his insights.

Developed in part from Grime's extensive observations of limestone outcrops and limestone grasslands, his theory added an important dimension to life-history theory by considering not only competition and disturbance but also environmental stress. Stress is not a concept beloved of those population and community ecologists to whom competition for limiting resources is foundational to all theory. As Grace (1991) and Goldberg and Barton (1992) have implied, Grime could have been more careful in drawing the important distinction between resources and conditions as sources of stress, where both are productivity-limiting factors, but only resources are consumed and competed for. Grime was justified, though, in drawing greater attention to environmental gradients driven by conditions, or productivity-limiting factors that are relatively uninfluenced by the plant community and its resource uptake. Through observation and reasoning, he concluded that plant communities change along gradients of conditions such as cold, salinity, mineral imbalances, sometimes aridity, and so forth, in ways that are more reflective of species' relative tolerances than of their abilities to compete with one another for limiting resources. How much of the world's plant community variation can be predicted by resource competition versus stress tolerance is far from resolved, but it seems inherently likely to me that tolerance will tend to predominate at larger scales.

Here I will admit to a substantial pro-Grime prejudice arising from my interest in serpentine ecosystems, which (as Grime himself also noted) resemble limestone outcrops and grasslands in their low productivity and rich native floras. Through observational and experimental studies, my collaborators and I and others have found a long list of Grimean qualities in serpentine plant communities, which

consistently support species with classic stress-tolerant functional traits (Fernandez-Going et al., 2012, 2013; Spasojevic et al., 2014). Compared with their more productive nonserpentine neighbours, serpentine ecosystems are less responsive to disturbance, in the sense that experimental removal of above-ground biomass has little effect on their diversity or their invasibility by soil-adapted species of natives (Elmendorf & Moore, 2007) or exotics (Grace et al., 2017). In shrublands, wildfire removes less biomass, stimulates less increase in diversity and is associated with less specialized plant adaptation on serpentine than nonserpentine soils (Safford & Harrison, 2004). Plant community composition responds less to climatic variability on serpentine than nonserpentine soils, whether one considers natural temporal variability, geographic variability or experimental variability in climate (reviewed in Damschen et al., 2012, Harrison et al., 2014). We thus share the hope of Grime and his colleagues that ecosystems on infertile soils may be relatively resistant to some human impacts.

While I have focused on what Grime called the 'vexed' question of stress gradients and competition, his papers are a rich source of other insights, some of which later became well-known theories more strongly associated with other ecologists. Regional species pools as controls over local community diversity (Cornell, 1985; Cornell & Harrison, 2014; Ricklefs, 1987) appear for the first time, to my knowledge, in Grime's 1973 *Nature* letter as an explanation for the low diversity of extremely harsh environments. The Resource Availability Hypothesis (Coley et al., 1985), perhaps the most successful general theory of plant antiherbivore defence, is predicted by Grime's statement in his 1977 *American Naturalist* paper that 'it would not be surprising' to find stress-tolerant plants are well-defended against herbivory as an evolutionary response to their limited recovery ability. The Dynamical Equilibrium Hypothesis (Huston, 1979) is foreshadowed by Grime's ideas, and its prediction that optimal levels of disturbance depend positively on productivity appears to hold up well in contemporary settings including forest fire management (Brodie et al., 2021).

I will conclude by offering the subjective opinion that the most lasting ecological theory originates not from deductive reasoning based on first principles, but by a blend of broad-ranging and deep observation of nature's variation together with sound analytic thinking. Darwin could not have been our leading theorist had he not also been such an obsessive and brilliant empiricist. Rereading Grime's work, with its extensive descriptions of plant communities and their species and traits, leads me to regard him as a member of that tradition of empirically-intelligent theorists. His ability to essentially predict the results of a climate change experiment long before climate change was recognized is as good a testimony as any to the success of his approach.

9 | SANDRA LAVOREL: THE ORIGIN OF TRAIT-BASED COMMUNITY ECOLOGY

Grime fathered modern trait-based approaches to community ecology (Grime, 1977; Hendry & Grime, 1993), setting the scene for contemporary big-data based approaches in functional ecology.

Organizing the plant world along two axes was a visionary innovation from the *r*-*K* framework (Southwood, 1988), by decoupling the economics of resources in plant organs (Bazzaz, 1979; Chapin III, 1980; Chapin III et al., 1990, 1993) and disturbances as drivers of fast vs. slow lifestyles. First, identifying disturbances as constitutive and independent components of ecosystems was the core innovation of the CSR framework (Pickett et al., 1989). Secondly, the triangular concept recognized that resource availability constrains regimes for disturbances linked to ecosystem productivity (e.g. herbivory, fire) and determines the ways and rates at which plants can recover from disturbance.

Grime initially conceptualized discrete strategies within this triangular space. However, nature is rarely discrete. The Integrated Screening Programme moved forward by acquiring standard, continuous measurements for anatomical, morphological, physiological and biochemical traits (Hendry & Grime, 1993). The first ever trait-based species classification validated the resource-driven axis, and confirmed the independent axis separating vegetative from regeneration traits (Grime et al., 1997). Later refined under the Leaf-Height-Seed (LHS) scheme (Westoby, 1998), but challenged by global trait analyses (Díaz et al., 2016), this remains one essential consideration in a world of more extreme and novel disturbance regimes.

The CSR scheme remains a fundamental, sometimes implicit, foundation of functional ecology, with contemporary incarnations and applications.

First, early global change research applied the plant strategy scheme to represent complex plant communities in climate and carbon cycling models (Grime, 1992; Smith et al., 1997; Woodward & Diament, 1991). There is a highly active legacy of trait-based approaches to large-scale vegetation and ecosystem modelling (e.g. van Bodegom et al., 2014). Yet these models rarely acknowledge disturbance responses and continuous, adapting trait values required to represent them (Scheiter & Higgins, 2009). This disconnect from field-based research may compromise our ability to predict vegetation change within biomes. As a fine field ecologist with an intimate knowledge of plant communities and an agile master of multiple methods including standardized approaches (e.g. trait screening), surveys along environmental gradients, and clever experimental approaches, Grime demonstrated with his collaborators complex climate change responses and their subtler mechanisms (e.g. Fridley et al., 2016; Ravenscroft et al., 2014).

Second, astute insights into plant community dynamics from functional approaches allowed Grime to uncover trait-based mechanisms underpinning the effects of plant diversity on ecosystem functioning. To date, the mass ratio hypothesis—that dominant traits in communities, rather than species richness, determine outcomes for mass-based ecosystem functions (Grime, 1998)—is strongly supported (e.g. Smith et al., 2020), although theory (Díaz et al., 2007) and evidence suggests that it combines with other mechanisms (Ali, 2019; Bello et al., 2021; Le Bagousse-Pinguet et al., 2019). A comprehensive understanding of the interplay between diverse trait-based mechanisms depending on abiotic context, evolutionary history or environmental legacies is still elusive.

This will certainly continue to build on insights into how traits affect community assembly (Grime, 2006), and how this cascades to ecosystem functioning through response-effect linkages (Lavorel & Garnier, 2002). Finally, trait-based approaches are not always the most predictive, nor the most parsimonious for linking biotic responses to ecosystem functions (Orwin et al., 2022; van der Plas et al., 2020).

Three directions merit further progress in functional, trait-based ecology. First, the plant resource economics spectrum (Reich, 2014) has proved a powerful mechanism controlling the distributions of species and communities along environmental gradients, and effects on ecosystem functioning. Has this hegemony blinded us to other mechanisms? Time is ripe to assess the extent and covariates for its explanatory power, and to discover the role of yet unimagined mechanisms and associated traits.

In addition, one may wonder what happened to the disturbance axis. With the notable exception of fire (Pausas, 2019; Pausas et al., 2017), resource-oriented plant functional approaches largely suffer from two limitations. Regeneration traits, and their roles for community assembly (Grubb, 1977) with onwards effects to ecosystems, have remained in the shadow of functional biogeography or vegetation modelling, hence widening the gap with population ecology or dispersal ecology. More serious perhaps, we must address our collective amnesia that the plant strategy scheme and its trait-based developments rest on a strong equilibrium hypothesis. Identifying the critical role of disturbance and environmental stochasticity in non-equilibrium dynamics was the most major advance in the late 1970s and 1980s (Chesson, 2000; Pickett & White, 1985) and is still core to parts of community ecology.

Finally, plant strategies have considered trophic interactions, including vegetative traits determining plant susceptibility to herbivory, floral traits for pollinators, and mycorrhizal status (Grime et al., 1997). Each are fertile research fields (Malik et al., 2020; Suárez-Mariño et al., 2022; Weigelt et al., 2021) and we are only starting to grasp the role of plant traits for multitrophic community and ecosystem ecology (Bartomeus et al., 2016; Bauer et al., 2021; Lavorel et al., 2013). In this pursuit the two above limitations will deserve caution.

Grime's work highlighted the complexity of biodiversity, clearly demonstrating it is not a single, species richness 'planetary boundary', but needs to be considered in all its texture in policy (Díaz et al., 2020; Mace et al., 2014).

10 | ZHIMIN LIU: THEORETICAL ADVANCEMENTS THROUGH TRADEOFF THEORY

Grime was one of several key figures developing plant ecology as an extensively integrated science. His major achievements in theory are plant functional trade-offs in resource use, the HBM of species richness/productivity, CSR plant strategy theory, linkage of

plant functional traits to ecosystem properties, mass ratio theory and the twin filter model (Pierce & Fridley, 2021). Although there have been deep debates concerning Grime's ideas, in my opinion, since ecological theories are drawn from specific case studies, it is inevitable that what is right in one case can be seen as wrong in other cases. Each theory has its own range of application. In any case, Grime's theories have modified our perspective of ecological study in the modern world, and he is among the most widely appreciated scientists whoever worked in the field of plant ecology or vegetation science (Pierce & Fridley, 2021). One of Grime's lasting impacts was his view that ecology needs to be practical and operable, especially considering local impacts caused by land use change and climate change.

Grime's scientific approach had several hallmarks. These include: (1) the pursuit of generalities by describing complex and detailed phenomena in a simplified framework, putting numerous driving factors into a simple classification system; (2) combining observation, experiment and hypotheses, and putting observation of natural phenomena center-stage in ecological study (Pierce & Fridley, 2021); (3) introducing the concept of 'function' in ecology study in order to understand how plants interact with each other and with the environment; (4) paying attention to the role of trade-offs in evolutionary science; (5) distinguishing the roles of disturbance and stress in governing vegetation processes; and (6) distinguishing growth and reproductive phases in determining plant strategies (Grime et al., 1997).

Several aspects of Grime's work will contribute to ecological research in the future. First and foremost is the screening and application of plant functional traits. In comparison with plant functional types, which are based on the classification of genetic characteristics, plant traits, playing a key role in shaping and maintaining the habitat, are more easily obtained and used in the management of local and specific vegetation types and ecosystems. Screening and application of plant functional traits will continue to be a common concern of both theoretical and applied ecologists. Second is the identification and application of trade-offs. A trade-off is an evolutionary dilemma whereby genetic change conferring increased fitness in one circumstance inescapably involves sacrifice of fitness in another (Grime, 2002). Trade-offs deeply affect the way plant ecologists see things, facilitating a deep understanding of the nature of plant evolution. Third concerns the differentiation of disturbance and stress as drivers of vegetation processes. According to Grime (2002), stresses are external constraints limiting the rate of dry matter production, while disturbance destroys plant biomass. This conceptual framework provides a basis for making predictions about how land use and climate change affect vegetation processes and ecosystem functioning. Fourth are the roles of the established (mature) regenerative (immature) phases in plant adaptation (Grime, 2002). Recent studies have supported the hypothesis that 'plants tend to use regenerative strategies to deal with disturbance and to use physiological strategies to deal with stress', which deepens our understanding of plant evolution.

11 | SIMON PIERCE: INTRASPECIFIC VARIATION AND THE IMPORTANCE OF ECO-EVOLUTIONARY DYNAMICS

Grime is associated with interspecific comparisons and the impact of species on community processes and ecosystem properties. However, the role of *intraspecific* trait variation was a key topic during the latter part of his career (Pierce & Fridley, 2021). Alongside collaborators, he assembled microcosms including different individual genotypes of grassland species, concluding that intraspecific variability mitigates local species extinction, reinforcing community stability (Booth & Grime, 2003; Whitlock et al., 2007). As any biology student will recognize, intraspecific variability is also essential to Darwin and Wallace's (1858) mechanism of evolution, because natural selection requires variation in individual phenotypes and thus fitness. Indeed, defining plant functional traits as 'morpho-physio-phenological traits which impact fitness indirectly via their effects on growth, reproduction and survival' (Violle et al., 2007) recognizes that intraspecific functional trait variability affects the outcome of natural selection; a crucial link between evolutionary biology and community ecology. Furthermore, as ecological processes can occur over the same timescales as individual lifetimes (the timescale on which natural selection 'selects'), evolutionary and ecological processes can be investigated jointly by the field of eco-evolutionary dynamics (e.g. Pelletier et al., 2009)—the implications for community assembly are illustrated by the 'twin-filter model of eco-evolutionary dynamics' (Grime & Pierce, 2012).

Eco-evolutionary dynamics encompasses intraspecific functional variability and links evolutionary processes (e.g. speciation via diversifying selection and cladogenesis) to ecological processes (filtering of the local species pool), explicitly considering evolution in the context of the community and ecosystem. Indeed, evolutionary selection and ecological filtering are essentially the same process, involving differences in the fitness and persistence of the individuals that locally represent each species (Grime & Pierce, 2012). While such dynamics are usually interpreted as fine-scale processes, intraspecific functional variability and Darwinian evolution are phenomena occurring within, and affecting, larger biological units such as ecosystems.

What is the future of Grime's insights into intraspecific variation? More specifically, can we improve realism when modelling large-scale processes in ecology, based on the underlying fine scale eco-evolutionary dynamics?

One possibility concerns species distribution models (SDMs), which integrate datasets to predict how distributions respond to environmental factors (e.g. Gargiulo et al., 2019). A recent drive to improve precision involves 'informing' SDMs using intraspecific variability (e.g. Chardon et al., 2020). SDMs can also be informed by remote sensing, generating detailed map layers of 'response variables' (He et al., 2015). Grime's (1974, 1977) CSR strategies are relevant to both approaches: capable of quantifying intraspecific variability (e.g. May et al., 2017; Vasseur et al., 2018) and of being remotely sensed (e.g. Kattenborn et al., 2017; Schmidt et al., 2017). At the largest

scale, global maps of CSR-related traits and the 'global spectrum of plant form and function' (Díaz et al., 2016) have been produced using a neural network, combining databases of citizen science plant photographs, functional traits and climate (Schiller et al., 2021). Biodiversity that cannot be detected by these methods (invertebrate or microbial communities) can be characterized from environmental DNA in diverse habitats (e.g. Kirse et al., 2021; Xie et al., 2021).

This encourages speculation that an eco-evolutionary biosphere model could be developed that, based on Darwinian and Grimean principles (selection and function), would offer a high degree of precision in predicting biological responses to environmental processes across scales. The particular value of the model would lie in its ability to determine complex interactive effects leading to tipping points unforeseeable by simpler models. As a detailed simulation of species, communities, ecosystems and biomes world-wide, such a model could faithfully represent reality and provide a testbed for *in silico* experiments. One can imagine ten-thousand virtual Earths replicated in an experiment predicting the responses of grassland or cereal species to climate change scenarios, or estimating the conservation status of each of the Earth's species over the next hundred years in response to human socio-political 'experimental treatments'.

At our current levels of knowledge and technology, this may sound like science fiction. Earth system simulations currently have resolutions measured in kilometres, involving exabytes of data distributed across data centers (e.g. the U.S. Department of Energy's 'Energy Exascale Earth System Model'; Burrows et al., 2020). A biosphere model with a resolution at the scale of single organisms, spanning the microscopic to the megascopic, ranging from the ocean floor to the nival zone, would require significant technical advances. However, Grime's achievement of linking broad-scale ecological phenomena to the individual-scale detail of evolutionary biology allows us to conceptually span disciplines and scales, inspiring us to imagine these possibilities. While it is easy to see Grime as the originator of one particular theory or another (CSR theory, Universal Adaptive Strategy Theory, the HBM, Mass Ratio theory, the scale-precision trade-off in spatial resource foraging, the Twin-Filter model; see Pierce & Fridley, 2021) these insights are only offshoots of his main objective of understanding the 'how and why' of plant communities, rather than being content simply to describe them. This mechanistic and functional approach is Grime's legacy; one that offers a steady guiding hand for future generations of ecologists.

12 | BERNARD SCHMID: UNDERSTANDING NATURE AS IT IS, NOT AS IT SHOULD BE

Studying the life history of *Carex flava* in Switzerland in the light of *r*-selection, my colleagues told me that the new CSR typology of Grime would be a more useful concept. I believe European continental ecologists liked Grime's pragmatic approach because it seemed to fit well with their own approach to classify vegetation. Reading Grime's original paper (1977), I was reconciled that he added to the disturbance gradient of *r*-selection an orthogonal stress gradient,

increasing the potential life-history poles to four. However, by deleting the high disturbance-high stress pole as not occurring in nature, he moved the theoretical concept to a phenomenological CSR triangle. In my view this was useful for classification but less so for understanding.

As a postdoc in John Harper's (1977) lab in North Wales, I unwillingly got caught between the two heroes of plant ecology. In Harper's lab we carefully avoided the word stress, because we could not sensibly define it, in particular not if it was related to the environment rather than the plant's response to it. It seems in the long term Grime's pragmatic approach prevailed, as obviously environmental stress gradients persist or have even become more frequent in recent ecological literature.

Grime was an empiricist who wanted to understand nature as it is, not as it should be under particular theoretical assumptions. But as an empiricist he used very creative experiments to explain effects of environmental factors on plant communities. One clever invention, which has not been adopted by others, perhaps because again it is pragmatic yet violates some statistical design principles, were his matrix experiments, where plants were grown in a physical matrix crossing a disturbance gradient with a fertilizer gradient (Burke & Grime, 1996), similar to fan-design experiments once suggested by a famous statistician (Nelder, 1962).

Being interested in understanding nature as it is, Grime was highly critical of the new wave of biodiversity–ecosystem functioning experiments that started in the 1990s (Grime, 1997). He found it unrealistic to think of large-scale extinctions that would perhaps leave a few subdominant species together in a plant community on fertile ground. At the beginning of the new millennium, Grime, together with others, was invited to discuss a new large biodiversity experiment in Jena, Germany. Perhaps typical for him, he made very constructive and interesting comments about the design, yet after returning home he wrote a strong e-mail, warning that the planned experiment would only reveal the so-called sampling effect as main explanation of claimed biodiversity benefits. His remark: 'the occasional inclusions of dominants like *Arrhenatherum* or *Alopecurus* will be like entering Mike Tyson in a high school boxing tournament'.

As a consequence, we added to the main experiment a so-called dominance experiment where only nine dominant species were used as pool to form all monocultures, all two-species mixtures and more species-rich communities, with all species equally represented at all diversity levels. However, biodiversity effects were even stronger in the dominance than in the main experiment; and they were not simply due to sampling effects (Roscher et al., 2005). Grime also provided us with detailed descriptions for the main experiment about which species would become dominant, yet interestingly even for his two 'Tyson' grasses he predicted various dominance ranks depending on planned species compositions. Again, his pragmatism was winning out over theory. In particular, his view (as that of many others), that a single functional type should always become dominant under constant environmental conditions in plant communities, did not apply in the biodiversity experiments in Jena. Rather, communities tended to maintain high functional diversity even after invasion (Petermann et al., 2010).

Typical for Grime, even though he was highly critical of biodiversity experiments, he did some of the most innovative ones himself, including an early study where grazing and mycorrhiza increased biodiversity by reducing the biomass of the canopy dominant (Grime et al., 1987). Later on, he set up probably the first species x genetic richness biodiversity experiment and combined it with a soil-depth treatment (Fridley & Grime, 2010). The results were highly complex, indicating many possibilities of interactive effects that should be studied in further experiments.

Overall, I admire Grime for his openness toward ecological problems even when he had very strong opinions about the right answers. Whenever it came down to the concrete situation, he would be the empiricist who objectively observed nature and creatively manipulated it to find out more about the causes behind the observed phenomena. For me, demonstrating this methodological approach is the lasting impact of Grime's contributions.

13 | CARLY STEVENS: THE ORIGINS OF PLANT STRATEGY THEORY IN SHEFFIELD GRASSLANDS

The introduction to *An Ecological Atlas of Grassland Plants* (Grime & Lloyd, 1973) begins 'If maximum use is to be made of our knowledge of the relations of individual species to factors of the environment it is essential that comparisons between species of similar or contrasted ecology should be possible. Such comparisons are valid only where the procedures of sampling, measurement, analysis and presentation have been standardized'. This quote relates the main reason behind the value of the surveys of the Sheffield region. Initiated in 1967, few previous works, especially in the UK, had taken such a methodological approach to collecting data with random sampling and a focus on common species. The survey was not perfect; it focussed on a single region of the UK and even within that, my own experiences of revisiting sites (Stevens et al., 2016) suggested that the authors may have been reluctant to stray too far from bus services or too far up hills, but the value and impact of the data have been undeniable. In this survey, labelled 'survey I' by Grime, Hodgson, et al. (1988), the approach taken is referred to as a comparative autecological approach. Grime and Lloyd (1973) provide individual species accounts that give detailed accounts of pH preference, substratum, slope, aspect, data that were not widely available at the time and remain useful to plant ecologists today. Two years later, survey II built upon Survey I with 2748 quadrats covering a much wider range of habitats and a more targeted survey approach. There is a great value in spending time collecting data in the field through extensive surveys and while not unique to Grime, his work demonstrates the value such large datasets can bring. Furthermore, spending so much time in the field examining the same species in different locations and circumstance provides a great way to learn about plants and their variation, as well as the time to consider their generalities and drivers. Such an approach to plant ecology raises many questions and provides the material to address them, something which Grime capitalized on very effectively.

The data from these surveys led Grime to formulate the CSR model (Grime, 1974). The CSR model classified plants on three axes based on their tolerance of stress and disturbance. When high stress, high disturbance exists, the habitat was considered uninhabitable for plants leaving three habitats. In a low stress and low disturbance habitat, we find the competitors, in high stress, low disturbance habitat we find the stress-tolerators and in low stress, high disturbance environments we find the ruderals. CSR theory has been criticized for a number of reasons including criticism of the functional trade-off approach (Grubb, 1985), that stresses and disturbances are perceived differently by different species (Grubb, 1985; Steneck & Dethier, 1995) and that plant survival may depend on alternative mechanisms (Tilman, 1988). Criticisms are summarized in Wilson and Lee (2000). While there is no doubt that the CSR model is a simplification and some aspects of how plants interact in communities may be missed, plant communities are complex and simplification is sometimes a necessity if we are to gain understanding. CSR theory remains a useful tool in assessing how plant communities have responded to global change and management and it is still widely applied in plant ecology and beyond. A quick search of Web of Knowledge reveals over 80 papers using CSR theory in the last 10 years (2012–2021, search terms 'CSR and Grime' and 'competitor, stress tolerator and ruderal' with and duplicates removed) addressing a range of topics including invasive species, habitat restoration and bacterial communities. In my own research, I have used CSR scores combined with Ellenberg values to indicate that in acidic grasslands acidification from atmospheric nitrogen deposition may be more important to changes in species composition than eutrophication (Stevens et al., 2010). CSR theory has also been applied all over the world and recent work has aimed to make CSR scores easier to calculate using readily available trait data (Pierce et al., 2016).

Throughout his career Grime sought to explain what he saw in the field through generalities. This is not necessarily an approach that Grime and I were in agreement with, and debate around his theories and models is likely to rage for years to come, but this is how science advances. I believe that CSR theory will remain useful but whether his ideas survive the test of time or not, there is no doubt that his research has contributed significantly to advancing the field of plant ecology.

14 | DAVID WARDLE: MOVING THE FIELD OF ECOLOGY FORWARD WITH NEW WAYS OF THINKING

Grime's contribution to the field of plant community ecology, spanning over six decades, has firmly cemented him as a true pioneer in this area. Before Grime's contributions in the 1970s, plant ecology was dominated by a classical population biology perspective driven by Prof. John Harper, which was focused heavily on studying plants in terms of their demographics. Grime's contribution helped to alter this, with quite some resistance from the establishment at the time, through spearheading a comparative approach to plant ecology

which aimed to shift the focus of plant ecology to understanding differences between plant species, for example in terms of their strategies, their interactions with their herbivores, soil biota and each other, as well as their impacts on ecosystem functioning. His CSR triangular strategy theory has probably gotten the most airtime (indeed it was my first exposure to his work, as a second-year undergraduate student in 1983), but his contribution is much broader than that. As such, many currently trendy or very active topics in ecology owe their origin in a large part to his work—including the whole field of plant functional traits, the leaf economics spectrum, plant-soil feedbacks, how plant species affect ecosystem functioning, the relationship of plant diversity with productivity and disturbance, and much more. For example, Grime deserves the credit for proposing the first conceptual model of the 'intermediate disturbance hypothesis' (Grime, 1973); Connell's and Huston's more sophisticated versions of this hypothesis did not appear until a few years later. I know it was a source of some amusement to Grime that his priority over others in proposing this model seem to somehow be frequently overlooked, especially on the other side of the Atlantic.

There are two areas in particular that Grime helped pioneer which intersect with some of my own research interests. The first involves my own core area of linking above-ground and below-ground processes. Specifically, his work was among the first to recognize that communities of soil biota (notably mycorrhizal fungi) drive plant community properties (Grime et al., 1987), as well as that certain plant functional traits may be able to serve as drivers of ecosystem functioning. This includes revealing that similar traits are able to drive both above-ground and below-ground ecosystem processes (Grime, 2002); for example plant species that produce the most palatable foliage for herbivores also produce the fastest decomposing plant litter (Grime et al., 1996). His early work on this topic helped underpin my own subsequent thinking and work in this area (e.g. Wardle, 2002; Wardle et al., 2004), as well as a now widely recognized line of thinking that the linkages between above-ground and below-ground elements of ecosystem functioning are reinforced by functional traits of the whole plant community because these traits simultaneously underpin ecosystem processes driven by both the producer and consumer subsystems.

The second involves the diversity-function debate and the mass ratio hypothesis. Since the mid-1990s there has been considerable effort, vigorously driven and supported by several 'establishment' ecologists, to demonstrate that plant species richness is one of the main drivers of ecosystem functioning. Grime took a different view and one that I have consistently shared (meaning that we, along with Michael Huston, unwittingly ended up together and on the same side of a somewhat polarizing debate in the late 1990s), which is that while species richness may indeed play a role in driving ecosystems, the effects of richness are inconsistent and often not large and are frequently overridden by other drivers, and that the importance of species richness as a major ecosystem driver was being heavily over-sold (Grime, 1997; Huston et al., 2000; Wardle et al., 2000). Grime's biggest and longest lasting scientific contribution to this debate was his 'mass ratio' hypothesis (Grime, 1998), proposing that ecosystems

should be driven primarily by the traits of the dominant species, and which provides a convincing and plausible reasoning as to why plant community composition rather than species richness may be a powerful driver of ecosystem functioning.

Grime's ideas were often controversial and he defended them fiercely, but despite unrelenting and sometimes vocal attempts by several well-known ecologists to disprove them, his most important theories (e.g. CSR strategy theory, the humped-back relationship between diversity and productivity, whether plants compete less in stressed environments, the intermediate disturbance hypothesis, the mass ratio hypothesis and the relative role of plant composition versus diversity in driving ecosystem functioning) have still never actually been unequivocally disproven even decades later. Even if I did not share his views on every issue, I am firmly of the view that plant community ecology is a whole lot more interesting because of him, and the fact that ideas that he proposed around 50 years ago continue to be debated in the literature are testament to his enduring legacy in plant ecology.

15 | MARK WESTOBY: FROM LOCAL TO GLOBAL ECOLOGICAL GENERALIZATION USING TRAITS

From 1960s through 1990s, three poles of plant ecology coexisted in UK. Plant demography was led by John Harper. Harper's overview papers and keynote addresses were very influential, as was the magisterial 1977 book. The research was characterized by descriptive field demography for related sets of herbaceous species. Also by elegant manipulative experiments, for example creating different microsites to study their influence on seedling establishment.

A second pole was a continuation of older field-botany traditions where the ideal plant ecologist could identify and comment knowledgeably on any plant anywhere. To the extent this tradition had an identifiable leader it would be Peter Grubb. The tone was captured by phrases from titles of two of Grubb's papers: 'problems of generalization' (Grubb, 1985) and 'positive distrust in simplicity' (Grubb, 1992). The third pole was Phil Grime and the Sheffield Unit of Comparative Plant Ecology. Their CSR triangle aimed to summarize ecological strategy differences across species. The two dimensions underpinning the triangle were not controversial. Everyone can agree that growth potential of the site and disturbance regime are important influences on plants. But the words competitor and stress applied to extremes of the triangle have loose common-English meanings, as well as being widely used in other scientific contexts. There was always going to be scope for argument about what exactly they meant within the CSR scheme. CSR was a conceptual scheme, but it was implemented in detail for Sheffield-region vegetation, and backed by the Integrated Screening Program for trait data.

These alternative research styles seemed to be in competition at the time. Looking back, it is clear they should be complementary. Detailed knowledge about particular species and vegetation types

will always be an essential component of ecology. Demography is at first glance attractive. Success or failure of a population is demographic. But it is not plausible to quantify demography across all the world's species. And demography is not really a species trait, rather an outcome from traits in particular years and sites. Demographic data do not by themselves help us to understand why a species with particular traits is successful in some settings and not in others. Whereas a trait-based framework to summarize the diversity of ecological lifestyles does offer the prospect of understanding species worldwide.

While the CSR framework did invoke species traits, it became evident during the 1990s that there was no actual algorithm leading from trait measurements to a quantified position along CSR dimensions. In this context, the suggestion arose to use traits directly as strategy dimensions (Westoby, 1998), opening up the potential for comparing strategies quantitatively across different continents and biomes. In this way 'trait ecology' emerged both from CSR and also from the limitations of CSR.

Using traits directly as strategy dimensions has been a roaring success in some respects. Over the past 20 years there has been a spate of trait papers with authors from several continents and with 'global' or 'worldwide' in the title. From piecing together 3–4 studies and a few hundred species in the 1990s, we have moved to tens of thousands of species, via collaborative databasing initiatives like TRY and BIEN. Nevertheless, trait ecology so far has had limited success with the question of what configurations or mixtures of traits can come together in assemblages. The limiting-similarity expectation that species will be overdispersed in trait space is not right. Many people are working on the question how traits translate into competitive exclusion or coexistence but strong predictive power has yet to appear.

I think Grime's influence will be long-lasting. Especially important was his sustained advocacy for ecological strategy schemes as a pathway toward interpreting the world's ecosystems short of detailed study for every species. Or to put that more broadly, for the importance of finding ways to generalize.

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The authors declare no conflicts of interest. Jason Fridley and Xiaojuan Liu are on the Editorial Board of *Journal of Ecology* but took no part in the peer review and decision-making processes for this paper.

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This work does not include data.

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