

Plant growth and defense

In their review of the growth–differentiation balance hypothesis (GDBH), Lerdau *et al.*¹ misrepresent the general model of plant defense outlined in our review². They fault the model as a 'source-driven GDBH model' which 'predicts allocation of carbon to terpenes based on resources' rather than a 'demand-side model', which 'stresses how allocation varies in response to phenological or herbivory demands'.

This is not the case. In fact, our model is very highly 'demand-side', with explicit emphasis on the adaptive evolution of phenotypic plasticity in, and interspecific patterns of, growth and secondary metabolism. Herbivores create the demand for defense, and competitors create the demand for growth.

Lerdau *et al.* failed to distinguish between the original concept of growth–differentiation balance proposed by Loomis³ and our integration of these constraints with optimal defense theory. Loomis predicts trade-offs between growth and secondary metabolism because (1) ontogenetic constraints limit secondary metabolism in developing cells, and (2) resource demands of growth limit secondary metabolism at the whole-plant level.

While the success of a particular resource allocation strategy is environmentally dependent, our model assumes explicitly that 'the importance of herbivory can vary within an environment independently of resource

availability'. There are no inherent constraints that limit secondary metabolism in resource-rich environments as there are on growth in resource-limited environments. But many studies show plants to increase their growth in response to resource enrichment. We argue this to be adaptive, the result of strong demand for growth created by competitors that would otherwise usurp the plant's resources. It is only because plants grow that secondary metabolism is constrained. Chemical defense diverts resources from growth, thus any benefit derived from increased secondary metabolism must exceed this opportunity cost. Induced resistance is a defensive adaptation with a particularly high benefit:cost ratio. We review the (scant) evidence that GDB constraints apply to induced, as well as constitutive, secondary metabolism.

Lerdau *et al.* argue that analysis of seasonal patterns of growth and secondary metabolism within an individual is ideal for testing the GDBH, and the frequent observation that expanding leaves have both the highest growth rates and the highest concentrations of secondary metabolites is inconsistent with the GDBH. We disagree. Secondary metabolism by mature cells within immature leaves is not inconsistent with constraints on secondary metabolism in immature cells. We review some of the developmental 'tricks' plants use to overcome this constraint.

Furthermore, such phenological correlations ignore the opportunity cost of secondary metabolism resulting from resource trade-offs at the whole-plant level. While high concentrations

of secondary metabolites in small immature leaves do not represent large investments based on the total carbon pool driving canopy expansion, even small annual diversions from canopy expansion may yield substantial compounding losses over the life of the plant⁴. When comparing genotypes differing only in the secondary metabolite concentrations of their expanding foliage, the GDBH predicts that the genotype with the lowest concentration will grow faster.

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Editor's Note

A reply from Lerdau *et al.* will appear in the next issue.

Taxonomic minimalism

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Biological surveys are in increasing demand while taxonomic resources continue to decline. How much formal taxonomy is required to get the job done? The answer depends on the kind of job but it is possible that taxonomic minimalism, especially (1) the use of higher taxonomic ranks, (2) the use of morphospecies rather than species (as identified by Latin binomials), and (3) the involvement of taxonomic specialists only for training and verification, may offer advantages for biodiversity assessment, environmental monitoring and ecological research. As such, formal taxonomy remains central to the process of biological inventory and survey but resources may be allocated more efficiently. For example, if formal identification is not required, resources may be concentrated on replication and increasing sample sizes. Taxonomic minimalism may also facilitate the inclusion in these activities of important but neglected groups, especially among the invertebrates, and perhaps even microorganisms.

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It is widely believed that biological surveys require the identification of species by means of Latin binomials. We explore this belief in the light of a series of emerging methodologies that we call collectively 'taxonomic minimalism'. This is the use of taxonomic ranks other than species for application to environmental

monitoring, conservation evaluation and ecological research. A related discipline, parataxonomy, trains technicians to collect and prepare specimens for formal taxonomic treatment. Taxonomic minimalism differs from this approach because it accepts that such formal treatment may never be complete or even possible and

seeks taxonomic alternatives for a variety of research and monitoring activities.

At least two kinds of taxonomic minimalism are used (most frequently with invertebrates). The first is common in environmental monitoring and impact studies and is thoughtfully reviewed by Cranston¹. Taxa that respond in predictable ways to changes in environmental variables can be accurately monitored at the level of genus, family, order or even phylum. A great variety of invertebrates has been used for this purpose^{2–5}. Frequently the taxonomic rank employed is the genus, and species are given numbers⁶, but it is often the case that the members of entire families or orders behave in a similar and predictable manner which greatly simplifies the taxonomic effort^{2,7}. The rank used has been referred to as the 'taxonomic penetration' or 'taxonomic resolution' required^{1,8,9}.

A second kind of taxonomic minimalism is the use of morphospecies which are also known as Operational Taxonomic Units (OTUs) or Recognizable Taxonomic Units (RTUs)^{1,10}. Species are formally identified by Latin binomials, which are subject to international conventions on nomenclature. By contrast, morphospecies are assigned according to easily observable morphological criteria that are required to distinguish between the specimens in question with

little or no reference to established classifications^{11,12}. The criteria for distinguishing between species are global but those for distinguishing between morphospecies are local or regional. Once the global requirement is abandoned, morphospecies that occur within a locality or region are often relatively simple to distinguish one from another.

The identification of morphospecies involves exactly the same methods as alpha taxonomy. It differs in that it requires only the data to hand and is more or less independent of existing Latin binomials, their associated hierarchies and phylogenetic trees. Difficult characters are often not required for the separation of specimens from local collections. In addition, at the local or regional scale, the sorting process often reveals many alternative character states (polychotomies) that quickly separate specimens into operational groupings. Dichotomies are generally slower and less useful. In this way, alpha taxonomy of morphospecies generates local, operational polychotomies (LOPs). The development of interactive computer keys that use LOPs will accelerate the process of identification to morphospecies.

Morphospecies can be used as surrogates for species in data analysis provided the correspondence between morphospecies and species is approximately one to one and that each morphospecies is unique. Correspondence is established by trials in which non-specialists and specialists sort the same samples. For example, it has been shown that the correspondence between species and morphospecies can be high in ants and spiders, but low in marine polychaetes and mosses¹³. In aquatic systems there may be good correspondence for Ephemeroptera (mayflies) but not for Odonata (dragonflies) or Chironomidae (non-biting midges)¹⁴. Uniqueness is an essential criterion for any kind of alpha taxonomy. In conventional taxonomy, species previously identified are described in the literature and specimens deposited in museums or herbaria. It is equally important that morphospecies have voucher specimens carefully labelled and stored by standardized methods¹⁴.

Taxonomic minimalism requires a partnership between specialists and non-specialists. It is an uneven partnership because specialists can function without non-specialists but not *vice versa*. However, most specialists face immense workloads and vast backlogs of specimens. If specialist focus is on the training of technical staff and the verification of morphospecies (see Box 1) then taxonomic minimalism may ease the burgeoning demands on taxonomists for in-

Box 1. A taxonomic partnership

The benefits of collaboration between specialists and non-specialists are illustrated by our recent Environmental Impact Assessment (EIA) of different forest management strategies on litter invertebrates. In this study, non-specialists sorted 29 463 specimens into 431 beetle morphospecies, 144 ant morphospecies and 146 spider morphospecies. Although not required for the bulk of the sorting, professional taxonomists were crucial for training and verification of morphospecies.

Training lasted half a day with each of three professional taxonomists. It identified the most useful characters and the most obvious sources of error such as sexual and developmental polymorphism. As a result, sorting was accurate to five percent for ants and several spider and beetle families. A paper presenting the details of this process is still in preparation but the practical problems encountered in this kind of work are outlined elsewhere¹⁵.

Sorting of specimens yielded two smaller collections for specialist verification, first, the voucher specimens and second, sub-samples consisting of random samples of specimens of each morphospecies. These collections represented a major reduction in the number of specimens to be examined. They guarded against two sources of error. The first was splitting, in which more than one morphospecies was assigned to a species. The second was lumping, in which a morphospecies contained more than one species. In this way the specialists determined how many species were, in fact, present. Monitoring of subsamples by specialists can lead to very close correspondence between morphospecies and species¹⁵. The time spent by the specialists on the collections was relatively short as Latin binomials were not required.

An important function of the subsamples was the detection of species turnover both in time and space. Specialists were able to distinguish specimens that differed from voucher specimens, sometimes in subtle ways. However, as our expertise developed, subsampling was confined to the most difficult groups and the necessity for specialist examination of vouchers and subsamples diminished.

Analyses of the data have shown that estimates of the species richness of ants, beetles and spiders in different types of forest were consistent regardless of whether morphospecies or species were used. Further, numerical classifications of forest types using Semi-strong Hybrid Multidimensional Scaling (SSHMS) and Analysis of Similarity (ANOSIM) on the two kinds of inventory were not significantly different (I. Oliver and A.J. Beattie, unpublished).

ventory work and so also promote the fundamental goals of systematics¹⁵.

Applications

One crucial advantage provided by taxonomic minimalism is that it facilitates the allocation of resources to replication rather than identification. Environmental monitoring, impact assessment, conservation evaluation, biodiversity assessment and the testing of ecological theory germane to these activities generally suffer from insufficient sampling both in time and in space. This is often because funds are in short supply and there is a trade-off between paying for taxonomic services and paying for additional samples.

Environmental impact assessment and environmental monitoring

Taxonomic minimalism is widely used for these purposes often because the trade-off between identification and replication can be manipulated according to need. Impacts or changes may be detected only by extensive sampling in space and time and the precise identity of species is often unnecessary¹⁶. For the same reason it is likely to be widely employed in the testing and implementation of new sampling designs and statistical procedures including the new generation of multivariate analytical methods being developed for environmental impact studies^{17,18}. The quantification of the effects of disturbance is a research priority identified by the Ecological Society of America¹⁹ and the identification of indicator taxa and test systems may be greatly facilitated by the increased

sample size, replication and statistical power that taxonomic minimalism can provide.

Most monitoring involves selected vertebrates and angiosperms. Such inventories fall short of newer requirements, many legislated, for monitoring biodiversity in more representative ways, for example, by the inclusion of selected invertebrate groups. It is now recognized that invertebrate monitoring is crucial but taxonomic resources are often in short supply or simply not available. In circumstances such as these, various forms of taxonomic minimalism are the only options. Projects as diverse as monitoring forest management strategies, the effects of pollutants from factory outfalls and the restoration of mine sites are increasingly dependent upon LOPs.

Conservation planning and management

In reserve selection procedures, most conventional inventories cover selected vertebrates and angiosperms. Individual cases are likely to be strengthened by extending sampling to important invertebrate groups²⁰. In addition, recent evidence that reserves selected for their contribution to vertebrate or angiosperm diversity do not make equal contributions to the conservation of invertebrate diversity^{20,21} suggests that assessment of invertebrate groups using the methods outlined here will be of increasing importance.

The effects of conservation management strategies and habitat fragmentation can be evaluated by broadscale sampling of invertebrates using taxonomic

minimalism^{6,22}. The same procedures and criteria may also measure (morpho)species richness and detect (morpho)species turnover in space and time. The determination of rarity and endemism among many invertebrate groups is extremely difficult but morphospecies may be of use. Rare morphospecies are simple to detect and may be sent to the specialist for formal identification. Subsequent monitoring will use the Latin binomial. Possible endemic morphospecies may be treated in the same way. Alternatively, provided the criterion of uniqueness for morphospecies holds, it is feasible to determine the geographic range of a suspected endemic by comparison across local and regional collections of voucher specimens. The discovery of possible rare or endemic morphospecies may help focus taxonomic effort on the most critical specimens.

Community and conservation ecology

The meaning and usefulness of some basic community concepts such as diversity indices, species-abundance curves and island biogeography have been questioned^{23,24}. In some cases insufficient data sets appear to have been the problem, where the trade-off between replication and identification has favoured the latter²⁵. This may be avoided by reducing taxonomic input. In this context, hypotheses used in conservation biology can be more rigorously tested. For example, the 'umbrella hypothesis' asserts that by conserving a particular species (often a charismatic megavertebrate) most other species in the habitat will also be conserved. There is disconcerting evidence that this may not be the case²⁶. The 'biodiversity indicator' hypothesis which asserts that the measurement of the diversity of one group explains the diversity of others is also suspect and should be tested. In both of these cases, taxonomic minimalism will facilitate the use of the large sampling programs and data sets that are required. Research into the possible value of ecological indicators is also a major priority for the Ecological Society of America¹⁹ and studies probing the use of invertebrates rather than vertebrate or angiosperm taxa as selective indicators show some promise²⁶.

Geographic Information Systems and ground-truthing

Geographic Information Systems are powerful tools for the identification of potential conservation reserves and the development of conservation strategies. However, output is usually a pattern of vegetation types which means that decisions are made based on the subset of

flowering plants to which the satellites respond. As this is a small proportion of overall biodiversity in any location, the diversity of vertebrates, invertebrates and other kinds of plants should be determined by sampling programs on the ground (ground-truthing)²⁷. Thus, for example, when there is a choice of areas for the conservation of endangered species, broadscale sampling of other organisms using taxonomic minimalism, facilitates the ranking of those areas for their contributions to the conservation of total biodiversity.

Future technologies

The use of computers in the processes described here is greatly enhancing their efficiency. Details of voucher specimens can be entered on a database and information on individual morphospecies and their distinguishing characters located by means of bar codes²⁸. Machine-readable bar code labels may form the basis of regional or even national databases of morphospecies. In the event of major increases in funding for taxonomy, these may become vital resources for the future.

Identification of organisms, such as selected invertebrate groups, can be greatly facilitated by image-based software packages²⁹ and software developed for conventional taxonomic work could be adapted for the procedures described here³⁰. It will be important to integrate regional voucher specimen databases with those in museums, herbaria and other taxonomic institutions.

Understanding the diversity of micro-organisms is a major problem, not least because the species concept is generally inapplicable to them. Some aspects of taxonomic minimalism are useful in this situation, for example, characters revealed by flow cytometry, especially in combination with nucleic acid or antibody technology, have considerable potential for evaluating microbial diversity by means of phenetic clustering techniques^{31,32}. Physiological, molecular and biochemical characters can be used to generate operational microbial taxa.

The majority of biodiversity comprises micro-size organisms whether they are bacteria, fungi, tiny plants or tiny animals. Although they are ubiquitous, abundant and vital to ecosystem processes, they are often ignored because of taxonomic difficulties. Taxonomic minimalism may facilitate research into these groups and so include them in the frontline of conservation efforts.

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