

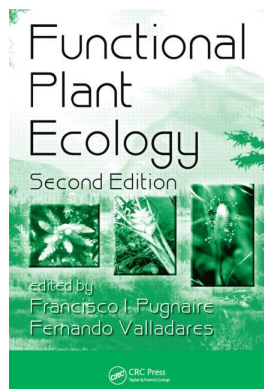
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Francisco I. Pugnaire, Fernando Valladares

Generalization in Functional Plant Ecology: The Species-Sampling Problem, Plant Ecology Strategy Schemes, and Phylogeny

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Mark Westoby

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23 Generalization in Functional Plant Ecology: The Species-Sampling Problem, Plant Ecology Strategy Schemes, and Phylogeny*

Mark Westoby

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INTRODUCTION

This chapter is about how we generalize across species, and how we choose species for study.

If a process is universal, it should not matter in which species we study it. An expectation that the processes under study should be universal is implicit in much physiological or developmental genetic work. Correspondingly a single species is studied, chosen for experimental convenience, perhaps tobacco, or *Arabidopsis*. In functional ecology, on the other hand, most generalizations are conditional and comparative. Functional ecology aims to work out how things operate differently in pioneer versus shade-tolerant species, on low-nutrient versus high-nutrient soils, among monocots versus dicots, in rare compared with widespread species.

Functional ecology makes progress through the struggle to generalize, to understand what is similar and what is different about species and situations. Progress is manifested at two levels in publication. In primary journal publications reporting fresh data, comparisons may be between as few as two species, up to tens of species, depending which traits were

*This chapter has not been updated since the first edition of the Handbook.

studied and how difficult and time-consuming it was to characterize them. However, later on, in literature reviews or meta-analyses, numbers of such primary studies are gathered together and generalizations are sought. It is really at the stage of compiling literature reviews that knowledge can be said to become consolidated and reliable. At this stage evidence may be available about tens to hundreds of species (e.g., edited review books about ecophysiology such as Lange et al 1984, Lambers et al 1989, Roy and Garnier 1994, Schulze and Caldwell 1994, Mulkey et al 1996). Similarly many hundreds of field experiments have now been conducted on the major interactions between species such as competition, herbivory, and predation (Connell 1983, Crawley 1983, Schoener 1983, Sih et al 1985, Price et al 1986, Hairston 1989, Goldberg and Barton 1992, Gurevitch et al 1992, Wilson and Agnew 1992, Goldberg 1996). Generalizing across the many primary studies has now become an outstanding problem for ecology.

This chapter argues in the following sequence. First, the reader is briefly reminded of the rules for inferring generalizations from samples. These rules are familiar to ecologists in contexts such as vegetation sampling, but curiously, they have been almost completely ignored in the context of selecting species for study. Some problems in applying the generalization rules to species selection are acknowledged, and the distinction between papers reporting primary data collection and subsequent review and meta-analysis papers becomes important here. Then to arrive at a conditional generalization, species have to be categorized in some way. The three main types of categorization are habitat, ecological strategy (traits of the species itself), and phylogeny. For primary data collection, anyone could use their own basis for categorizing species, but during subsequent meta-analyses, only widely-adopted categorization schemes can come into play. Hence, achieving consensus on at least some categorization schemes should be an important part of the research agenda of comparative functional ecology. A new ecological strategy scheme is proposed for this purpose. Finally phylogeny: species with recent common ancestors are more likely to have similar traits. A brief outline is provided of the recent debate about whether phylogeny should be regarded as an alternative explanation to present-day functionality. More constructively, phylogeny provides a potential tool for choosing study species to arrive more efficiently at generalizations, and to place better-defined boundaries around the generalizations.

INFERENCE RULES FOR GENERALIZING FROM A SAMPLE

The rules for inferring a generalization from a sample have been well appreciated by ecologists for many years, in the context for example of describing vegetation by means of quadrat sampling. The rules are

- Quadrats are placed at random, in other words each possible location within some category should have an equal chance of being sampled.
- Accordingly, the scope and boundaries of the category itself need to be defined. Is it a particular patch of forest that is described, or is it all patches of that forest-type within a continent? As well as conceptual decisions about the scope of the category, there usually need to be some exclusion rules—perhaps sites are not sampled on cliffs because of the practical inconvenience, or in the middle of forest tracks because these are not thought interesting.
- There needs to be some replication of the samples, to give a sense of the range of variation. I will not digress to discuss different indices of the range of variation; biometry texts provide recipes for calculating these and discuss their merits and assumptions. The point is only that all recipes require replication, because the logic by which we generalize about a category requires some indication of the range of variation within the category.

These rules come into play during the design of a sampling procedure. Generalization rules forge the link between the sampling procedure and the scope of the generalizations that can subsequently be inferred. The design of the study is shaped by contemplating what conclusions one might be seeking to draw. The decision what category to sample, together with the exclusion rules, draws boundaries on the conclusions that can be drawn. The legitimacy of the conclusions depends on the equal-chance-of-being-sampled principle, and the replication allows the strength of the conclusions to be assessed.

APPLICATION OF THE INFERENCE RULES TO GENERALIZATION ACROSS SPECIES—AN ISSUE THAT HAS BEEN UNDERESTIMATED

In contexts such as vegetation sampling and manipulative field experiments, the inference rules have been thoroughly assimilated into the practices of ecological researchers. All the more remarkable, then, that choice of species to study still seems not to be perceived as a sampling problem where the rules for generalization need to be applied. Some researchers may quite legitimately argue that they have chosen particular species because they are interested just in them, they have no interest in generalizing. Alternatively they may believe the mechanism they are studying is universal, so it does not matter in which species they study it. However, many studies of the functional ecology or ecophysiology of plants seek to interpret their results by references to categories of plants—shade-tolerant versus pioneer, low versus high altitude, annual versus perennial, inhabitants of low-nutrient versus more fertile soils, rare and endangered versus widespread, and constitutively slow-growing versus capable of rapid growth—in other words, the species are to be interpreted as samples from some category. Nevertheless, these studies rarely address explicitly the representativeness and replication criteria. If the inference rules were followed, the methodology of these papers would first define categories of species—listing all the low-nutrient species in NSW, for example—then indicate exclusion rules that had to be applied—for example, only species available from seed merchants could be considered, and among those, some had to be eliminated because they could not be persuaded to germinate in reasonable numbers within a few days of each other—and then within those boundaries, would confirm that the species studied were chosen at random. However, in reality, most papers in comparative ecophysiology hardly comment at all on the choice of species, and it is quite common for two categories to be compared by means of two species, with no replication. Imagine if a manuscript were submitted in which two vegetation types were compared by means of one quadrat in each, placed at the location the investigator thought most representative or convenient?—it would get short shrift from referees and editors. However, many papers that have been successfully published and are respectfully cited in comparative ecophysiology do exactly this with regard to choice of species.

How have these differences in research culture, in expectations about sampling, come about? Probably one factor has been the physiologist's expectation that truly interesting processes occur reliably in whatever species is studied. Surely the other main factor must have been the sheer difficulty and laboriousness of some types of measurement. Remember also that for an investigator seeking to dissect mechanisms, there are always strong incentives to measure more processes and at more frequent intervals within one species, rather than to extend to further species. Consider investigations of complete carbon budgets for example, including dissecting root respiration into growth and maintenance components. Within the framework of a Ph.D., it is unreasonable to expect more than a couple of species to be studied. Then since there are too few species for replication within categories, it must seem unimportant to apply the equal-chance rule within each category. There are also strong reasons to use species where seeds are available and are known to germinate readily,

which can lead to a few species used repeatedly by successive investigators. So in summary, the tradition of using few species and those not chosen according to explicit rules of sampling is entirely understandable, within ecophysiology and indeed in other areas such as genetics and demography of rare species.

Nevertheless, subsequent literature review or meta-analysis has to face the issue: is species coverage in the primary research reports representative, and of what categories? As more and more primary research reports accumulate, this issue is becoming more pressing. One way of defining the problem in species selection is to say that species should be selected to make better generalizations possible to the person who comes along 5–10 years after and writes the literature review.

How might this come about? At one extreme could be imagined a grand overall species-selection design, decided by a well-meaning dictator or committee. Each lab worldwide would be then instructed which species to select. I feel confident this is not going to happen (and indeed should not be allowed to, because the slackening of competitive energy would surely outweigh the benefits of coordination). At the other extreme, and far more likely, is that primary research publications move toward discussing their species selection explicitly, in relation to the inference rules. Explicit discussion could be very valuable. Even when there can be little replication, and when many exclusion rules have been required so that there is only a small choice of species, compilers of literature reviews will nevertheless be better placed if the primary studies have spelled out their species-selection criteria explicitly. Related to explicit discussion, authors should be encouraged to make available as much background information as possible about their species. By background, I mean information that is not referred to in the paper for the purpose of proving a conclusion, but that might subsequently be useful to reviewers or meta-analysts seeking to investigate different questions. The limited page-space in journals need no longer discourage authors and editors from reporting background information about traits and habitats of the study species, since such material can now be placed at websites.

CRITERIA ON WHICH TO COMPARE SPECIES

If species-sampling is one side of a coin, the other side is categories into which species are grouped for comparison. Criteria on which species might be compared fall under three main headings:

- Habitat
- Attributes of the species themselves—ecological strategies
- Phylogeny (or in practice, usually taxonomy)

The distinction between primary research reports and reviews or meta-analyses is important here also. Individual research groups can and do categorize species according to whatever criteria they think meaningful for the question in hand. However, at the stage when knowledge is consolidated across many primary reports, the reviewer can use only categories that were adopted in common by all the primary reports, or alternatively that are simple enough for species to be attributed to them by the reviewer. As a consequence, most reviews group species into rather simple categories: herbaceous versus woody, deciduous versus evergreen, temperate versus tropical and so forth. For categories to be used at review that captured a subtler degree of difference between species, consensus on the categorization scheme would need to be achieved in advance. Developing wider consensus on more expressive categorization schemes is thus a major priority for improved generalization in functional ecology.

HABITAT

I will comment only very briefly on habitat descriptors. Rainfall and temperature are not, nowadays, too much of a problem to attribute to plant species. Maps or climate-interpolating software can produce estimates of yearly means or various seasonal patterns or extremes, for a given location where a species is known to occur. Shading under canopies used often to be described in qualitative categories, but measurements on an absolute scale of PAR have become more typical over the last couple of decades, and have been important in clarifying seedling performance in the shade.

Soil nutrients remain an unresolved problem. Many papers have compared species from infertile versus fertile soils, within particular landscapes. However, synthesis across these papers is very difficult because they do not share common measurements that describe soil fertility of the sites where the species is successful. There is some reason to believe that relatively fertile soils in Australia might fall into an infertile category in northwest Europe, for instance, and this complicates any attempt to relate Australian to European studies. Certainly there are many complexities in measuring soil fertility, but still, it would be a step forward if even one or two lowest-common-denominator measures could be agreed.

TRAITS OF THE SPECIES THEMSELVES—ECOLOGICAL STRATEGY SCHEMES

The literature on plant ecological strategy schemes can be summarized into three main strands of thinking. One strand categorizes species by reference to distribution (realized niche) on one or more gradients, for example, Dyksterhuis (1949) for grazing, Noble and Slatyer (1980) for time after disturbance, Ellenberg (1988) for soil and other habitat features. A second strand categorizes species according to physiognomy (e.g., Raunkiaer 1934, Dansereau 1951, Mueller-Dombois and Ellenberg 1974, Box 1981, Sarmiento and Monasterio 1983, Barkman 1988, Orshan 1989, Prentice et al 1992) and has been active especially within plant geography. In a third strand axes or categories are named according to concepts (as distinct from naming them according to traits or realized niche). Examples include the *r-K* spectrum (Cody 1966, MacArthur and Wilson 1967) and several schemes that have developed this spectrum into a three-cornered arrangement (Greenslade 1972, 1983, Grime 1974, Whittaker 1975, Southwood 1977). The three-cornered schemes add a category of opportunities where the physical environment permits only slow acquisition of resources. This situation is called stress in Grime's CSR triangle (1974, 1979, Grime et al 1988), the best developed three-cornered scheme for plants. The CSR triangle has two dimensions, the *C-S* axis reflecting adaptation to opportunities for rapid growth versus continuing enforcement of slow growth (Competitors to Stress-tolerators), the *R*-axis reflecting adaptation to disturbance (Ruderals).

Among conceptual strategy schemes the CSR triangle is the most widely cited in textbooks (e.g., Cockburn 1991, Colinvaux 1993, Begon et al 1996, Crawley 1996, Ingrouille 1992), reflecting wide acceptance that exploiting opportunities for fast versus slow growth, and coping with disturbance, are two of the most important forces shaping the ecologies of plants within landscapes. Yet papers in functional ecology do not routinely report CSR axis scores for the species studied, for the reason that there is no explicit quantitative protocol for scoring a species from anywhere worldwide (see qualitative and partly subjective keys in Grime 1984, Grime et al 1988). In other words, the CSR scheme is widely cited for conceptual discussion but not widely adopted for practical comparisons. The only general-purpose scheme that has been widely adopted is Raunkiaer's life-form categorization (1907, English translation 1934), based on the location of the buds where regrowth arises after the unfavorable season of the year. Raunkiaer life-forms are very easily attributed for most

species (that is why the scheme is widely adopted), but the scheme conveys only a modest amount of information about differences between species.

In summary, then, those existing schemes that can easily be applied worldwide capture very few of the differences between species, especially with regard to how they exploit different opportunities within multispecies vegetation and between different sites in a landscape. On the other hand, schemes that seek to be more expressive about these differences between species are not so designed that species anywhere can readily be categorized. Consequently schemes such as the CSR triangle have not been able to be used to group species worldwide during literature reviews or meta-analyses. In this context, I have recently (Westoby 1998) proposed a new LHS (leaf-height-seed) scheme (Box 23.1) designed to express at least some of the differences between species addressed by the CSR triangle and related schemes, while using axes readily measured on the plant itself, and therefore offering the potential for worldwide comparison.

BOX 23.1

Proposed LHS Plant Ecology Strategy Scheme

The LHS scheme (Westoby 1998) would consist of three axes:

- Typical specific leaf area (SLA) (of mature leaves, developed in full light, or the fullest light the species naturally grows in)
- Typical height of the canopy of the species at maturity
- Typical seed mass

The strategy of a species would be characterized in the scheme by a position in a 3D volume. Each dimension is known to vary widely between species at any given level of the other two, thus the volume occupied by present-day species extends considerably in all three dimensions. Each of these traits is correlated with a number of others, but they have not been chosen only as conveniently measured indicators. Rather it is believed that they themselves are fundamental trade-offs controlling plant strategies. They are fundamental because it is ineluctable that a species cannot both deploy a large light-capturing area per gram and also build strongly reinforced leaves that may have long-lives; cannot support leaves high above the ground without incurring the expense of a tall stem; cannot produce large, heavily provisioned seeds without producing fewer of them per gram of reproductive effort.

As would be expected for traits of such ecological importance, plants have some capacity to shift trait values in response to the circumstances they find themselves in. In other words, none of SLA, height at maturity, or seed mass are absolute constants within species. Nevertheless, variation between species is much greater than within species, and many previous authors have seen no insuperable difficulty in recording characteristic species values for comparative purposes (e.g., for height at maturity Hubbell and Foster 1986, Grime et al 1988, Keddy 1989, Bugmann 1996, Chapin et al 1996). All three axes would be log-scaled, reflecting the fact that the difference between 30 and 31 m (to take canopy height at maturity as an example) is not nearly so important as the difference between 30 and 130 cm.

SPECIFIC LEAF AREA

SLA is the light-catching area deployed per unit of previously photosynthesized dry mass allocated to the purpose. SLA is like an expected rate of return on investment. High SLA permits (given favorable growth conditions) a shorter payback time on a gram of dry matter invested in a leaf (Poorter 1994). At first glance it might appear that a low rate of return on investment would not be evolutionarily competitive, but low SLA species achieve greater leaf life span (Reich et al 1992, 1997),

BOX 23.1 (continued)**Proposed LHS Plant Ecology Strategy Scheme**

through extra structural strength and sometimes through allocation to tannins, phenols, or other defensive compounds. Therefore light capture per gram invested can be at least as great in a low-SLA species when considered through the whole life of the investment. Reich et al (1997) have shown across six biomes that SLA is closely correlated with mass-based net photosynthetic capacity and mass-based leaf N as well as leaf life span. Higher leaf water content and reduced lamina depth can both contribute to higher SLA (Witkowski and Lamont 1991, Garnier and Laurent 1994, Cunningham et al 1999). Grime et al (1997) found SLA to be among the major contributors to the primary axis of specialization they identified by ordination of 67 traits among 43 species, corresponding to the *C-S* axis of the CSR scheme.

Potential relative growth rate RGR, measured on exponentially growing seedlings given plentiful water and nutrients, has been seen as an indicator of responsiveness to favorable conditions (e.g., Grime and Hunt 1975, Leps et al 1982, Loehle 1988, Poorter 1989, Reich et al 1992, Aerts and van der Peijl 1993, Chapin et al 1993, van der Werf et al 1993, Turner 1994). Because potRGR is made up of net assimilation rate \times leaf fraction \times SLA, variation in SLA necessarily influences potRGR. Indeed, in most comparative studies SLA has been the largest of the three sources of variation in potRGR (Poorter 1989, Poorter and Remkes 1990, Poorter and Lambers 1991, Lambers and Poorter 1992, Reich et al 1992, Garnier and Freijns 1994, Saverimuttu and Westoby 1996, Cornelissen et al 1996, Grime et al 1997, Hunt and Cornelissen 1997, Poorter and van der Werf 1998). High SLA species can have strategies associated with rapid production of new leaf during early life. Faster turnover of plant parts permits also a more flexible response to the spatial patchiness of light and soil resources (Grime 1994b). On the other hand, species with low SLA and long-lived leaves can eventually accumulate a much greater mass of leaf and capture a great deal of light in that way; and the long mean residence time of nutrients made possible by leaf longevity permits a progressively larger share of nitrogen pools to be sequestered (Aerts and van der Pijl 1993).

CANOPY HEIGHT AT MATURITY

Height obviously conditions how plants make a living, in different ways depending on vegetation dynamics. In some vegetation types a characteristic vertical profile of leaf area and light attenuation persists over time, through the turnover of individual plants. Species with canopies at different depths in this profile are operating at different light incomes, heat loads, wind speeds, humidities, and with different capital costs for supporting leaves and lifting water to the leaves. In other vegetation types disturbances, or the death of large individual trees, destroy canopy cover and daylight becomes available near the ground. The successional process that ensues can be understood as a race upward for the light. Because light descends from above, the leading species at a given time have a considerable advantage. In this race, unlike a standard athletic contest, there is not a single winner determined after a fixed distance. Rather any species that is among the leaders at some stage during the race is a winner, in that being among the leaders for a reasonable period permits a sufficient carbon profit to be accumulated for the species to ensure it runs also in subsequent races. The entry in subsequent races may occur via vegetative regeneration, via a stored seed bank, or via dispersal to other locations, but the prerequisite for any of these is sufficient carbon accumulation at some stage during vegetative growth. Races are restarted when a new disturbance destroys the accumulated stem height. The duration of an individual race can be measured in years, or ideally in units of biomass accumulation, calibrating intervals between disturbances to the productivity of a site. However, within a race-series with some typical race duration, one finds successful growth strategies that have been designed by natural selection to be among the leaders early in a race, and other successful strategies that join the leaders at various later stages. Species that achieve most of their lifetime photosynthesis with leaves deployed at

(continued)

BOX 23.1 (continued)**Proposed LHS Plant Ecology Strategy Scheme**

10–50 cm have different stem tissue properties from those designed for 1–5 m, and those in turn are different from species that achieve 30–40 m. The canopy height that species have been designed by natural selection to achieve is the simplest measure of this spectrum of strategies.

SEED MASS

Seed mass variation expresses a species' chance of successfully dispersing a seed into an establishment opportunity, from a given area of ground already occupied by a species. Seed mass is also quite a good indicator of a cotyledon-stage seedling's ability to survive various hazards.

Species with smaller seed mass can produce more seeds from within a given reproductive effort, and seed mass therefore is the best easy predictor of seed output per square meter of canopy cover. It might be thought that distance of dispersal would be the major influence on a species' chance of dispersing a seed to a forest gap or another establishment opportunity. However, dispersal distances have not proved tidily related to dispersal morphology, to seed mass, or to any other plant attribute (reviewed in Hughes et al 1994). Among unassisted species, larger seeds do not travel as far from a given height of release, but on the other hand larger seeds tend to have wings, arils, and so on or to be released from a greater height. Similarly among wind assisted species, larger seeds tend to have larger wings or longer pappuses. Because reduced dispersal associated with larger seed mass tends to be counteracted by extra investment in dispersal-assisting structures, or sometimes by being released from a taller plant, the net effect is that dispersal distance is not tidily related to any of these attributes. Seed mass (as a surrogate for seed output per ground area occupied) is the best predictor, for the present, of the chance that an occupied site will disperse a propagule to an establishment opportunity.

Species with larger seed mass have been shown experimentally to survive better under a variety of different seedling hazards (tabulated in Westoby et al 1996), including drought, removal of cotyledons, and dense shade below the compensation point. The tendency to survive longer applies only during cotyledon phase, whereas seed reserves are deployed into the fabric of the seedling (Saverimuttu and Westoby 1996). Capacity to continue growth into later seedling life under a low-light level is determined more by canopy architecture and leaf properties (Kitajima 1994). It seems likely that tolerance of seedling hazards is endowed not by seed mass as such, but by a tendency for larger seeds to retain more metabolic reserves uncommitted to the fabric of the seedling over a longer period, and therefore available to support respiration when in carbon deficit (Westoby et al 1996).

LHS SCHEME IN RELATION TO GRIME'S CSR TRIANGLE

Where each axis of the CSR scheme implies a complex of plant traits (e.g., Grime et al 1997), the LHS scheme has axes defined by single quantitative traits. The benefit of the LHS scheme's simple protocol for positioning a species outweighs any loss of information content in the LHS axes compared with the CSR axes, for the purpose of facilitating worldwide comparisons of species.

The CSR scheme has been made triangular rather than rectangular because the most stressful and most frequently disturbed corner is said not to be occupied (Grime et al 1988), or because ineluctable trade-offs are said to prevent a species from getting highly adapted to more than one of the three primary strategies *C*, *S*, or *R* (Grime 1994a). The idea that a whole quadrant is missing due to the combination of high stress and high disturbance has been criticized (Grubb 1985) and experiments with crossed gradients of fertility and disturbance (Campbell and Grime 1992, Burke and Grime 1996) have not produced wholly unoccupied space at the low-fertility high-disturbance corner. The LHS scheme avoids prejudging the question whether any particular corner of the LHS volume is not viable.

BOX 23.1 (continued)

Proposed LHS Plant Ecology Strategy Scheme

Another difficulty in the CSR scheme is the ruderality axis. Adaptation to disturbance might in principle include adaptations for surviving individual disturbances, together with adaptations for completing life history within a short interval between disturbances, together with adaptations for dispersing through space or time to freshly disturbed locations. Grubb (1985) criticized the CSR scheme for not distinguishing continuing from episodic disturbance. According to Grime (Grime et al 1988, Grime and Hillier 1992) the scheme is for adults not juveniles: a given adult strategy can occur in combination with several different juvenile strategies, which has the effect of separating out dispersal and seed bank strategies from the main CSR categorization of a species. The LHS scheme disentangles these disparate elements to some extent. The canopy height at maturity axis reflects adaptation to the interval between disturbances (calibrated in units of height growth rather than time). The seed mass axis (more exactly its inverse, seed number per mass allocated to seed production) reflects the potential for dispersal to freshly disturbed locations. Adaptations for continuing the lineage through particular types of disturbance (e.g., lignotubers for resprouting after fire, soil seed banks with a light requirement for germination following soil turnover, basal tillering in graminoids for grazing tolerance) have deliberately been left outside the LHS scheme, since they do not lend themselves to any simple generalization.

In summary of Box 23.1, the LHS scheme captures a substantial part of the same spectra of strategy variation as the CSR scheme, while resolving some difficulties with it. SLA variation (the L dimension) is crucial to the CS axis (Grime et al 1988, 1997), which is to leaf longevity, mean residence time of nutrients, soil nutrient adaptation, and potential RGR. Canopy height at maturity (the H dimension) is arguably the most central single trait that needs to be adjusted to the duration of the growth opportunity between disturbances (*R*-axis); it is also treated by Grime et al (1988) as a significant predictor of *C* versus *S* strategy. The LHS scheme does not prejudge what parts of the LHS volume will be occupied, compared with the CSR triangle, which decides a priori that the high-*S*-high-*R* quadrant is not a viable strategy. By separating out seed mass (*S* dimension) as a distinct axis, it expresses something about dispersal to new growth opportunities, independently of what is expressed by canopy height about the duration of the growth opportunity between disturbances. Seed mass also expresses some significant differences between species about seedling establishment. Most importantly, the LHS axes chosen require little enough effort to estimate that experimentalists may be willing to report them for their species with a view to subsequent meta-analysis by others, even though they have no immediate use for the data themselves.

PHYLOGENY

Regrettably, phylogenetic relatedness is often interpreted as an alternative reason (sometimes called phylogenetic constraint) why species should be similar (Hodgson and Mackey 1986, Kelly and Purvis 1993, Harvey 1996, Silvertown and Dodd 1996). Common ancestry or phylogeny is seen as a source of confounding or error that requires controlling for; in competition with explanations that invoke natural selection or functionality continuing into the present day.

This competing explanation approach is incorrect, with regard to explaining present-day ecological function. Phylogenetic niche conservatism is commonplace; hence, species can often have similar trait combinations *both* because they are phylogenetically related, *and* because they are subject to similar continuing forces of natural selection. The issues of interpretation have been debated elsewhere, for example in a Forum in *Journal of Ecology*

(Ackerly and Donoghue 1995, Harvey et al 1995a,b, Rees 1995, Westoby et al 1995a–c, 1996, 1998, Price 1997) and are summarized in Box 23.2 to Box 23.4.

Precisely because functionally important traits are sometimes phylogenetically conservative, phylogeny can and should be seen not as a source of confounding, a technical difficulty

BOX 23.2

Frequently Asked Questions (FAQs) about Phylogeny and Functional Ecology

FAQ1: When related species tend to be similar (e.g., seed mass more similar within than between genera), should this be attributed to phylogenetic constraint?

Answer to FAQ1: No. The term constraint clearly implies that the trait has been under directional selection toward different values, but nevertheless has failed to respond to selection. (Remaining unchanged due to absence of directional selection, or due to continuing convergent selection, cannot usefully be called constraint, or inertia, an alternative sometimes seen.) There are two reasons why similarity of species with a common ancestor should not be regarded as positive evidence for constraint or failure to respond to directional selection.

First, given that differences between species, genera, or families are under consideration, the hypothesized constraint needs to have applied over millions, perhaps tens of millions of years. Thus features of genetic architecture that might be measured in a present-day population and might restrict response to selection over tens of generations, such as low heritability or genetic correlations between traits, could only account for constraint in this context if the low heritability or the genetic correlations survived a million years of mutation and genetic rearrangement under directional selection. This would be sufficiently surprising that it certainly should not be accepted as a null hypothesis, especially not for quantitative traits such as seed mass. Rather it is a decidedly strong biological hypothesis: a definite mechanism for the constraint should be proposed, and means sought to test it.

Second, there are alternative well-established mechanisms through which species could tend to maintain similar traits over time after diverging from a common ancestor. Therefore correlation of a trait with phylogeny cannot be regarded as evidence for constraint rather than for continuing functionality. Phylogenetic niche conservatism is a process whereby because ancestors have a particular constellation of traits, their descendants tend to be most successful using similar ecological opportunities, and so natural selection tends to maintain the same traits among most if not all descendant lineages. Niche conservatism is at least as likely a cause of similarity among related species as constraint—more likely, for quantitative traits—and explicitly invokes ecological functionality continuing into the present day.

Sometimes one will see the term “phylogenetic effect” used to refer to the tendency for phylogenetically related species to have similar traits. This term is defensible provided it means “effect” only in a purely statistical sense, a label for variation correlated with phylogeny. However, the temptation seems strong to see a phylogenetic effect as somehow an alternative causal interpretation to ecological functionality, and this is wrong. The term phylogenetic effect was better eschewed (Westoby et al 1995c). If constraint is inferred, a specific mechanism should be proposed. If not, one might refer to phylogenetic conservatism, identifying the pattern in the outcome without hinting at any particular mechanism.

FAQ2: Is it true that phylogenetically related species are nonindependent as evidence for present-day ecological function?

Answer to FAQ2: Yes in part, but mainly no: actually formulating the question around the term independence is not helpful (see Box 23.3). The grain of truth in this idea is that a correlation across present-day species between traits X and Y might be caused through a cross-correlation with Z rather than reflecting a direct functional relationship between X and Y . Related species are more likely to have similar values for Z . However, the argument usually connected to the claim about nonindependence is that radiations, separate divergences on the phylogenetic tree, are

BOX 23.2 (continued)**Frequently Asked Questions (FAQs) about Phylogeny and Functional Ecology**

independent events, and therefore that a test for correlated divergence deconfounds the X – Y correlation to a large extent (Harvey et al 1995a) from third-variable influences (see Box 23.4 for further discussion of the sense in which correlated-change analysis deconfounds or partials out third variables). This implication that analyzing divergences rather than present-day species is an improved, phylogenetically corrected method for assessing ecological function is unsafe for two reasons.

First, the problem of cross-correlation with third variables is not confined to related species. Hence analyzing for correlations in divergence rather than correlations across present-day species does not overcome the well-known problems of inferring causation from correlation.

Second, just because an X – Y correlation is cross-correlated with Z , this does not necessarily mean Z is the true cause. It remains just as likely that the true mechanism runs from X to Y , and Z is a secondary correlate, so far as anyone can tell from the correlation pattern alone. In such cross-correlated situations, it is not conducive to sensible interpretation to deconfound X – Y from any influence of Z without at the same time looking at the raw X – Y correlation. This is all the more so when the third, fourth, and so on variables from which X – Y is deconfounded are not explicitly identified, but rather are an aggregate of all variables that have been conservative down the phylogenetic tree.

In summary, evolution by natural selection has given rise to cross-correlated patterns of traits among present-day species. Selection for ecological functionality has inherently been confounded with phylogeny during the history of evolution, and statistical corrections are not capable of converting that inherently confounded history into the ideal experiment in which phylogeny is orthogonally crossed with present-day function. In this situation the credibility of a hypothesis connecting traits to ecological functions cannot be judged according to the pattern of correlation and cross-correlation alone, but must rest also on whether the physiological or morphological mechanism is convincing, and the outcomes are well tested in field experiments. While everyone should be aware that correlation cannot prove causation, it is important to remember also that disappearance of correlation after correction or partialling does not *disprove* causation.

The qualification “as evidence for present-day ecological function” in FAQ2 is important. If the issues under study were to do with the historical process of evolutionary divergence, then naturally data about present-day species should be transformed by hanging on the phylogenetic tree (Grafen 1989) to give rise to inferred data about the radiations.

FAQ3: Is it obligatory to correct for effects of phylogeny?

Answer to FAQ3: No (when concerned with present-day function). Although advocates of phylogenetic correction or correlated-divergence analysis (Kelly and Purvis 1993, Rees 1993, Harvey 1996, Silvertown and Dodd 1996) have taken the view that cross-species correlation analysis has been superseded, correlated-divergence analysis cannot be considered obligatory because: (a) Tests for correlated evolutionary divergence (phylogenetic correction procedures) do *not* reliably control for all potentially confounding third variables, see FAQ2, and (b) Phylogenetic correction *does* remove from consideration correlations that have been phylogenetically conservative, many of which may also reflect present-day function (phylogenetic niche conservatism), see also FAQ2. A trait can perfectly well be functional, but have arisen in only one or a few separate radiations, so that a correlated-divergence analysis would never show statistical significance. Conversely, a trait can be repeatedly correlated with an ecological outcome across many radiations or phylogenetically independent contrasts, but nevertheless not be the true cause.

to be overcome, but more positively, as a basis on which to select species for study. Through better species selection we may hope to arrive at generalizations more efficiently and with better-defined boundaries on the generalization. People concerned with methods of phylogenetic analysis have mostly been using datasets already in existence, and have not as yet paid

BOX 23.3**Meanings of Independence and Adaptation**

The debate over phylogenetic correction has (like most debates) gotten issues of how we obtain reliable knowledge mixed together with issues of semantics. Certain key words need comment:

Independence: Arguments for phylogenetic correction typically begin from the formulation by Felsenstein (1985), where species do not represent independent data points, on the grounds that related species will have similarities by reason of common ancestry. To claim that species lack independence purely because they have similarities cannot be justified. If correlation with another trait were sufficient to vitiate independence, either two species that both occurred in Europe could not be considered independent, or two species that both had alternate leaves. Carried to its logical conclusion, evidence could never be found for anything, because some correlate could always be found that would be regarded as vitiating the independence.

In general, independence is not an absolute property, but makes sense only in the context of a particular model of causation. The issue is whether two species represent separate items of evidence for that causation process. The model connected with the Felsenstein formulation of nonindependence focuses on the process of change in a trait. The present-day trait value is viewed as caused by the past process of change, rather than the process of change being caused by an attraction toward the present-day trait value, an attraction arising from ecological functionality. The claim that species are not independent items of evidence, rather the change along each phylogenetic branch is an independent item, makes sense only in the context of this particular model of the generating process. Price (1997) gives an example of a model where the evolutionary process positions species in trait space according to the present-day ecological context, and shows formally that a better test of that process is obtained by considering each species an independent case than by considering each radiation an independent case.

Adaptation: A sector of the scientific community wishes to reserve adaptation to refer only to the natural selection under which a trait first emerged, excluding natural selection that may be maintaining it in the present day (Gould and Vrba 1982, Harvey and Pagel 1991). Although others continue with a broader usage of adaptation that can refer also to ecological functionality in the present day (see Williams 1992, Reeve and Sherman 1993 for balanced discussion), advocates of phylogenetic correction have chosen to insist that tests for adaptation must exclude trait-maintenance (Harvey et al 1995a). In practical effect, this definition of adaptation insists that questions about the emergence of traits are legitimate, whereas questions about trait maintenance are not.

Under these circumstances the word adaptation is best avoided, for the present. Throughout this chapter traits have been referred to as functional, or those that have ecological significance, to avoid getting sidetracked by this issue of the definition of adaptation.

much attention to species-selection designs. However, for experimentalists who collect new data, sufficient effort is involved for each species that it is worth thinking carefully about how that effort should be allocated.

Species-selection design, like any other aspect of design, depends on the question under study. It is important to be careful about the exact formulation of questions invoking phylogeny. A range of different question formulations and corresponding species-selection designs are discussed in Westoby et al (1998), where a more general overview is provided.

A traditional idea is that one should compare species within a genus rather than more distantly related species, for the reason that other unmeasured attributes are less likely to vary in such a comparison. This idea is actually not a very good compromise. On the one hand, it is

BOX 23.4**Relationship between Correlated Divergence Analysis (Phylogenetic Correction) and Partialling Out the Cross-Correlation with a Third Variable**

According to people who believe correlated-divergence analysis should be obligatory (e.g., Harvey 1996), one of its major benefits is in deconfounding an X - Y correlation, partialling out potential influences of whatever third traits Z_1 , Z_2 , and so on may be phylogenetically conservative. Westoby et al (1995a) described phylogenetic correction as extracting variation in this sense and discarding it from consideration as potentially related to ecological function, but in response Harvey et al (1995a) asserted that correlated-change procedures should not be regarded as extracting any component from the cross-species dataset. What, then, are the similarities and differences between correlated-divergence analyses and partial correlation analysis?

Correlated-divergence analysis transforms a species \times traits data table by hanging it on the tree (Grafen 1989), producing a new dataset where each row is a radiation or node in the phylogenetic tree, and each column is a measure of divergence in a trait at the radiation in question. In the simplest case, the measure of divergence would simply be the difference in the trait between the two species descended from a branch-point. (There are various complications where three or more branches descend from a node, or where branch-lengths are not assumed equal, but the essential logic is the same for these more complicated cases.) The question is whether divergence in Y is correlated with divergence in X , tested by fitting a regression through the origin to the data-points derived one from each radiation.

Thus correlated-divergence analysis has similarities to a paired design, such as if one set out to study 1000 biology students, and paired each one with a humanities student, matched for age, gender, and University. Then if one wished to analyze for a relationship between biology versus humanities and attending live drama, the number of plays attended during the preceding year for each biology student would be subtracted from the number attended for the corresponding humanities student, and one would test whether the difference in plays attended was significantly different from zero. In correlated-divergence analysis, species are similarly matched into pairs, using the criterion of common ancestry, which has the effect also of pairing them according to any number of phylogenetically conservative traits. Depending on the species-selection design, pairs may be deliberately contrasted on some attribute, for example, soil habitat, or may simply be random species descended from a branch-point in the phylogenetic tree. In any event, the point of subtracting trait values between pair-members is to remove from consideration trait-variation associated with matters for which pairs have been matched, such as age, gender, and University. Although this has advantages for some questions, looking only at the differences also has distinct disadvantages. Suppose there was some tendency for humanities students to attend more live drama, but the tendency of females rather than males to attend live drama was much stronger—this second fact, putting the first in perspective, would be rendered invisible by the pairing and subtraction process. Further, if one then drew the conclusion that the average humanities student attended more plays than the average biology student, this might be quite wrong if a greater proportion of biology students were female.

not a safe means of controlling for the influence of third variables. Other unmeasured variables are quite capable of varying within genera as well as between genera. On the other hand, there is no way to tell how far a generalization from a within-genus study extends to other lineages. The within-genus study sacrifices all power to assess generality across lineages, without decisively controlling for third variables.

To assess the consistency of a pattern across lineages, typical designs are based on phylogenetically independent contrasts or PICs. A phylogenetic contrast, or radiation, is a branch-point in the phylogeny and the set of branches descending from it (Felsenstein 1985, Grafen 1989, Harvey and Pagel 1991). In the simplest case it is a pair of species descended from a common ancestor. (Using pairs maximizes the number of PICs in the design relative to

the number of species required.) The independence refers to the set of contrasts within a particular study being independent of each other, representing separate divergences or radiations in the phylogenetic tree. Each PIC then provides one replicate for testing whether a divergence in attribute X has consistently been associated with a divergence in Y across separate evolutionary divergences.

Suppose the phylogenetic tree adopted is simply the existing taxonomy, and the aim is to select say 20 PICs from a pool of candidate species. A simple rule for obtaining further PICs is to include new genera in preference to more than two species within a genus, new families in preference to more than two genera within a family, new orders in preference to more than two families within an order, and so forth. The effect of this rule is to spread sampling out across the phylogenetic tree, so any PIC-based design will have some degree of breadth of coverage of different lineages. Nevertheless, unless there are a very large number of PICs some lineages may go unrepresented, and nothing in the simple rule described allocates equal representation to different major branches. To achieve these design aims one might spread PICs through the phylogenetic tree more systematically, for example by treating as blocks major branches of the angiosperm tree such as rosids, asterids, and palaeoherbs. No study known to me has implemented such a design as yet.

PIC-based designs are good for assessing consistency of a relationship across many lineages, but have countervailing disadvantages (several complications of using PICs are discussed in more detail in Westoby et al 1998). Probably the most important is that they will usually not satisfy the equal-chance-of-being selected rule in the species selected from a particular habitat or strategy. Suppose, for example, we wish to contrast species from infertile soils with species from more fertile soils (e.g., Cunningham et al 1999, Wright and Westoby 1999). For each species chosen from an infertile soil, a related species will be sought on fertile soil to form a phylogenetically independent contrast. This means that from the list of all species on fertile soil, species are more likely to be chosen if they belong to genera or families that are also present on infertile soil. The species chosen according to a PIC-based design will not give a fair representation of the overall shift in the frequency distribution of (say) species leaf sizes between habitats. Specifically, they will tend to underestimate the contribution from families and orders that are present in one habitat but not the other.

One can select PICs branching across higher as well as lower taxonomic levels, so in principle it might be possible to select species in such a way that they both constituted a set of PICs between two habitats, and also were proportionately representative of the phylogenetic species-mixture occurring within each habitat, but such a design has never been attempted to my knowledge. This is on the premise that a PIC between (say) orders within a superorder is constructed by selecting one species at random from each order. In some designs such a PIC can also be constructed by estimating each order's trait value from species within that order that have also been used to build PICs between families, genera, or species. However, this is only possible when the species have been randomly sampled from the phylogeny within each order, not when the PICs have deliberately been contrasted for (say) leaf size, or soil habitat (Westoby et al 1998). No doubt species-selection on the basis of phylogeny is an area where many further developments and improvements can be expected over the next few years.

CONCLUSION

The current situation in functional plant ecology is that quite a large number of detailed field experiments and ecophysiological studies on one or a few species have accumulated, more than have been satisfactorily digested, interpreted, and generalized. Emerging wide-area

applied problems, notably global change of climate and land use, are creating urgent demand for plant functional type classifications that might permit worldwide generalizations (Steffen et al 1992, Körner 1993, Woodward and Cramer 1996, Smith et al 1997). The gradual accumulation of comparative information in electronic databases is reaching critical mass, allowing patterns to have their generality quantified much more widely and quickly than a decade ago. Together, these trends mean that generalization across species and the associated topic of ecological strategy schemes are becoming keys to research progress in functional plant ecology over the next 10–20 years.

In this context the selection of species for study is an issue deserving closer attention than it has received up to the present. The maxim is to be explicit. This means describing explicitly the boundaries on categories of species that are to be compared in any given study. Ideally one would then select replicate species at random within those categories. This is a counsel of perfection that will be hard to meet in practice, but again, authors should be encouraged to think about and list explicitly whatever exclusion rules they have found it necessary to use, that prevented them from choosing at random from the whole list of species within a particular category. The work of subsequent literature review and generalization must surely become more rigorous and powerful once reviewers have available to them a clearer knowledge of what sort of species have been studied and what sorts have been avoided.

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