PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Preface

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PREFACE

The great Darwinian truth that underlies our attempts to discover rhyme and reason in the diversity of life on Earth is that natural selection has shaped the form and behaviour of organisms. The search for the evolutionary pathways that lead to the present diversity of life, the study of phylogeny, was among the most powerful forces in the development of biological science in the latter part of the 19th and first half of the 20th century. It provided a fascinating intellectual exercise to draw out putative evolutionary sequences and gave the excuse for quite violent conflicts of interpretation. Comparative morphology was the main (and often the only) source of data for such phylogenetic speculation. It acknowledged that some features, 'conservative characters', were more resistant than others to evolutionary pressures and so were more reliable for tracing lineages. To establish phylogenies it became vitally important to identify these 'conservative' characters and to distinguish them from features that responded more quickly to selective pressures and therefore indicated only recent ancestry.

Two particularly important developments stemmed from the historic passion for phylogeny. First, and of great significance for many papers in this collection, was the perceived need for systematics and taxonomy to reflect evolutionary lineages and to be more than efficient systems for classification and pigeon-holing. A second development from the post-Darwinian passion for phylogenetic speculation was a deep distrust of what had sometimes become 'the gin-palaces and brothels of unbridled hypothecation'. Disillusionment with some of the more extreme phylogenetic 'just-so stories' forced a quite dramatic shift in interest from macroevolutionary speculation to microevolutionary empiricism. Evolution in action became the focus for the study of biological diversity. The science of ecological genetics, pioneered for example by E.B. Ford among zoologists and Turesson among botanists, emphasized the role of present environmental forces (both biotic and abiotic) in natural selection. Studies of melanism in moths and metal tolerance in plants were just two examples among many that emphasized the power and speed with which natural selection operated. The process of evolution had become part of the present ecological scene. It has been tempting to see the ecological match between organisms and their present environments as the result of present evolutionary processes, and to forget their phylogeny.

This volume was born out of the conviction that the time is ripe to re-examine in phylogenetic perspective the perceived patterns of relationship between different plant life history traits, and between those traits and the presumed selective pressures that shaped them. This re-examination takes two forms; in the first it simply recognizes that because evolution is a branching process, traits are not randomly distributed across taxa and that therefore analyses of trait correlations cannot treat species as independent data points. One solution to this problem is essentially (though not literally) to factor-out phylogeny so that trait correlations that arise from convergent evolution can be distinguished from those due to common descent.

The second form of re-examination is almost the reverse of the first and, instead of attempting to factor-out phylogenetic relationships between species it uses these relationships to reconstruct the evolutionary pathways of traits. Phylogeny allows us to infer whether a particular change occurred once or a number of times, whether change has been in one direction or another, whether change in one character has been associated with change in another, whether associated changes have occurred in a particular sequence, and whether particular changes are associated with shifts in diversification rates

The volume is organized in five sections; the first section is chiefly intended to demonstrate the uses and hazards of taking a phylogenetic perspective on trait-trait and trait-habitat correlations. Sections two, three and four examine a range of traits from the reproductive phase of the life cycle through seed production and dispersal to recruitment and growth. In each of these sections papers variously emphasize the two forms of phylogenetic perspective, trait-trait or trait-habitat correlations, and relevant life history theory. The fifth and final section recognizes that important features of plant life history involve interactions with competitors, herbivores and microbial symbionts and that these interactions have an evolutionary history; sometimes an ancient one.

Phylogenetic perspectives

In an introductory paper Silvertown and Dodd ask what they see as the fundamental questions in any comparative study of plant life histories: 'Which traits are correlated with each other?' and 'Are these correlations the result of common descent or have they arisen repeatedly as a result of convergent evolution?'. They distinguish between comparisons that treat species as independent data points (the tips of the phylogenetic tree, TIPs) and those that take account of the phylogeny and the lack of independence that common ancestry may confer on samples (Phylogenetically Independent Contrasts, PICs). This theme appears repeatedly in other papers in this collection and Silvertown and Dodd show, with some worked examples, how phylogenetic information can be used to correct comparisons for phylogenetic independence. They show that secondary chemistry and life form (woody *vs.* herbaceous), two traits which are conserved in angiosperm phylogeny, are significantly correlated due to convergent evolution, providing important support for theories of anti-herbivore defence. Lest ecologists rely too much on specific evolutionary trees Donoghue and Ackerly caution that 'It is highly likely in fact that, virtually every phylogenetic tree found in the literature is wrong in one way or another.' and they describe the use of sensitivity analyses to explore the robustness of phylogenetic conclusions.

A major part of the eco-evolutionary game has been explored by demonstrating what it is about particular species that enables them to live where they do and what it is about them that makes them seem the best (or the best compromises) in the best of all possible worlds. Extraordinarily little effort has been put into ecological and evolutionary explanations of why almost all species are always absent from almost everywhere! One explanation is presumably that evolutionary specialization progressively narrows the range of habitats and environments that provide the conditions needed for survival and growth. However another reason for the absence of most species from most habitats is that geographic isolation has prevented colonists from ever reaching them.

Species of plant and animal that are new invaders to a territory, especially to an island, must of necessity have acquired the necessary properties elsewhere. They cannot become subject to natural selection in their new habitat until after they have proved that they can survive in it. Comparisons between alien and native floras and faunas are therefore a particularly rich source of material for studying the nature and origins of the traits that govern the ecology of species. Crawley, Harvey and Purvis use this approach for an analysis of the British flora for which there is detailed information about the time of alien invasions. Using PIC they find traits such as the mating system and method of seed dispersal to be apparently irrelevant to successful invasion and that successful invaders are characterized by being big (large seeds, large plants) and having protracted seed dormancy. Their analysis also suggests that the flora of Britain is unsaturated because new invasions have not depended upon the ousting of previous inhabitants.

In various papers in this collection authors have used taxonomy as a surrogate for the better resolved but rarer phylogenies that are derived from molecular analyses. How far this surrogacy is reliable is a crucial issue discussed by several authors. Kelly and Woodward press the contrast between taxonomies and cladistically derived phylogenies by applying both methods of structuring data to traits such as clone size, life form (trees and shrubs) and features such as the ecological range and the commonness and rarity of species.

Reproductive traits

A wide variety of mating systems is found among flowering plants, often within the same family or genus and so even before the advent of molecular phylogenies it had become clear that shifts between selfing and outcrossing must have occurred frequently within lineages. Molecular phylogenies now make it possible to unravel the story of mating system evolution in much greater detail. Barrett, Harder and Worley compared species within the family Polemoniaceae to determine the degree of independence of phylogenetic and ecological correlates of self- or cross-fertilization. Using a molecular (*matK*) phylogeny they show that in the temperate herbaceous clade of Polemoniaceae the annual life cycle evolved at least seven times, and reverted to the perennial habit on three occasions. Selfers evolved from outbreeders at least 14 times but there is no evidence of the reverse.

Schoen, Morgan and Bataillon examine the clues that both floral ecology and molecular genetics offer to answer the puzzling question of why self-pollination has evolved repeatedly within different lineages. Their analysis of various theories shows that a century of study has left us still in the dark about this central problem in plant reproductive biology (as in our understanding of the significance of sex itself). While the first two papers in this section deal with mating system as an evolving trait, the third paper by Hamrick and Godt analyses the effect of this trait, amongst others, on genetic diversity and genetic structure.

Seeds

Seeds for the plant scientist are (like eggs for the zoologist) convenient starting points for the analysis of life histories. There is abundant evidence from simple controlled experiments that large seeds confer a clear advantage in intraspecific competition and individuals whose seedlings are smaller or emerge later are commonly disadvantaged in a population of the same (or a closely related) species. Seed mass is part of a classic example of evolutionary compromise in which any increase in individual seed mass is thought necessarily to involve a compensating decrease in seed number. Increased seed mass almost inevitably makes dispersal more costly but by providing the embryo with greater reserves increases the chance of establishment in environments where resources are hard to gather. Delayed germination implies that time spent dormant might, in theory, have been employed in growth and reproduction and the disadvantage is usually assumed to be offset by an increased probability of survival as a result of the delay. There are extensive data sets from the British flora which Rees analyses using PICs to explore the correlations between seed mass, dormancy life span and clonality, finding general support for theoretical expectations.

The paper by Westoby, Leishman and Lord is broadly concerned with detecting correlations among the same series of traits but provides a contrast with Rees' paper because greater weight is given to the informative value of TIPs analyses. PIC only detects evolutionary change and is hence insensitive to the consequences of stabilizing selection. Westoby *et al.* make the important point that variation in seed size within species is typically very narrow, implying that in each species seed size (mass) is tightly canalized and presumably subject to strong stabilizing selection. In contrast the mass of individual seeds differs quite dramatically from species to species within the same communities. It looks as though natural selection may act powerfully to favour uniformity within species but ecological forces act to favour seed niche diversity within communities.

A crucial question is when and whether any property (form or behaviour) of an organism, population or species can usefully be analysed in isolation from others. Perhaps the most interesting 'traits' are trade-offs in which the balance between two or more attributes is more interesting (both for phylogeny and ecology) than each attribute itself. The relationship between the size and number of seeds may, for example, be a far more informative 'trait' than either size or number alone. Venable discusses models that can be used to help understand how and when different components of the reproductive process constrain and selectively impact each other.

Recruitment and growth

Early land plants grew clonally and clonality is clearly an ancestral trait in the plant kingdom. We need therefore to explain how and when it has become lost from some groups and what the ecological consequences are. Van Groenendael *et al.* analyse both the phylogeny (at the level of families and higher systematic categories) and the present ecology of clonality using a unique data set of 2,000 plants from Central Europe. One important finding is that clonality is over-represented among plants of wet habitats, but that this is essentially due to the preponderance of monocots in such habitats.

The whole pattern of a life history can be regarded as a trait, selected in evolution and constraining the ecology of species. But, of course, most individuals never experience their life history: most die young. However, among those that survive, the pattern of adult mortality differs quite markedly between species and various authors have recognized, among animals, a continuum of life histories ranging from organisms with 'fast' (high adult mortality, fast development, high fecundity and short life cycles) to slow life histories (low adult mortality, slow development. low fecundity and long life cycles). Franco and Silvertown ask whether such a continuum can be detected in the life histories of higher plants and they conclude that the modular growth of plants (which enables them, at least in theory, continuously to increase their size and fecundity as they age) means that some trait correlations found in unitary organisms are not seen in plants.

We may recognize individual species as having characteristic life histories that we can classify or order. But in reality nature is made up of environments that are heterogeneous, patchy mosaics and in these genetically identical individuals act out their life histories in quite different fashions. The 'characteristic' life history of a species is defined by a variance as well as a mean. Sibly reviews the body of theory that has developed to model the evolution of life histories in environments that are heterogeneous in space and also in time. Once again, there are peculiarities about higher plants, such their plasticity and the potential increase in fecundity with age, that make classic models based on unitary animals inappropriate.

Interactions

Ecologists see competition, predation and parasitism as powerful forces in present population and community dynamics that determine the present (proximal) significance of traits in both form and behaviour. It would be unreasonable to disregard their potential role in phylogeny. It is to be expected that past biotic interactions (ultimate factors) will have left their mark in present (proximal) performance as limits and constraints on the ecological versatility of species. A classic paper by Ehrlich & Raven (1964) on the evolutionary consequences of interactions between insects and their food plants was seminal in the development of the theory of coevolution. Insect herbivores are conservative in their diet often to the extent of strict monophagy. Indeed biological control programmes that use insects to control weeds depend on this monophagy for their success. Such dietary specialization is often deeply rooted in the history of the clades of both the insect herbivores and in their plant prey where it is often reflected in biochemically versatile modifications of particular classes of alkaloids, glucosinolates, terpenes etc. Futuyma and Mitter review the state of knowledge about the evolution of dietary specialization among insects and point out, for example, that some cladistically basal groups which feed on conifers and other gymnosperms have probably been associated with their special hosts since before the Cretaceous. Where there is evidence that specialists moved to new host plants and lineages have consequently branched it has usually been from one food plant to another that is closely related. There are few better demonstrations of phylogenetic constraint acting upon what selection can accomplish.

The associations between microbial symbionts and plant roots are even more ancient than the majority of plant-herbivore associations. Fitter and Myersoen discuss the phylogeny of root symbioses and point out that endo-mycorrhizal associations are primitive but the non-mycorrhizal habit is a derived, specialized condition that appears to have evolved repeatedly. Ectomycorrhizal associations have evolved at least twice. By contrast, the ability to form N-fixing root symbioses appears to be restricted to a single clade but within this clade the ability may be gained or lost.

Haldane (1932) wrote 'The fitness of plants in the Darwinian sense must be tested with the plants grown in competition' and as Sakai (1961) pointed out 'This stimulating statement implies the existence in plants of heritable differences in competitive ability. Sakai went on to compare the performance of varieties of rice in pure stands and in all combination of varieties in pairs. From this simple experimental design he concluded that competitive ability is a genetic character controlled by polygenes with low heritability. Since that time the study (even the definition) of plant competition has developed into a minefield of problems — some semantic and some that pose daunting problems in experimental design and analysis. Competitive ability might be regarded as a trait in itself, it clearly also encapsulates a whole spectrum of individual traits that interact to determine success or failure in a struggle with neighbours. There is certainly no way in which we can hope to identify traits associated with competitive effect and competitive response or to partition 'competitive ability' into proximate (ecological) and ultimate (phylogenetic) elements until we have some agreement on what it is that we are measuring and comparing. Goldberg reviews many of these problems with a succinct survey of a vast literature and suggests simple (though very large) experimental designs that might provide a solution.

A phylogenetic perspective reminds us that there is a unity of common origins underlying the diversity of plant life history. This volume is intended to uncover some of that unity, but in the attempt it is inevitable that the holes in the fabric of our knowledge become apparent too. Lest the holes seem larger than the cloth, we should pinpoint some of the more general trait correlations revealed by the use of the comparative approach in this volume: longevity is a trait of central importance that is negatively correlated with reproductive allocation (Silvertown & Dodd) and seed dormancy (Rees), and positively correlated with outcrossing (Barrett *et al.*), genetic diversity (Hamrick & Godt), age at first reproduction (Franco & Silvertown), and seed mass (Rees). Seed mass is another very important trait that is correlated negatively with dormancy (Rees), specific leaf area and relative growth rate (Westoby *et al.*) and positively among herbs with the presence of VA mycorrhizas (Fitter & Moyersoen). Life form (herbaceous/woody) is a third trait of general importance, being correlated with leaf chemistry (Silvertown & Dodd), mating system (Barrett *et al.*) and ectomycorrhizas (Fitter & Moyersoen). This is an incomplete list and not all the correlations are simple ones (for example the negative relationship between seed mass and dormancy occurs only in species with specialized dispersal mechanisms), so one of the most important questions we have to ask is 'How general are these patterns?'. Some, like the correlations with longevity, may be quite general, others like those involving symbionts may be more clade- or habitat-specific. Although it is still too early to answer the question, this volume demonstrates that now at least we have the means to address it.

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