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Evolution and Ecology: a Janus Perspective?

> The large scale is likely to have at least some characteristics that we cannot predict at all from a knowledge of the small scale . . . Scaling up is not part of our tradition.
>
> (Grace *et al.*, 1997)

A popular name used in universities across the world is 'Department of Ecology and Evolutionary Biology'. At many sites this title is associated with productive interactions between the two major sub-disciplines. In particular, where the shared objective is to gain a detailed understanding of population processes, there are many opportunities for fruitful collaboration. Often, however, the activities of evolutionary biologists and ecologists are so different that we may be reminded of the divergent perspectives of the bifocal Roman god, Janus (see Fig. 1.1). It has become apparent (Grime, 1993) that to address certain of their key objectives, many ecologists will not easily progress by uncritically adopting the mindsets and methods of evolutionary biology. New alignments and initiatives may be necessary if ecology is to emerge as a coherent, useful science. To see why some divergence is inevitable it is helpful to examine the recent trajectories of both sub-disciplines and to visit some of the misunderstandings between them.

Evolutionary biology

One of the most treasured of the discoveries among the Darwin papers is the notebook page upon which Darwin mused about the evolution of species by drawing a diagram resembling the branching system of a tree. Nearly two

The Evolutionary Strategies that Shape Ecosystems, First Edition. J. Philip Grime, Simon Pierce.

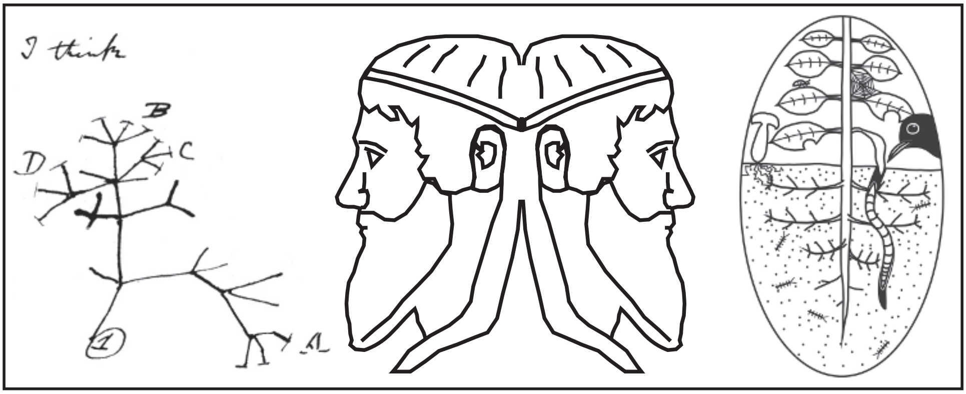

Fig. 1.1 Janus surveys Evolution and Ecology.

hundred years ago this simple sketch foretold the method that later, but with significant elaboration, would be used by taxonomists and molecular biologists to depict the origins and evolutionary affinities of the organisms that compose the world's biota. A feature of Darwin's theoretical tree, amply validated by modern investigations allowing the construction of 'real' evolutionary trees, is their highly irregular and unpredictable structure. Some branches appear to persist from early epochs to the present day whilst others have experienced bursts of recent speciation producing clusters of surviving species. The construction of evolutionary trees does not, of course, rely exclusively upon comparisons of extant organisms; palaeo-biologists through the discovery and examination of fossils continue to refine our understanding of extinct groups, some of which may provide the missing relationships between surviving taxa.

Evolutionary biology is not confined to the investigation of past connections between surviving or extinct organisms. Many practitioners are concerned with the ongoing processes of evolution within contemporary populations (e.g. Grant & Grant, 2008). Some are attempting to intervene to breed or engineer organisms with specific benefits to human society. Others are investigating evolutionary processes in plants and animals as an aid to their conservation and management; these scientists often prefer to be described as evolutionary ecologists.

Ecology

We can safely conclude that one substantial legacy from the theory of evolution by natural selection is a large college of scientists operating across the world as evolutionary biologists. Whatever the scale of their research, from processes within single populations to large-scale taxonomy, their science rests securely under the Darwinian umbrella. At present, no such unifying perspective encompasses the whole of ecology. In the opening paragraphs of this book we point to the much more diffuse nature of our science particularly where it seeks to understand the structure and functioning of communities and ecosystems. The struggles of ecologists to comprehend the community are ably summarized by Weiher & Keddy (1999) and even at one point famously provoked from Lewontin (1974) his despairing reference to 'the agony of community ecology'. The situation has often been much worse with frequent complete disjunction between evolutionary concepts and the ecosystem.

It is remarkable to record that in the highly influential textbook *Fundamentals of Ecology* by Eugene Odum (1953) the reader must wait until page 210 before Charles Darwin and the theory of evolution appear, only for them both to vanish immediately! Moreover, it is fascinating to observe that this cameo appearance of Darwin refers exclusively to palaeontology: the ongoing role of evolution in the biosphere draws no comment. It would be a mistake, however, to attribute all the travails and remaining challenges in ecology to the problems of scaling up to the complexities of communities and ecosystems. Difficulties can arise even when our research objective is confined exclusively to populations and species. In the 1990s a vivid example unfolded in the pages of the *Journal of Ecology* when evolutionary biologists objected to the comparative methods used by many ecologists in attempts to identify the factors determining the field distributions and habitat preferences of plant and animal species. Some indication of the depth of the differences aroused by this argument is apparent from the title of one of the papers published at this time: 'Why ecologists need to be phylogenetically challenged' (Harvey *et al.*, 1995). So what prompted such a critical observation by evolutionary biologists about the conduct of ecological research? Careful reading of this paper reveals that it was addressed to circumstances where ecologists had reported the occurrence of consistent differences in morphological, physiological or biochemical traits that coincided with differences in both ecology and phylogeny. Harvey and his co-authors cautioned against the assumption that such correlations were a reliable basis for ecological interpretation. In this they were likely to find support from the majority of ecologists who were equally aware that comparisons of groups of organisms differing in their ecology are often consistently distinguished by many other traits and that, at best, such comparisons merely serve as an inconclusive preliminary to experimental work in field and laboratory. Remarkably and controversially, however, Harvey *et al.* (1995) recommended the use of procedures in which attempts to establish the reliability of traits in explaining ecology should be based upon the statistical consistency with which specified trait differences were maintained in comparisons within large numbers of taxa. There can be little doubt that in some laboratories this technique, sometimes described as '**phylogenetic correction**' was regarded as a means of distinguishing between ecological and phylogenetic effects.

The protocol advocated by Harvey *et al.* (1995) drew a swift response from Westoby *et al.* (1995) who recognized that many relationships between phylogeny, traits and ecology were extremely unreliable concluding that: 'in future authors should eschew phrases such as phylogenetic effect' (Westoby *et al.*, 1995). This was a conclusion that drew strong support from many experienced ecologists:

> . . . taxonomic approaches are often beset with problems . . . closely-related species often show more marked differences in response to environmental factors than taxonomically unrelated species. (Duckworth *et al.,* 1997)

Briefly this argument cast a shadow over the comparative approach to ecology and there was an episode in which some journals rejected studies in which reported differences in the traits selected for study had not been subjected to 'correction'. This was particularly unfortunate in the case of studies confined by necessity to a few species.

These arguments had exposed a fundamental difference in objectives and methods between evolutionary taxonomists and ecologists. For the evolutionary biologist and taxonomist, comparisons of DNA could meet the objective of providing a quantitative, definitive proof of relatedness between organisms. However, the same information scarcely began to address the needs of an ecologist. It was essential that the foundations of ecology should remain firmly rooted in an evolutionary perspective, but in many laboratories there was a growing conviction that to drive their subject forward ecologists would have to embark on some bold construction work on their own account. Thus, notwithstanding the interests and priorities of evolutionary biologists, many ecologists now claim the right without hindrance to recognize and explore the consequences for communities and ecosystems of universally occurring convergences in adaptive strategy even when these occur between taxonomically distant organisms.

The emergence of a science of adaptive strategies

In retrospect it can be seen that the '**phylogeny disputes**' of the 1990s originated as a well-intentioned attempt to apply some inappropriate working methods of evolutionary biology in ecology. However, such methodological differences were trivial in comparison with another substantial issue that, after persisting in the background for more than a hundred years, had begun to push slowly forward over the last quarter of the 20th century and could be recognized as a distinctively ecological initiative. The stimulus for this divergence had two main origins:

1. Recognition that classification of organisms by evolutionary affiliation did not provide all the necessary insights into the ecological role of species and populations. Functional classifications that usefully addressed communities and ecosystems did not reliably correspond to taxonomic classifications.
2. There was a need to devise a theoretical framework and database that was capable of analysing the structure and dynamics of communities and ecosystems, predicting their future states in changing conditions and eventually contributing to our understanding of biosphere functioning.

As we shall see in succeeding chapters a majority of the pioneers of the functional approach were plant ecologists, but zoologists and microbiologists have also made highly significant contributions to this rapidly expanding branch of ecology.

Summary

1 In studies of the population biology of individual species many productive interactions are taking place between ecologists and evolutionary biologists.
2 In physiological ecology and in attempts to investigate the structure and functioning of communities and ecosystems, evolutionary affinities are an unreliable predictor of the characteristics and behaviour of component organisms.
3 Because evolutionary relationships are not consistently related to ecology we require an alternative basis for prediction and elucidation of ecological phenomena. There is a need for a theoretical framework that recognizes the existence of universal constraints on evolutionary specialization that result in widely recurring adaptive strategies with predictable effects on ecosystem structure and functioning.