1913 2013
British Ecological Society
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100 INFLUENTIAL PAPERS – LONGER COMMENTARY

09 Harper, J. L. (1967)

A Darwinian approach to plant ecology. *Journal of Ecology*, **55**, 247-270.

As stated by Roy Turkington, John Harper taught us a whole new way to study plants. In *A Darwinian approach to plant ecology*, John Harper synthesised the fundamental principles defining a discipline and drafted the path for later research in the area. He recalled our "distinguished parenthood", which we share with population geneticists, and advocated Darwin's quantitative approaches to ask why demographic thinking hadn't yet permeated plant ecologists' agendas. He established the quantitative bases for plant ecology, building in analogies with quantitative genetics in a way seen in some recent advances in theoretical ecology, e.g. Hubbell's biodiversity theory. Harper's work has been, in my view, among the most important foresights for the development of modern ecological science. In his presidential address, he proposed to extend plant ecology well beyond the limits imposed by the "vegetationalist" approaches outlined by Schimper and Warming, largely based on correlational analyses. The detailed observation of individuals, Harper argued, "*brings measurements of flux into ecological studies in terms which are meaningful to the selection geneticist and the evolutionist*." (my italics).

Nature is made up by numbers and, more specifically, by the balance among them. Harper argued that numbers can be difficult to translate directly into the real essence of plant populations. But he used the pioneering studies of Tamm, Sagar, and Antonovics on declining plant populations to advocate the usefulness of plant numbers. Tallying numbers is the only way to estimate the actual turnover (the balance between added and disappeared individuals) in a way that can be readily translated into genetic selection studies or estimates of ecosystem fluxes. When coupled with studies of plant vigour, numbers can be invaluable to assess processes of population regulation. Harper used a series of linked examples to discuss in sequence population regulation by mortality factors, size hierarchies, and patterns of allocation to vegetative as opposed to sexual reproduction.

Harper defended the importance of comparative analyses of allocation patterns and seed production to understand the evolution of plant life histories. Recent analyses at large scales, encompassing vegetation types and species from all continents, form the basis of recent developments in functional plant ecology.

Harper showed how the allocation patterns of vegetative/reproductive structures subtly influence density-dependence by determining population turnover rates, and he provided a range of predictions about life-history patterns. He further elaborated these ideas by building a convincing case for experimental approaches to the study of plant coexistence under field conditions. This approach has been used successfully by others to assess experimentally the long-term competitive dynamics of plant communities.

He discussed, although only briefly, a number of themes that now are central topics in plant ecology, such as the complementarity of plant species. Besides this Presidential Address, which is clearly not a data paper, Harper championed quantitative analyses with an extraordinary series of studies in plant demography (i.e. the 1960-1964 series on density dependent regulation of plant demography) that have been extremely influential in recent ecological thinking.

Harper ended with a very humble assertion highlighting the importance of plant-animal interactions in Darwin's ecological thinking: "I have wholly omitted the fascinating matter of animal-plant interactions that play so large part in Darwin's ecology. I am not amongst those very few ecologists since Darwin who are intellectually equipped to deal with the plant-animal interface."

Frequently, the interactions with animals - either mutualistic or antagonistic - translate into fitness effects because of their pervasive effects on plant numbers: their outcomes can be measured as number of propagules lost, dispersed, removed, attacked, or otherwise manipulated by animals, with either positive or negative consequences. The study of these outcomes in terms of numerical balances under different ecological scenarios has fuelled plant ecology in the last 50 years. This was Harper's vision. I'm convinced that, contrary to his unpresuming statement, he was more than well equipped intellectually to deal with the pivotal relevance of these interactions to understand plant numbers. It is always worth revisiting A Darwinian view of plant ecology.

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