100 INFLUENTIAL PAPERS

Published in 100 years of the British Ecological Society Journals

by Peter Grubb and John Whittaker

1913 2013

British Ecological Society

CELEBRATING 100 YEARS

Authors of Papers

"A journal of wide scope and high standard, which would furnish both a record and a continuous criticism of ecological work...furthering the interests of ecologists throughout the world"

Sir Arthur Tansley

Sir Arthur Tansley FRS

Sir Arthur Tansley, the founder and first president of the British Ecological Society wrote these words in the first issue of the *Journal of Ecology*, published in March 1913 and are still relevant today. When the Society was founded 100 years ago it had two fundamental aims, to "foster and promote in all ways the study of ecology" and to "present a record of and commentary upon the progress of ecology throughout the world".

The Society has kept to the vision of its Founders and since 1913 the *Journal of Ecology* has been joined by *Journal of Animal Ecology* in 1932, *Journal of Applied Ecology* in 1964, Functional Ecology in 1987 and in 2009 our newest and first purely online Journal, *Methods in Ecology and Evolution*. The first journal editors recognised the need for reporting international research and the journals continue to publish the best ecological research from around the world.

The membership is the heart of the Society and to celebrate our centenary we asked 100 eminent ecologists to nominate the paper they felt to be the most influential either personally or in the science of ecology. It has led to a truly inspiring and interesting selection with commentaries reflecting our shared interest in the science we all enjoy.

I hope you will join in celebrating our centenary; we've developed a full programme of activities and an online version of the papers so you can join in the discussion and nominate your own choice.

Professor Georgina Mace CBE FRS

www.britishecologicalsociety.org

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CELEBRATING 100 YEARS

In early 2012 the Committee of Council planning the Society's 100th Anniversary Celebrations in 2013 asked us to prepare a booklet and website bringing together a selection of the most influential papers published in the Society's journals. The committee agreed to our suggestion that an appropriate number would be 100 papers.

How should the papers be chosen? Some ecologists suggested that we should use only objective criteria such as the number of citations and/or the number of downloads. This procedure would not have done justice to the earlier papers, say those published in the first fifty years, when the number of ecologists writing and reading papers was so much smaller and before the advent of electronic searching.

We should remember that the membership of the BES was little over 1000 in 1960 but has now reached almost 4000.

We chose to use a mixture of criteria, including numbers of citations and downloads, but placing a strong emphasis on the suggestions of respected ecologists around the world because we felt that as researchers and teachers they could inform us of what had most influenced them in their thinking. We invited nominations from 113 correspondents representing the breadth of ecology, pure and applied, and a wide age range. Each was invited to name the one paper they felt absolutely must be in any such list, and then suggest another paper which might not occur to large numbers of correspondents but was thought highly significant by them for one reason or another. All correspondents were asked to consider all the BES journals which embrace some 17000 papers since 1913.

We imagined that a list of papers that absolutely must be included might be short. In fact that did not happen, and for three journals no paper received more than one or two nominations. The exception was Journal of Ecology for which Harper's Presidential Address attracted eight nominations, and Watt's seven. Given the criteria we set, it is unsurprising that there were few papers suggested from the last five years so the Society's fifth journal Methods in Ecology and Evolution, launched in 2009, is not represented in this selection. However, several of the selected papers from the longer established journals fell within the remit of this new journal so we would expect Methods to be well-represented in any future lists.

In the end we were able to include virtually all papers cited more than 500 times by 31 March 2013 (a total of 26) and most of the papers nominated by our correspondents. We added a number in order to cover under-represented fields, the earlier years, and high down-loads, and to reach our total of 100. There is, of course, overlap between these criteria. Where we had a title, but not a submitted piece of text, we invited other ecologists to write about them. We are very grateful to them and to all those who nominated papers in response to our invitation.

We considered grouping the papers by decades, but decided to do it by fields within ecology. These are necessarily somewhat arbitrary, but we hope they will be helpful. It is worth saying that the selected papers represent a good spread over the 10 decades with an average of six per decade in the first 50 years when the two journals then being published had grown relatively modestly in number of pages per year, and 13 per decade in the last 50 years when there were four journals and many more pages.

The desire during the last few decades for high citation rates has inevitably led some prospective authors to send papers which might otherwise have been published in BES journals to others with a high citation index . At the same time, subjects related to Ecology have launched or increased promotion of their own journals. Despite these trends, our journals have maintained high citation rates, and perhaps just as important, long half-life of papers. It is this latter point which underpins the success of many if not all of the papers included here. We have every reason to think that they will continue to be accessed and cited for years to come, as will many other papers in the Society's journals.

All the commentaries included here are also being published on the Society's website, often in more extended format, many with references to related work, and all with links to the papers themselves. Our hope is that website users will interact with that material, giving their views about the papers we have included, and writing about papers that they would have included. We hope that readers of this booklet will engage actively in this exercise.

The staff at the BES who are engaged in planning the Centenary events were extremely helpful to us in the preparation of this booklet and the web-site. We are particularly indebted to Lindsay Haddon for editorial work in the early stages of the project and to Julie Hodgkinson for extensive help in the later stages.

Peter J Grubb and John B Whittaker

British Ecological Society Journals

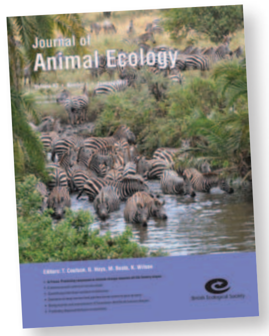
The British Ecological Society publishes five high-impact journals, covering a broad range of ecological science and connected disciplines. Containing over 100 years of content, these journals are ably directed by teams of expert Editors, and supported by over 200 Associate Editors and a number of experienced editorial office staff. There are many benefits to publishing in BES journals, including:

- High impact
- No page charges
- Rapid high-quality review
- Fast publication times
- Excellent promotion of papers via social media channels
- Additional press and media coverage on selected papers
- Option to publish open access

Functional Ecology
www.functionalecology.org

Functional Ecology publishes high-impact papers that enable a mechanistic understanding of ecological pattern and process from the organismic to the ecosystem scale.

Because of the multifaceted nature of this challenge, papers can be based on a wide range of approaches. Thus, manuscripts may vary from physiological, genetics, life-history, and behavioural perspectives for organismal studies to community and biogeochemical studies when the goal is to understand ecosystem and larger scale ecological phenomena. Functional Ecology is open-minded about the variety of data, research approaches and types of studies it publishes. Certain key areas continue to be emphasised: studies that integrate genomics with ecology, studies that examine how key aspects of physiology (e.g. stress) impact the ecology of animals and plants, or vice versa, and how evolution shapes interactions among function and ecological traits.



Journal of Animal Ecology
www.journalofanimalecology.org

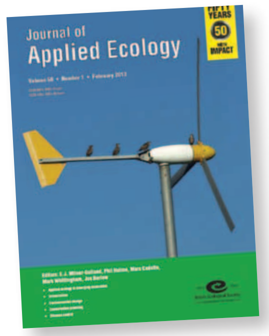
Journal of Animal Ecology publishes the best original research on all aspects of animal ecology, ranging from the molecular to the ecosystem level. These may be field, laboratory and theoretical studies utilising terrestrial, freshwater or marine systems.

It is our aim to publish articles detailing novel and important work that will challenge the way animal ecologists think. We encourage submission of papers that (i) make significant advances to the field of study in terms of development of ecological theory or methodology; (ii) address questions of importance and/or current interest; and (iii) generate insights that extend beyond the study system utilised.

Journal of Ecology
www.journalofecology.org

Journal of Ecology publishes original research papers on all aspects of the ecology of plants (including algae), in both aquatic and terrestrial ecosystems.

We aim to bring important work using any ecological approach (including molecular techniques) to a wide international audience and therefore only publish papers with strong and ecological messages that advance our understanding of ecological principles. Experimental and theoretical studies of plant communities, populations or individual species are accepted, as well as studies of the interactions between plants and animals, fungi or bacteria, providing they focus on the ecology of the plants. The research presented must transcend the limits of case studies and must be of general interest to ecologists.



Journal of Applied Ecology
www.journalofappliedecology.org

Journal of Applied Ecology publishes novel papers that aim to drive forward the field of applied ecology by providing a high-quality evidence base for scientists, managers and policymakers.

The high-impact papers contained in this journal are on the interface between ecological science and the management of biological resources. Contributions are encouraged that use applied ecological problems to test and develop basic theory, although there must be clear potential for impact on the management of natural systems. The Journal covers all major themes in applied ecology, such as conservation biology, global change, environmental pollution, wildlife and habitat management, land use and management, aquatic resources, restoration ecology, and the management of pests, weeds and disease, but does not normally publish papers that are purely methodological in focus. Articles that interact with related fields are welcomed providing that their relevance to applied ecology is clear.

Methods in Ecology and Evolution
www methodsin ecologyandevolution.org

The BES's newest journal, Methods in Ecology and Evolution, promotes the development of new methods in ecology and evolution, and facilitates their dissemination and uptake by the research community.

An online-only journal, Methods in Ecology and Evolution brings together papers from previously disparate sub-disciplines to provide a single forum for tracking methodological developments in all areas, publishing papers in any area of ecology and evolution, including phylogenetic analysis, statistical methods, conservation & management, theoretical methods and practical methods, including lab and field.

01

Elton, C. & Nicholson, M. (1942)

The ten year cycle in the number of Lynx in Canada. *Journal of Animal Ecology, 11, 215-244.*

Modern population ecology seems far removed from the early days of the subject. Today, sophisticated theory is brought together with rich, long-term datasets to help us understand how and why populations are responding to environmental change. We are now able to explore simultaneously the coupled ecological and evolutionary dynamics of populations, and delve into the detail of individual life histories and the factors that shape them. The 'roots' of modern population ecology are much more modest by comparison. The earliest papers were purely descriptive, simply reporting the observed patterns of population change over time. In many ways, the paper by Elton & Nicholson is unremarkable because it simply reports data on Lynx numbers in Canada. Its importance really lies in the cyclical patterns it documents; patterns that demanded a mechanistic explanation, and which subsequently stimulated the development of a rich array of theoretical population dynamics models. We now know that population cycles can be generated by a wide range of ecological mechanisms, but none of this work would have happened without the pioneering studies of early ecologists such as Elton & Nicholson. Observations of ecological systems matter! In an age of austerity, we would do well to remember this

Ken Norris

02

Varley, G.C. (1947)

The natural control of population balance in the knapweed gall-fly, (Urophora jaceana). *Journal of Animal Ecology, 16, 139-187.*

Density dependence is one of the central concepts in ecology : it is critical to the growth, persistence and dynamics of populations. This idea introduced by AJ Nicholson, was extended by Nicholson and V.A.Bailey [*Proceedings of the Zoological Society of London* ,**3**, 551-598 (1935)] to show theoretically how natural enemies, and in particular, parasitoids, influence the stability and dynamics of populations. Varley's1947 paper based on his Cambridge thesis of 1938 provided the first and definitive field test of the concepts of Nicholson and Bailey on the stability and persistence of host-parasitoid interactions. Varley documented the ecological effects on the interaction between the knapweed gall-fly and a range of parasitic natural enemies. By carefully investigating different ecological processes acting on *Urophora Jaceana*, Varley showed that three factors control population size: direct density dependent early larval mortality and delayed density dependent parasitism by two different parasitoids. While the use of mathematical theory and statistical methods of analysis (to account for both deterministic and stochastic factors) have advanced enormously since Varley's study, the necessity for clear, carefully planned field experiments to test concepts has never been in dispute. Varley's paper remains a testament to this approach of challenging contemporary theory with experimental and observational tests

Michael Bonsall

03

Birch, L.C. (1948)

The intrinsic rate of natural increase of an insect population. *Journal of Animal Ecology, 17: 15-26.*

Charles Birch (1919-2009) wrote this paper while visiting Elton's Bureau of Animal Population at Oxford. By 1948 he had joined Sydney University. As of 2012, this paper has 1,445 citations. It urges that 'The intrinsic rate of increase [r, as introduced by Lotka for human populations] is a basic parameter which an ecologist may wish to establish for an insect population'. The paper shows, in detail that looks excruciating by today's standards, how r is calculated from age-specific survivorship and fecundity data (l_x and m_x) from $\int_0^\infty e^{-rx} l_x m_x \, dx = 1$. Birch discusses the ecological usefulness of r, and gives a very detailed illustration of its calculation from data for the rice weevil *Calandra oryzae*. Notably, this is one of the first quantitative analyses of the demographic behaviour of an animal population, albeit one which was growing exponentially under laboratory conditions. More generally, Birch was a major figure in ecology's earlier days. With Andrewartha he wrote The *Distribution and Abundance of Animals* (Chicago University Press, 1954), the world-wide leading ecology textbook of the 1950s and 1960s. In the late 1960s he founded the Social Responsibility in Science Movement in Australia (to which I owe my subsequent career). He also was an influential and ego-free leader of anti-Vietnam-war activism in Australia.

Robert May

04

Solomon, M.E. (1949).

The natural control of animal populations. *Journal of Animal Ecology,18, 1-35.*

Although influential, this paper had a slow start, only 327 citations being recorded for it between 1949 and 1993. Since 2000, however, it has averaged about 28 citations a year. To the modern reader this paper comes across as wordy and discursive, more like a popular article than a scientific paper. This does not, however, mean that the science and the man behind the article were not first class. Journals had less pressure on their space in those days and scientists had more time to think and read. If only it were so now. This paper has had an immense influence on the study of population dynamics, although for my generation who were undergraduates in the 1970s, Solomon's little Study in Biology book, *Population Dynamics*, published in 1969, was our main, if not only, encounter with his work. Today we recognise this paper as the first one to formalise the term 'functional response' and the first to draw together the disparate conceptual strands of pre-war population dynamics in one coherent whole. This was an inspirational paper and inspired early modern mathematical ecologists such as Holling, Watt, Gradwell and Varley and through them more recent past BES presidents such as Mike Hassell, Bob May and John Lawton. A truly influential piece of writing.

Simon Leather

05

Varley, G.C. & Gradwell, G.R. (1960)

The natural control of population balance in the knapweed gall-fly, (Urophora jaceana). *Journal of Animal Ecology, 16, 139-187*

This paper provided the first methodology that was widely used to dissect the immediate causes of changes in population size. Following Morris's concept of key mortality factors, Varley and Gradwell developed a quantitative approach based on Haldane's logarithmic method for comparing the contribution of successive mortality factors to total mortality. The method was originally applied to time series for winter moth populations in Wytham Wood, where variation in winter disappearance was the key factor responsible for most of the variation in numbers. It was subsequently used by others to explore the dynamics of other invertebrates, birds and mammals. It proved particularly useful in relatively long-lived species where it provided a way of identifying the relative impact of mortality in different categories of individuals on changes in population size. Today, this approach has been largely abandoned in favour of more powerful and sophisticated techniques and it is appreciated that complex patterns of dynamics can emerge from systems where population growth rate depends on population density in a non-linear manner. Nevertheless, both the new methods and our understanding of the demographic impact of mortality at different stages owe much to Varley and Gradwell's original paper and the approach to population dynamics that they pioneered.

Tim Clutton-Brock

06

Roland, J. (1994)

After the decline- what maintains low winter moth density after successful biological control? *Journal of Animal Ecology, 63, 392-398*

In the 1950's the winter moth, *Operophtera brumata* became well known to population ecologists as the subject of one of the first life table analyses of an insect population [Varley, G.C. and Gradwell, G.R. *Journal of Animal Ecology*, **29**, 399-401 (1960)]. At about the same time winter moth was discovered to be defoliating oak woodlands in Nova Scotia in eastern Canada, and 20 years later it moved west to Victoria, British Columbia. The tachinid fly, *Cyzenis albicans* was introduced to Canada as a biological control agent. Because parasitization was low for British winter moth populations, Varley thought this fly would not be a successful biocontrol agent. But it was. Using both a life table approach and experiments, Jens Roland carried out one of the most comprehensive experimental investigations of a successful biological control programme. His work showed that winter moth populations can have two distinct density equilibria, a higher one in the absence of a specialized parasitoid and a lower one regulated by ground beetle predation on pupae. The important messages from this work are that 1) successful biological control agents do not have to be density dependent, 2) factors that limit and regulate populations can be different, and 3) parasitoids that are relatively rare in the native habitat can be successful control agents.

Judith Myers

07

Perrins, C.M. (1965)

Population fluctuations and clutch-size in the great tit, Parus major L. *Journal of Animal Ecology, 34, 601-647.*

The long-term study of great tits, Parus major, at Wytham Wood, near Oxford, has contributed a great deal to our understanding of population dynamics, and this paper by Perrins which formed the foundation for much of the work that followed, is still widely cited nearly 50 years after its publication. It was written at a time when there was much debate about how natural selection operated; whether on the individual or on the group. Perrins provided clear evidence that great tits did not limit their reproductive effort for the good of the species. Instead, individual birds maximised their lifetime reproductive success according to the resources available to them, and population size was limited by food supply rather than the birds themselves. It has since become one of the classic examples used in teaching to explain the fallacy of 'good of the species' arguments and group selection in general.

Ian Hartley

08

Murton, R.K., Isaacson, A.J. & Westwood, N.J. (1966)

The relationships between wood-pigeons and their clover food supply and the mechanism of population control. *Journal of Applied Ecology, 3, 55-96.*

Employed by the Ministry of Agriculture, Fisheries and Food to study woodpigeons as pests, Murton and his team carried out an extensive study. Whilst this could easily have just been a useful piece of research, their thoughtful approach to population ecology and behaviour resulted in a study with pioneering methods and concepts. By simultaneously studying the clover food supply and the bird's behaviour and ecology they determined the functional response, the aggregative response between food density and woodpigeon distribution, the impact of food on annual abundance and within flock variation in intake. Other components of this remarkably complete study included examining the dynamics of clover within pigeon-proof exclosures, determining the response to severe weather, measuring body condition and assessing the long term response of the clover population to grazing. Combining these elements leads to their theory as to how the population is regulated: most birds are in good condition but when the population is high relative to the food supply the few birds in worst positions gain insufficient food, lose mass and either die or leave. By integrating behaviour with ecology, theory with fieldwork, observations with experiments, condition with demography, and local distributions with interannual changes, the paper set the stage for the study of vertebrate responses to their food supply and for answering a range of applied questions.

William J Sutherland

09

Harper, J.L. (1967)

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

Harper synthesised the fundamental principles defining a discipline and drafted the path for later research. He recalled our 'distinguished parenthood', shared with population geneticists, and he advocated Darwin's quantitative approaches to ask why demographic thinking hadn't yet permeated plant ecologists' agendas. 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 value of plant numbers. Tallying numbers is needed to estimate the balance between added and disappeared individuals in a way that can be translated into genetic selection studies or estimates of ecosystem fluxes. When coupled with studies of plant vigour, numbers are invaluable in assessing processes of population regulation. 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 built a convincing case for experimental approaches to the study of plant coexistence under field conditions. Harper doubted his ability to deal adequately with the part played by plant-animal interactions, but I think he had the ability (see web site account).

Pedro Jordano

10

Sarukhán, J. & Harper, J.L. (1973)

Studies on plant demography: Ranunculus repens L., R. bulbosus L. and R. acris L. I. Population flux and survivorship. *Journal of Ecology, 61, 675-716.*

In his seminal 'Darwinian approach' paper [see (1967) *Journal of Ecology*, **55**, 247-270; on p. 10] Harper highlighted the almost total neglect of studies on plant numbers, a neglect that had hindered development of plant ecology within both population dynamics and life history evolution. A surge of papers on plant demography followed, and in the early 1990s the time was ripe for a first general synthesis of plant demography [see Silvertown et al. (1993) *Journal of Ecology*, **81**, 465-476 see below). An essential inspiration for this tremendous growth of knowledge on the details of plant population dynamics was the study on three buttercup species by Jose Sarukhán in a field in Caernarvonshire, Wales. During a period of two years from spring 1969, Sarukhán made continuous detailed recordings of every single plant in permanent plots, from seedlings to mature adults, using a pantograph. This methodology would set the standards for later studies on plant demography. The two years of trying field work rewarded Sarukhán with several new insights into the life of plant populations, e.g. the large dynamic flux of individuals despite rather stable population sizes, detailed estimates of plant turnover, life-length and reproductive output, and, perhaps most important for later population analyses, the basis for estimates of vital rates.

Ove Eriksson

11

Silvertown, J., Franco, M., Pisanty, I. & Mendoza, A. (1993)

Comparative plant demography – relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. *Journal of Ecology, 81, 465-476.*

How can ecologists make meaningful comparisons of the demography of plants as contrasting in life history as annual weeds and giant redwoods? Such comparisons make apples and oranges seem like close cousins. This paper pioneered the use of stage projection matrices to compare large numbers of species, compiling data for 66 herbs, shrubs and trees. It uses the finite rate of population increase (λ) and the elasticity of matrix elements (a measure of an element's contribution to fitness) to make meaningful comparisons of the growth, survival and fecundity of this diverse array of species, showing clear trade-offs among life-cycle components and a separation of functional groups in demography space. Over 300 plant matrix modelling papers have been published since 1993 using ever-more sophisticated techniques, but this paper remains as a leading example of how the technique can be used to compare the ecology of species.

David Coomes

12

Mohler, C.L., Marks, P.L. & Sprugel, D.G. (1978)

Stand structure and allometry of trees during self-thinning of pure stands. *Journal of Ecology, 66, 599-614.*

Self-thinning is one of the major phenomena of plant populations. Mohler, Marks & Sprugel evaluated the -3/2 power relationship between tree density and average tree biomass, proposed by Yoda, Kira, Ogawa and Hozumi, along the development of even-aged pure stands of pin cherry and balsam fir, with allometric properties between size dimensions that are used to estimate tree biomass, and the change in size structure with stand age. Their study was attractive for various reasons: (1) the two target stands were contrasted in that pin cherry is shade-intolerant whereas balsam fir is shade-tolerant; (2) a bivariate model fitting was employed, which is statistically appropriate; and (3) interaction between crowding and tree allometry was suggested. To relate individual architecture, resource competition, population structure and dynamics, and ecosystem properties in carbon accumulation and turnover is a central issue of ecology, and this paper keeps its significance for this reason. This study has been followed by many empirical and theoretical studies, including critical meta analyses, that encourage ecologists to employ stand biomass rather than average tree biomass for discriminating statistical problems, and in building the metabolic theory of allometry.

Takashi S Kohyama

13

Hassell, M.P. & May, R.M. (1973)

Stability in insect host-parasite models. *Journal of Animal Ecology, 42, 693-726.*

The population dynamics of predator-prey and other consumer-resource interactions have a natural propensity to oscillate. Predator numbers increase and drive down the population of their prey which leads to starvation and predator decline. With their predators rare, the prey population recovers and the cycle can begin again. Simple models often predict diverging cycles leading to the extinction of predator or prey. Understanding the biological mechanisms that allow consumer-resource interactions to persist has been a major goal of population ecology. Much of this research has involved parasitoids, insects that lay eggs in the bodies of other insects. Parasitoids are very important in biological control, and the relatively simple manner in which a successful attack results in typically one new parasitoid greatly simplifies modelling. Hassell & May summarised what was known about the factors that might stabilise parasitoid-host interactions and developed a series of models to unify and extend existing theory. They concluded that non-random search leading to refuges for hosts when parasitoids were at high density was the most biologically likely stabilising mechanism. Over the next twenty years the authors and other groups developed a sophisticated theory of parasitoid and predator searching upon which our current understanding of resource-consumer persistence is based.

Charles Godfray

14

Anderson, R.M. & May, R.M. (1978)

Regulation and stability of host-parasite population interactions. I. Regulatory processes. *Journal of Animal Ecology, 47, 219-247.*

The models described in this paper, together with its sister paper 'II. Destabilizing processes' (May and Anderson 1978), changed the way ecologists and epidemiologists viewed host-parasite associations as a special class of predator-prey interactions. The first paper showed (1) how overdispersion of parasite numbers per host, (2) non-linear functional relationships between parasite burden per host and host death rate, and (3) density dependent constraints on parasite population growth within individual hosts, stabilise the dynamical behaviour of host-parasite and enhance the regulatory role of the parasite. The second paper, on destabilizing processes, again identified three important categories of biological processes: parasite-induced reduction in host fecundity, parasite reproduction within a host which directly increases parasite population size, and time delays in parasite reproduction and transmission.

Both papers are citation classics, the former cited over 800 times in the last 35 years, and have provided the theoretical framework for empiricists to test hypotheses about the role of parasites in the population dynamics of their hosts. For example, work on the controversial mechanisms causing regular cycles in the population dynamics of both invertebrate pests and the game-bags of red grouse, as well as the role of parasites in the more chaotic dynamics of reindeer.

Steve Albon

15

Watt, A.S. (1947)

Pattern and process in the plant community. *Journal of Ecology, 35, 1-22.*

Although based on his extensive studies of grasslands in Breckland (eastern England), beech woods in the Chiltern Hills and heathlands on Scottish mountains, Alex Watt's paper highlights two essential aspects of the science of ecology. First, ecology is an observational science; people have attempted to identify patterns in what is observed. Second, ecology is an experimental science; by deducing the processes which created those patterns, hypotheses can be formulated and tested by experimentation. The dynamic nature of plant communities is a core consideration, with competition and stress, caused by disease or depletion of nutrients, being both explicitly and implicitly associated with 'cyclic change'. Perhaps for a botanist, it is surprising to find Watt's disappointment in the lack of literature demonstrating the "intimacy and integration between plants and animals" and "the life histories and food habits of microorganisms". How many times in the last decade or two have papers in the *Journal of Ecology* referred to plant-animal interactions, or to above-ground/below ground relationships? Half a century earlier, Watt was suggesting that these topics needed more investigation, but his thesis is that "problems in nature are problems of the ecosystem rather than of soil, animals or plants" (page 22), a strong pointer to the need for a systems approach in ecology.

Michael B. Usher

16

Botkin, D.B., Janak, J.F. & Wallis, J.R. (1972)

Some ecological consequences of a computer model of forest growth. *Journal of Ecology, 60, 849-872.*

Botkin, Janak and Wallis were pioneers in the application of simulation modelling to understanding successional processes in forests. The paper engenders the sort of excitement that arises when you stumble upon an old camera and cherished childhood photos. You stop everything you're doing for a few moments to admire them, opening up the camera's back and fiddling with the delicate lever which controls the aperture and gently pressing that all-or-nothing shutter; you feel you understand completely how it works and admire its simple beauty. The white-bordered photos are small and grainy with exaggerated colour, but they too have a remarkable quality to them. So it is with this particular study. The algorithm is straight forward, captured completely in a few simple equations and capable of running on any computer with at least 50 kbytes of available memory, yet it contains the major building blocks found in all later forest simulators: subroutines describing tree growth, recruitment and mortality with modifiers for site conditions. The presented outputs are little more than a few hand-drawn curves, yet they capture the essence of forest succession remarkably well, and herald an era when simulation models are used routinely as tools to integrate ecological knowledge and test hypotheses that cannot be explored by conventional experimentation.

David Coomes

17

Crocker, R.L. & Major, J. (1955)

Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. *Journal of Ecology, 43, 427-448.*

The study employed the chronosequence approach, whereby soils were sampled on terrain of increasing age since glacial retreat. Glacier Bay was ideally suited to the study because of the detailed history of deglaciation at the site, which allowed soils to be aged, and the rich knowledge of vegetation succession. Crocker and Major's most striking finding was the rapid rate of soil nitrogen accumulation, which was strongly related to vegetation distribution and development; during early succession, soil nitrogen was found to increase dramatically under plants believed to fix nitrogen, especially *Alnus*, and then decline in late succession following the replacement of *Alnus by Picea*. Such patterns of nitrogen accumulation during succession are now well documented and understood. However, this study firmly established the need to consider both plants and soils, and their intimate interactions, to fully understand how ecosystems develop and function. The paper is also an enjoyable read. Crocker and Major write in an engaging and very descriptive way about their experiences of sampling soils at Glacier Bay and the problems that they encountered; such writing is now lost from ecological literature.

Richard Bardgett

18

Noy-Meir, I. (1975)

Stability of grazing systems: an application of predator-prey graphs. ***Journal of Ecology, 63, 459–481.***

Three strands in Noy-Meir (1975) have continuing influence through to the present. Firstly, Figure 5e showed how two very different steady states can arise when a given herbivore stocking rate interacts with the forage production from vegetation. Across many different ecosystem-types, the 1970s were marked by increasing appreciation of alternative states, as also of disturbance regimes and of lottery processes. Noy-Meir (1975) manifested that same shift in outlook for grazing systems. Secondly, the Discussion gathered evidence together from range and pasture literature. As he put it 'While each of these pieces of evidence is rather meagre, cumulatively they indicate that some range and pasture systems are discontinuously rather than continuously stable.' But range management theory at the time did not provide for alternative persistent states. This discrepancy subsequently stimulated development of state-and-transition language (see web site) in order to describe ecosystem dynamics more realistically. Thirdly, Figures 8-10 showed how as the stocking rate approached closer to maximum sustainable yield, the plant-herbivore balance became more vulnerable to year-to-year variation. This idea that for natural resources there is a choice between maximizing yield and reducing vulnerability was an important motivation for the now-prominent concept of resilience in social-ecological systems.

Mark Westoby

19

Resetarits, W.J. & Chalcraft, D.R. (2007)

Functional diversity within a morphologically conservative genus of predators: implications for functional equivalence and redundancy in ecological communities. ***Functional Ecology, 21, 793-804.***

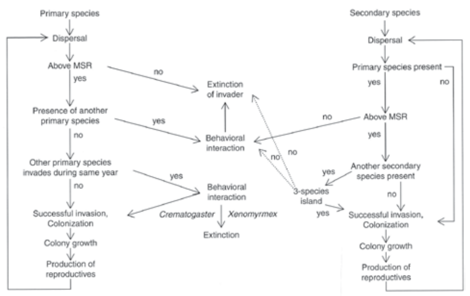
How far are species that are phylogenetically closely related, morphologically very similar, with the same type of life cycle, and found in the same habitat 'functionally equivalent'? The authors investigated this issue using the three species of sunfish in the genus *Enneacanthus*. These species are predators and are broadly sympatric in streams and pools on the eastern seaboard of North America; often two species cohabit, and rarely three. In a three-month experiment the various sunfish species were kept separately with three anuran species from the tadpole stage in artificial ponds outdoors. In terms of effects on larval anurans only one of three pairs of species could be considered functionally equivalent, and these two species showed the greatest differences in growth and therefore metabolic demand. In terms of relative yield total only one pair of species could be rated functionally equivalent, and their effects on larval anurans were very different. This paper goes to the heart of how communities are structured. In their analyses, the authors integrate physiology with ecology to test ideas about functional equivalence. They challenge the commonly held view that functional equivalence is widespread and should be expected. This issue is central to understanding the relationships between diversity and ecosystem function.

Duncan Irschick

20

Cole, B. C. (1983).

Assembly of mangrove ant communities: patterns of geographical distribution. ***Journal of Animal Ecology, 52, 339-347.***



21

Cole, B. C. (1983).

Assembly of mangrove ant communities: colonization abilities. ***Journal of Animal Ecology, 52, 349-355.***

Combining studies on distribution, habitat suitability, social behaviour, caste structure, colonizing ability, and ergonomics, Blaine Cole provided an unusually compelling argument on how an ant community is assembled. Using small mangrove islands in the Florida Keys, he generated experimentally mechanistic assembly rules for the five species involved, noting the presence of two competitively dominant species, termed Primary, others being less aggressive and avoiding encounters with dominant species. These rules were partially deterministic – competition and behaviour prevented coexistence of some species – and partly stochastic – establishment of one of the Primary species on an island precluded colonization by the other. This study exemplifies the detailed nature of investigations needed to establish a convincing mechanistic understanding involving coexistence of species in a natural setting. Even when small islands and few highly aggressive species are examined, the richness of factors impinging on assembly is impressive, suggesting that in other studies the detection of pattern with deduced assembly rules, without mechanistic studies, are too primitive to reliably interpret nature. The figure illustrates the assembly of the ant communities with constraints on the presence or absence of species and their coexistence. MSR denotes the minimum size requirement needed for an ant species to persist on a certain island size.

Peter Price

22

Gross, K.L. (1984)

Effect of seed size and growth form on seedling establishment of 6 monocarpic perennial plants. ***Journal of Ecology, 72, 369-387.***

This seminal study is based on a comparative experiment, in which Gross measured the relative growth rate (RGR, mg g-1 day-1) of six monocarpic herbs that share basal leaves but span more than two orders of magnitude in seed size. When plants were grown on bare soil, with or without litter, RGR decreased with seed size within and across species. When grown with a competitor, plants instead displayed an increase in RGR with seed size. These context-specific differences in RGR – combined with the usual advantages in seed number for smaller-seeded species at a given reproductive effort – have profound implications, suggesting that competition should favour small seeds in fugitive species that establish in recent disturbances, and larger seeds in species that establish in more crowded microsites. This study confirmed some earlier ideas regarding the adaptive significance of seed size, but surprisingly demonstrated an RGR advantage for small seeds in open microsites – a pattern supported by several later glasshouse studies. Gross' investigation should be replicated on a grand scale, with phylogenetically structured analyses and addition of several co-varying traits, and the basis of context-specific advantages in RGR sought in the allometry of allocation to different organs and correlations with photosynthetic traits.

Tom Givnish

23

Thompson, K. & Grime, J.P. (1979)

Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. ***Journal of Ecology, 67, 893-921.***

Great progress in ecological research has been facilitated by new methods, as for example GIS technology or microsatellite markers, or new theoretical concepts based on existing data. The paper by Thompson & Grime (1979) falls in the second category. Some field and laboratory studies on seed banks had already been done before the 1970s, but the differences in seed longevity were described without consistent theoretical basis. The suggested four categories of transient and persistent seed banks were based on seasonal variation in seed release, germination and seed abundance in the soil. This relatively simple but elegant scheme was readily accepted by the ecological community and stimulated thousands of empirical studies in almost all biomes and continents. The concept was attractive because it suddenly offered a terminology for communicating species- and site-specific differences in seed bank characteristics. The significance of the paper is not reduced by the fact that it later turned out to be not fully correct, and thus became replaced by a slightly modified set of seed bank types, incidentally from the same research group [Thompson, Bakker & Bekker (1997) *The Soil Seed Banks of North West Europe: Methodology, Density and Longevity*].

Johannes Kollmann

Bellamy's bank, Miller's Dale, Derbyshire one of the research sites

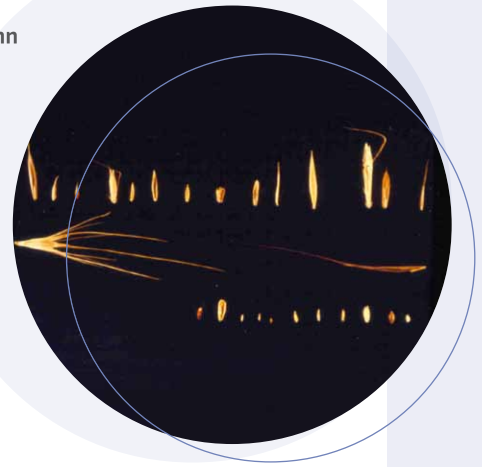
24

Thompson, K., Band, S.R. & Hodgson, J.G. (1993)

Seed size and shape predict persistence in soil. *Functional Ecology, 7, 236–241.*

I discovered this paper during preparation of a journal club session at the Eidgenössische Technische Hochschule Zürich, in a period when I had just done a number of seed bank surveys. I had a strong feeling that seed size was a key trait for understanding the contrasting abundances of seeds in the soil. Seed shape also looked like a suitable candidate for explaining seed movement into the soil. This paper used for the first time a simple but effective approach for predicting species-specific differences in persistence of the soil seed bank. This was achieved by plotting seeds of a range of British species in a two-dimensional diagram based on seed mass and variation of seed dimensions. In doing so the authors could demonstrate that there was a marked separation between species with large and elongated seeds resulting in transient seed banks compared with small and round seeds with high persistence. This concept has later been tested with several floras outside north-western Europe with variable results.

Johannes Kollmann



Seeds of a range of British grass species. Seeds in the bottom row have persistent seeds banks, while the rest are transient.

25

Grime, J.P. (1998)

Benefits of biodiversity effects on ecosystems: immediate, filter and founder effects. *Journal of Ecology, 86, 902-910.*

Since the mid 1990s there has been considerable focus on how plant biodiversity, including species richness, drives ecosystem processes such as productivity, nutrient cycling and decomposition. While many studies in the 1990s focused on immediate effects of biodiversity, Grime's 1998 paper was an important advance because it highlighted the importance of distinguishing immediate effects driven by dominant species from filter and founder effects emerging over longer periods when subordinate and transient species play a role. Based on this approach, Grime proposed a 'mass ratio hypothesis', predicting that the relative contribution of each species to ecosystem properties should be proportional to its contribution to total primary productivity. Then ecosystem processes should be driven primarily by traits of the dominant species (those contributing most to productivity) rather than species richness of minor components. This concept has had an enduring impact for three reasons. First, it provides plausible reasoning as to why plant community composition rather than species richness may be a powerful driver of ecosystem functioning. Second, it explicitly identifies a central role of plant traits in driving ecosystem processes, an area that is attracting considerable effort. Third, it provides the conceptual underpinning for increasingly widely used 'community weighted' approaches for quantifying plant traits and/or processes at the whole community level.

David Wardle

26

Smith, W.G. (1913)

Raunkiaer's "life-forms" and statistical methods. *Journal of Ecology, 1, 16-26.*

Smith reviewed two kinds of contribution by Raunkiaer: characterization of vegetation types in terms of 'life-form spectra', and studies on the merits of different-sized samples of vegetation. Here I cover only the first of these. Raunkiaer's work had previously been set out only in Danish, French and German. He wanted to get away from classification in terms of floristics, and find a means of expressing in terms of what we would now call structure and physiognomy the impact of the climate on vegetation (especially seasonal cold and lack of rain). He introduced 'life-forms' based partly on height attained at maturity, partly on the positions of the buds during any 'critical or rigorous season', and partly on whether the buds persist in waterlogged soil or under a body of water. These had the now-familiar names of phanerophyte, chamaephyte, hemicryptophyte, geophyte, helophyte, hydrophyte and therophyte. In his comparisons of different vegetation types (rain forest, temperate deciduous forest, semi-desert etc) summarized by Smith, Raunkiaer also used the established terms stem-succulent and epiphyte. His practice of comparing the life-form spectrum of each vegetation type with 'the normal spectrum' (a mean spectrum based on the whole world's vegetation) was not widely adopted, but his categories have been used by innumerable plant ecologists.

Peter Grubb

27

Oliver, F.W. (1913)

Some remarks on Blakeney Point, Norfolk. *Journal of Ecology, 1, 4-15.*

F.W. Oliver, Quain Professor of Botany at University College London, gave Tansley his first job and remained his patron. He was a member of the British Vegetation Committee (predecessor of the British Ecological Society), host at UCL in 1913 to the inaugural meeting of the BES, and its second President. He advocated, and energetically practised, the application of ecology in public affairs. With Tansley, he led student parties (1904-1906) to the Bouche d'Erquy in Brittany, and in later years to Blakeney Point on the north Norfolk coast (where he worked with E.J. Salisbury, commissioned the first use of aerial survey in ecology, acquired Blakeney Point and presented it to the National Trust). These student parties, which studied the ecology and ecophysiology of plants on shingle, sand dune, and saltmarsh, continue even today. Oliver here summarises the work of the early excursions. He describes the growth of the series of shingle ridges that resemble 'a dilapidated comb in which the surviving teeth occur in groups near the end'. He notes, with reservations, space as a surrogate for time in the study of successions. He recognises 'catastrophism' and continuous processes. He makes quantitative calculations of the shingle source. And he considers the autecology of *Suaeda fruticosa* and *Artemisia maritima*.

Dicky Clymo

28

Marsh, A.S. (1915)

The maritime ecology of Holme next the Sea, Norfolk. *Journal of Ecology, 3, 65-93.*

Coastal environments have been important theatres for research from the inception of plant ecology, the *Journal of Ecology* and indeed the Society. Salt marshes, shingle and dunes were manifestly dynamic systems, which exhibited striking environmental and vegetational gradients; arguably these are the ingredients that inspired the development of several fundamental concepts and particularly those related to succession. In volume 3 of the *Journal of Ecology*, Marsh reported substantial and intensive field investigations by a team that brought together a range of expertise and techniques. They recognized and mapped the different vegetation communities ('societies'), relating their distribution to sediment depth and texture, elevation, and the degree of tidal inundation. Having documented the shifting physiography of this coast from historical sources and his own surveys, Marsh appreciated the dynamic nature of coastal systems; he described the role of disturbance in maintaining the vegetational mosaic, and interpreted successional relationships between the plant communities – an early example of space-for-time substitution. This classic paper promises further instalments and the initiation of experimental work but, sadly, with the outbreak of World War I, he felt duty-bound to volunteer. Captain Marsh was shot through the heart by a sniper at Armentières in January 1916, a month short of his 24th birthday.

Tony Davy

29

Chapman, V.J. (1938)

Studies in salt-marsh ecology. Sections I to III. ***Journal of Ecology, 26, 144-179.***

This was the first paper in a series by V. J. Chapman in the journal, and introduces the studies based on the north Norfolk coast, and especially Scolt Head Island, which were to make a hugely significant contribution to our understanding of salt marsh ecology. Somewhat descriptive by today's standards, it outlines the main environmental factors which influence the distribution of plant species, emphasising the overriding effect of tidal submergence. In dividing salt marshes into two main types Chapman invites us to test, in future work, the idea that the downward spread of species of the upper marsh is limited by increasing submergence and the upward spread of lower marsh species is limited by the degree of non-tidal exposure. Whilst later research has emphasised the importance of dynamic processes such as facilitation and competition in assembling salt marsh communities, Chapman's careful analysis of the tidal and physical environment in this first paper set the scene for many subsequent studies of primary succession in a frequently zoned and highly structured environment.

Alan Gray

30

Summerhayes, V.S. & Elton, C.S. (1923)

Contributions to the ecology of Spitsbergen and Bear Island. ***Journal of Ecology, 11, 214-286.***

In 1921, a group of Oxford University biologists spent ten weeks in the Arctic carrying out ecological surveys on Bear Island and Spitsbergen. The group included Charles Elton, a 21 year-old second year student, recruited by his tutor, Julian Huxley. The species-poor communities allowed Elton, working with Victor Summerhayes, a recent graduate in botany who became an orchid expert at Kew, to realize that their ecology could most effectively be described by food relationships. This recognition [elaborated further in *Journal of Ecology* (1928) **16**, 193-268] persuaded Elton to focus on what he called the 'sociology and economics of animals' and to develop ideas about trophic levels and number pyramids. He refined these concepts on subsequent visits to Spitsbergen in 1923 and 1924 and led him on to investigate the factors that regulate population numbers – concepts which he set out in his seminal 1927 book *Animal Ecology* (written at Huxley's instigation in 85 days). Elton's experiences on his Arctic expeditions laid the basis for what became a key component of the 'British tradition' of scientific natural history.

R.J. (Sam) Berry

31

Tansley, A.G. & Adamson, R.S. (1925)

Studies of the vegetation of the English chalk. III. The chalk grasslands of the Hampshire-Sussex border. ***Journal of Ecology, 13, 177-223.***

This paper is not just an account of the floristics of the chalk grassland, chalk heath and juniper scrub of a part of the South Downs that Tansley loved. For many ecologists the chief interest is in the authors' pioneering experiment with rabbit-exclosures. The exclosures were big (390-820 m2) and not sufficiently replicated by modern standards (two only). Nevertheless they revealed effects found repeatedly by later researchers. The experiment was begun in 1908, showing that although Tansley did not generally carry out experiments on single species under garden or laboratory conditions [cf. p. 27], he recognized early on the need for field experiments. The 1925 paper documented the specific effects of close grazing by rabbits as opposed to sheep. Most characteristic is the great reduction in grasses relative to the dicot *Sanguisorba minor* so that the latter species becomes the dominant, and grass leaves are seen to be bitten off exactly at the level where they begin to poke through the *Sanguisorba* canopy. Exclosure led to a large increase in grass relative to *Sanguisorba*, and illustrated the variation in flexibility of growth form among the dicots that are common in very short turf – some can grow tall and persist without close grazing while others cannot grow tall and are overwhelmed.

Peter Grubb

32

Stephenson, T.A. & Stephenson, A. (1949)

The universal features of zonation between tide-marks on rocky coasts. ***Journal of Ecology, 37, 289-305.***

Marine biologists around the world described their local shores and emphasised the unique inhabitants. Alan Stephenson took a contrary view. While at the University of Cape Town he compared temperate shores to the west of the Cape with tropical ones to the east. He concluded that despite their differences there were underlying similarities and these were of widespread occurrence. He and his wife Anne studied more shores around the world than anyone before and since. In the 1949 paper he outlined his aim which was to introduce a system . . . 'which may be of universal application.' He defined four recurring zones that were characterised by types of organisms. The **supralittoral fringe** the area wetted by spray and inhabited by lichens and littorinid snails; the **midlittoral zone** of barnacles and limpets that was covered and uncovered daily by the tide, and so on. On shores not obscured by seaweeds the white band of barnacles and above it a band of black lichens are unmissable. Their scheme provided a standard nomenclature to enable researchers worldwide to specify exactly where they were working in a steep environmental gradient. This was particularly useful when from the 1960s onwards the seashore became a test bed for field-based experiments exploring the interactions between stress tolerance and interspecific competition.

Trevor Norton

33

Poore, M.E.D. & McVean, D.N. (1957)

A new approach to Scottish mountain vegetation. ***Journal of Ecology, 45, 401-439.***

This paper had a much wider impact than its title might suggest. It was outstanding in the way it contributed to the transition from a mainly floristic approach to research on Scottish plant communities to a better appreciation of the role of the ecological factors which determine their composition. Based on studies carried out by methods described by Poore in three papers closely preceding this one [*Journal of Ecology*, **43**, 226-269 and 606-651], the 'new approach' advocates a framework of five 'factor complexes' – altitudinal zonation, oceanicity, snow cover, base status, and moisture – and on this basis provides descriptions of a range of communities selected partly for 'their intrinsic interest and partly to illustrate how the patterns of Scottish mountain vegetation can be fitted into the ecological framework'. This offered a novel and practical basis both for future studies and for the further development and interpretation of this attractive and important set of communities. Poore and McVean deplore the fact that previous work in the UK on mountain vegetation makes scant reference to the extensive and relevant Scandinavian publications on this topic. They go some way to remedying this lack, and their lead has been fruitful in the recognition of important parallels or contrasts between Scandinavian and British findings.

Charles Gimingham

34

Webb, L.J. (1959)

A physiognomic classification of Australian rain forests. ***Journal of Ecology, 47, 551-570.***

No doubt one reason this paper has been cited more than 300 times is that it used structural and physiognomic criteria to classify vegetation, a lead later followed by many. It also echoed Beadle's view that soil fertility is a major determinant of vegetation structure and plant form in Australia. For me, however, Webb's description struck a deep chord because it crystallized the latitudinal and geological distributions of vegetation characterized by differences in leaf size and shape, in canopy stature, stratification, continuity, and deciduousness, and in the abundance of woody vs. herbaceous vines, tree ferns, palms, and vascular and non-vascular epiphytes. The obvious question in each case – though never articulated by Webb – was why? Why do plants with different leaf forms and growth habits dominate different climates and substrates? Why, over much of the Great Dividing Range, do sclerophyll *Eucalyptus* forests dominate the tablelands while rain forests dominate the gullies? Why does maximum tree height increase with latitude in Australian rain forests? Why are deciduous trees so uncommon in Australia? Such questions – and their physiological, population, and ecosystem-level ramifications – have long been an impetus to my thoughts, and Webb's paper is now increasingly cited for such reasons by other authors.

Tom Givnish

35

Hill, M.O. (1973)

Reciprocal averaging: an eigenvector method of ordination. ***Journal of Ecology, 61, 237-249.***

How can we best describe, quantify and compare the species composition of communities and relate variation in composition to the environmental and other factors that determine it? During the 1960s and 1970s there was considerable debate about how best to answer these questions; the available techniques included gradient analysis, polar ordination and principal components analysis. Using a combination of gradient analysis and the method of successive approximation, Hill introduced a methodology known as reciprocal averaging (or correspondence analysis) that is a particular uncentred form of principal components analysis with double standardisation. The technique can be used with both presence/absence and quantitative data and has the particular advantage of producing both stand and species ordinations. The duality of the species and stand ordinations is the chief advantage of reciprocal averaging; computationally it is also very efficient. The technique does, however, have two distinct faults. The first is the arch effect, a mathematical artefact, and the second is that equivalent differences in species composition are not represented by the same distances in the ordination. It was the elimination of these two faults by detrending and standardization that allowed Detrended Correspondence Analysis [Hill & Gauch (1980) *Vegetatio*, **42**, 47-58] to be developed. This became the dominant technique for the ordination of plant communities.

Andrew Watkinson

36

Condit, R., Hubbell, S.P., Lafrankie, J.V., Sukumar, R., Manokaran, N., Foster, R.B. & Ashton, P.S. (1996)

Species-area and species-individual relationships for tropical trees: a comparison of three 50-ha plots. ***Journal of Ecology, 84, 549-562.***

This paper was one of the first to describe comprehensive analyses from 50-ha forest plots in the tropics. It is based on 610,000 stems mostly identified and all mapped; before these 50-ha plots tropical ecologists thought that 1 ha was large and that tree species richness reached an asymptote at 1-3 ha. The three plots were from Malaysia, Panama and India, and from evergreen, semi-evergreen and dry forest respectively. Even at 50 ha new species were being recorded. One of the main reasons why this paper has been so widely cited is that the authors interpret the lack of an asymptote in the species area curves as evidence for the community drift model proposed by Hubbell in his 2001 book *The Unified Neutral Theory of Biodiversity and Biogeography*. That model has generated much discussion in the literature. A decade later it is widely accepted that there is a lot of ecological redundancy in tropical tree species though few accept that for all species in tropical forest 'life history trade-offs equalize per capita relative fitness of species' (page 346 in Hubbell's book).

Edmund Tanner

37

Anderson, M.C. (1964)

Studies of the woodland light climate. I. The photographic computation of light conditions. ***Journal of Ecology, 52, 27-41.***

Light is one of the most strongly varying environmental resources with major changes in light intensity occurring at time-scales as short as fractions of seconds to as long as days, months and seasons. The paper of Anderson (1964) has greatly advanced the understanding of the variability of light in plant communities and provided a methodology for light estimation that is used extensively today. The paper introduced the concepts of direct, diffuse and total site factor to describe the percentage of light availability and demonstrated that hemispheric photography can be reliably used to estimate all these light components. As a method for getting snapshots of canopy gap distributions, hemispherical photography has also played a major role in the development of radiative transfer theory for plant canopies. Furthermore, the study of Anderson (1964) has served as a springboard for development of a methodology for rapid optical estimations of vegetation leaf area index used today by a huge community of plant canopy researchers. Overall, the paper remains as a key reference for anyone attempting to use hemispherical photography for quantitative estimation of light availability in vegetation.

Ülo Niinemets

38

Newman, E.I. (1966)

A method of estimating the total length of root in a sample. *Journal of Applied Ecology, 3, 139-145.*

39

Tennant, D.M. (1975)

A test of a modified line intersect method for estimating root length. *Journal of Ecology, 63, 995-1001.*

Papers that describe widely adopted methods can attract many citations, as with these two. Their authors would not have claimed great scientific novelty, but their impact has been large. In 1966 it was well understood that the length of a root system was more important to many aspects of root function than its mass, but the excessive time taken to measure length of anything but a small, pot (or ideally solution)-grown plant ensured that few bothered. The gratitude of researchers to Newman (1966) and subsequently Tennant (1975) stems from the vast saving in time and the consequent opportunity to study length. Newman proposed a simple formula for measuring the length of a set of lines using their intersections with a fixed line and Tennant simplified that and showed how using a grid of lines was effective. Tennant's approach facilitated automation. The papers remain heavily cited, even though almost everyone now uses automated methods. A good example of the importance of measuring length is the study by Sanders and Tinker [(1973) *Pesticide Science*, **4**, 385-395] on mycorrhizal function in leek seedlings. The problem of phosphate uptake for plants is that each segment of root rapidly becomes surrounded by a depletion zone and the rate of uptake is then determined by the slow diffusion of phosphate ions from soil to root. A plant can enhance P uptake either by growing a longer root system that explores undepleted soil or by forming a symbiosis with a mycorrhizal fungus that can grow out of the depletion zone. Nye and Tinker [(1977) *Solute Movement in the Soil-root System*. Blackwell Scientific Publications, London] developed the concept of inflow, the rate of uptake per unit root length. Because of diffusion limitation, there is an absolute upper limit for inflow to a root, determined largely by moisture content and the buffering capacity of the soil for phosphate. In the experiment by Sanders and Tinker, that upper limit was 3.5 pmol m-1 s-1, which was approximately what they measured (3.6) for uncolonised leek plants. However, leek seedlings colonised by a mycorrhizal fungus had P inflow of 17 pmol m-1 s-1, five times faster than the theoretical maximum, which was possible because the mycorrhizal hyphae spread out beyond the depletion zone and relieved the diffusion limitation to P uptake. This seminal paper revealed the mechanism by which arbuscular mycorrhizal fungi worked; it would not have been possible without measurement of root length. Measurement of root length is now routine in all functional studies, and can be achieved quickly and easily.

Alastair Fitter

40

Bradshaw, A.D., Chadwick, M.J., Jowett, D. & Snaydon, R.W. (1964)

Experimental investigations into the mineral nutrition of several grass species. IV. Nitrogen level. *Journal of Ecology, 52, 665-676.*

Bradshaw et al. experimented with six native grass species of northern Europe that are associated with different types of soil, ranging from strongly acidic to appreciably alkaline, and varying greatly in contents of available major nutrients. In glasshouse experiments using sand and water culture, they determined first the responses of the six species to variation in pH, and availability of Ca and P [*Journal of Ecology*, **46**, 749-757 (1958), **48**, 143-150 & 631-637 (1960)]. In the 1964 paper they reported the responses to increasing concentrations of NaNO3. These experiments on an appreciable number of wild plant species, as opposed to crops, were some of the earliest precursors of the experimental studies in 'comparative plant ecology' carried out with such enormous impact by Philip Grime and colleagues using much larger numbers of species in later years. Some results were much as expected. For example, *Agrostis stolonifera* was able to respond to increase in N supply at concentrations higher than those at which *A. tenuis* (now *A. capillaris*) was saturated. Other results were unexpected, as when the 'eutroph' *Agrostis stolonifera* yielded more at the lowest NO3 concentration than the 'oligotroph' *Nardus stricta*. Importantly the authors' Discussion exemplifies ecologists' thinking in the 1960s about the significance of inherent differences in maximum growth rate.

Peter Grubb

41

Grime, J.P. & Hunt, R. (1975)

Relative growth rate: its range and adaptive significance in a local flora. *Journal of Ecology, 63, 393-422.*

Plant traits, and especially studies on the ecological significance of interspecific variation in plant traits, have been super hot for some years now. But it is fair to acknowledge that this booming research activity is firmly rooted in Grime and Hunt's 1975 paper in the *Journal of Ecology*. This is where they pioneered the standardised screening of multiple plant species for traits underpinning ecological strategies. They demonstrated that the inherent relative growth rate measured under standardized conditions in the lab (referred to as R_{max}), is a strong predictor of the quality of the natural environments that the species inhabit, and of the ecological roles they play in those environments. 'R_{max}' has been used to define a species' strategy along axes defined by stress and disturbance regimes. It is therefore no coincidence that 'R_{max}', and the traits underpinning it, have since become tremendously popular globally as powerful predictors of (changing) ecosystem functions and services related to carbon and nutrient cycling. These relationships are now being ubiquitously applied in, for instance, biodiversity conservation, agriculture and global change research. Grime and Hunt (1975) have certainly earned their invitation to the BES centenary party.

Hans Cornelissen

42

Cornelissen, J.H.C. (1996)

An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types. *Journal of Ecology, 84, 573-582.*

It has long been established that chemical and physical characteristics of plant litter (i.e., 'litter quality') are important predictors of litter decomposition rates, but work on this topic has historically been conducted without much consideration of the ecology of the plant species producing the litter. The paper of Cornelissen (1996) broke new ground, through being the first major study to attempt to link across-species variation in litter decomposability to the ecological attributes of these species. This work involved placing litters of 125 highly contrasting British plant species in a common soil environment or 'litter bed' and measuring their mass loss through decomposition over time. It showed that litter decomposability varied greatly according to plant life form, deciduous versus evergreen habit, leaf colour at litter-fall, taxonomic status, and level of evolutionary advancement. As such, this work revealed for the first time that plant ecological and taxonomic characteristics could have considerable predictive power for determining litter decomposition rates. This work has underpinned considerable subsequent activity aimed at understanding the comparative ecology of plant litter decomposition, including in relation to plant traits spectra (notably the 'leaf economics spectrum'), the impacts of global environmental change, coordination of strategies among different plant tissues, and linkages between decomposition and herbivory.

David Wardle

43

Lavorel, S. & Garnier, E. (2002)

Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology, 16, 545-556.*

The extensive number of species found in many ecosystems has been historically reduced to a few discrete groups of taxa sharing life form and some key, general traits. These groupings were refined over time by accounting for specific, individual traits that could be quantified and linked to certain ecological functions, which led to the notion of functional types or groups of organisms. The grouping was useful for studies in hyperdiverse ecosystems but its most attractive side was the potential link of these groups to different ecosystem properties and functions. Lavorel & Garnier (2002) made not only a useful review of the traits selected by previous authors but more importantly they suggested two main categories of traits, which they called response and effect traits, the former affecting community structure and diversity and the latter related to ecosystem functioning. The Holy Grail in search was to move forward from simply grouping plant species to unveiling processes and even mechanisms behind community dynamics and ecosystem functioning to gain generalization and predictive power. The paper fostered interesting research but had a number of limitations that were experienced by the many scientists following this trait dichotomy (see web version). The diffuse limits between the categories and other complexities make this Holy Grail still elusive.

Fernando Valladares

44

Clymo, R.S. (1973)

Growth of Sphagnum: some effects of environment. ***Journal of Ecology, 61, 849-869.***

Dicky Clymo has contributed more to our knowledge of *Sphagnum* than perhaps anyone else and, as he reminds us, it is important because there is a lot of it, its ecology and physiology are distinctive, and peat bogs are largely comprised of its remains. In this substantial study Clymo combines experimental manipulations in the laboratory with observations in the field to understand the ways in which physical factors (water table height and light) and chemical factors (H^+ and Ca^{2+} ions) influence the growth and niche separation of twelve species of *Sphagnum*, which are characteristic of a range of mire communities. The study elegantly demonstrates the importance of interacting factors and shows that variables cannot be simply combined in an additive way. Clymo elucidates the mechanistic basis of the species-specific responses to water table height and demonstrates that ecological and physiological optima do not necessarily coincide. Further, data from experimental perturbations are used to explain community level patterns in the field. On a personal note, the clarity and novelty of Clymo's research was reflected in his brilliant teaching, which inspired me to pursue my chosen career path.

Malcolm Press

45

Monteith, J.L. (1972)

Solar radiation and productivity in tropical ecosystems. ***Journal of Applied Ecology, 9, 747-766.***

The elegant concept developed by John Monteith was that plant productivity could be determined from the proportion of incident radiation absorbed, and converted into dry matter, by a crop canopy. Deriving this conversion efficiency was fundamental and far-sighted; this approach is now the basis for determining the annual productivity of crops and natural vegetation. Applications using 'radiation use efficiency' now include harvest index calculations for horticulture or agricultural crops; estimates of productivity and turnover in forest savannas, tropical forests, and boreal peatlands, as well as global biomass inventories. This concept is now incorporated into large-scale models from canopies to ecosystems, via eddy covariance and satellite remote sensing. Monteith (1972) also compared productivities of crops which we now recognize as C3 (rice, soybeans, groundnuts) or C4 (maize, millet, sorghum) as a function of light energy conversion. A schematic defining C3 and C4 energy conversion is now commonly used to define future agricultural demand. Although published in 1972, 25% of citations have occurred in the past three years! Given the current pressures on food production, carbon sequestration by natural vegetation and the need to predict and scale such processes for the future, the relevance of Monteith's logical insights, and the legacy of this paper, will endure.

Howard Griffiths

46

Hellkvist, J., Richards, G.P. & Jarvis, P.G. (1974)

Vertical gradients of water potential and tissue water relations in Sitka spruce trees measured with the pressure chamber. ***Journal of Applied Ecology, 11, 637-667.***

The paper by Paul Jarvis and colleagues has endured as a field-based study which married theoretical considerations of water-relations components in a quantitative, practical fashion. Gradients in water and solute potential, and the bulk modulus of cellular elasticity, were coupled to diurnal variations in evaporative demand within a Sitka spruce stand. Developing the theoretical considerations of Scholander and Tyree, the paper provided a robust confirmation of theory with some exquisite data and insightful analysis. Many subsequent studies building on these approaches now recognize that the hydraulic conductance of roots, stems and leaves form an equally important contribution to maintaining sap flow, together with chemical and hydraulic signals, in part regulated by aquaporins. Limitations imposed by water transport in the tallest redwoods or eucalypts can be viewed in the context of recent insights into the frequency of cavitation and associated dynamic repair processes. The hydraulic pathway in leaves is now seen to be an equivalent limitation to that imposed by stomata in regulating water fluxes to the atmosphere. Most recently, the notion that the turgor loss point, derived from P-V curves, serves as a drought tolerance index, has re-emphasised the fundamental importance of the work initiated by Hellkvist *et al*. (1974).

Howard Griffiths

47

Lloyd, J. & Taylor, J.A. (1994)

On the temperature dependence of soil respiration. ***Functional Ecology, 8, 315-323.***

Interest in decomposition increased enormously when it was widely realised that rising temperatures meant that the carbon cycle was no longer in equilibrium. In the late 1980s and early 1990s research on the carbon cycle had a new impetus. The measurement of 'soil respiration' became commonplace. The analysis of data sets had followed the well-trod path of fitting the Q10 model. The enquiry of Lloyd and Taylor turned out to be more than a statistical exercise. The authors delved deeply into the literature, going back to the original work on the temperature sensitivity of chemical reactions by van't Hoff and Arrhenius. They concluded that the Q10 model is 'inadequate' and that the relationship between respiration and temperature can be accurately represented by an Arrhenius type equation where the effective activation energy for respiration varies inversely with temperature. The success of the paper owes much to its timeliness (its exponential citation pattern from 1995 to 2011 follows closely the citation pattern of papers on soil respiration), and to its thoroughness (wise old supervisors everywhere recognise scholarship when they see it, and push such papers to their students). Many of today's students use the clearly 'inadequate' Q10 model but, they nevertheless cite the Lloyd & Taylor paper showing that they, too, respect scholarship.

John Grace

48

Körner, C. (1991)

Some often overlooked plant characteristics as determinants of plant growth: a reconsideration. ***Functional Ecology, 5, 162-173.***

Acknowledging the progress in photosynthesis measurement technology and rapid increase of information on leaf-level gas-exchange rates, Körner (1991) has importantly pointed out that a number of plant traits with major significance for productivity and competitiveness is often left out. In addition to traditional characteristics such as leaf area ratio, specific leaf area, and biomass allocation traits with already recognized importance for plant growth rate and plant size, Körner highlighted a series of other characteristics which at that time were not routinely studied. Among these key traits commonly neglected were leaf longevity, plant longevity, root turnover, and maximum plant height, meristem activities and cell sizes and division rates. By now, the research community has learned that all these traits have huge impact in determining plant ecological strategy. In an era of increasing use of technology in functional plant ecology - in particular, portable instruments for gas-exchange and chlorophyll fluorescence measurements, the paper of Körner (1991) made a major point that simple measures of plant performance should not be left out. This message is today as fresh as it was when the paper came out.

Ülo Niinemets

49

Koerselman, W. & Meuleman, A.F.M. (1996)

The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. ***Journal of Applied Ecology, 33, 1441-1450.***

Papers which provoke a sense of incredulity within a research community make a unique and valuable contribution to science by inspiring sceptics to prove them wrong and progressing understanding by doing so. The paper by Koerselman and Meuleman concerns a basic issue in ecology: whether particular communities are limited by the supply of N or P. Arguably the best way to test for nutrient limitation is a fertilizer experiment, but this is time consuming and expensive. Koerselman and Meuleman asked whether simple analyses of the N:P stoichiometry of leaves provides a useful alternative. Their results were elegant and compelling: they plotted the mean N and P concentrations of 40 European wetland communities, using different symbols to indicate whether fertilizer experiments had found N or P to be limiting. Remarkably, with only one exception, N:P > 16 indicated P-limitation, N:P < 14 indicated N-limitation and intermediate values indicated co-limitation. The authors proceeded to argue that variation in N:P among the species in a community may indicate species-level differences in nutrient limitation. Could it really be so simple? Do the same rules apply to other vegetation types? What is the physiological explanation for such patterns? This paper rekindled an old debate and inspired a new generation of ecologists to find out.

David Coomes

50

Wright, I.J., Reich, P.B. & Westoby, M. (2001)

Strategy shifts in leaf physiology, structure and nutrient content between species of high- and low-rainfall and high- and low-nutrient habitats. *Functional Ecology, 15, 423-434.*

The bulk of leaf trait adaptation in natural communities has yet to be quantified or understood. What we do know owes a great deal to this paper, which focused on how and why leaf structure and physiology varied across four contrasting Australian communities (high vs low rainfall, with high vs low nutrient supply). This paper presented key discoveries in ecophysiology. For example, this paper showed that higher N and P concentrations in leaves of drier sites enabled a high photosynthetic rate for a given stomatal conductance, and pointed to the current foci of ecological drought tolerance research: the physiological ability to maintain carbon balance, and the reduction of hydraulic demand to match a lower water supply. Second, this paper was fundamental in the field of 'leaf economics', i.e., the inter-relationships of leaf structure, composition and physiology, which emerged in the 1970s, and reached a crescendo with the powerful global biome comparisons in the late 1990s and early 2000s. For the specialist, this paper is of particular value, simultaneously addressing a large number of hypotheses for how physiological and structural traits should co-vary among diverse species within and across communities, providing a template for new research on the ecophysiological basis of species coexistence.

Lawren Sack

51

Tansley, A.G. (1917)

On competition between Galium saxatile L. (G. hercynicum Weige) and Galium sylvestre Poll. (G.asperum Schreb.) on different types of soil. *Journal of Ecology, 5, 173-179.*

Early in the 20th Century, British plant ecologists were largely concerned with vegetation description as evidenced by Tansley's *Types of British Vegetation* (1911). These studies raised questions over the factors affecting plant distribution. The starting point for this paper was Tansley's observation that two Galium species had contrasting distributions on the Carboniferous limestone with *G. saxatile* confined to the loess soils and *G. sylvestre* (now *sterneri*) to the rendzinas even when they were separated by as little as a few centimetres. Tansley describes experiments undertaken outdoors in the Cambridge Botanic Garden in 1911-17 to investigate the role of soil type and competition between the species in determining this distribution. He concludes that competition acted 'through the direct suppression of the shoots of one species by those of the other as the result of its more vigorous growth on its preferred soil.' The paper is important as the first 'laboratory' study designed to elucidate the factors affecting plant distribution in Britain. It is the starting point for many later studies, notably those designed to investigate the calcicole-calcifuge problem which later became a major preoccupation of British plant ecologists. Tansley went on to influence experimentation by many others, but this is the only example of his direct involvement in such a study.

John A. Lee

52

Salisbury, E.J. (1929)

The biological equipment of species in relation to competition. *Journal of Ecology, 17, 197-222.*

Salisbury began with a quotation from Darwin's *Origin of Species* acknowledging that it is generally very difficult to state precisely how one species outcompetes another, but then took a positive view of such understanding as had accumulated. He emphasized the often slight differences in conditions that tip the balance between species, a lesson lost on some experimenters of the late 20th century. He showed that many 'plants grow not where they would but where they must'. Many halophytes, aquatics and plants of summer-dry soils grow much larger on well-drained, non-saline moist soils than on their native soils; a warning to those who in the 1930s took a naïve approach to the 'adaptations' of plants to particular habitats. Salisbury reviewed carefully competition between plants for light and water, but then wrote 'of all the biological features that influence frequency, capacity for propagation and dispersal must obviously be of prime importance'. Many would dispute this assertion, at least for perennials, but there is truth in the idea of significant competition between plants at every stage of the life cycle, an idea that was lost sight of in much theorization of the 1970s-1980s. Salisbury pioneered collection of 'the vital statistics of plants', and in that way anticipated the great contribution of John Harper.

Peter Grubb

53

Gause, G.F., Smaragdova, N.P. & Witt, A.A. (1936)

Further studies of interaction between predator and prey. *Journal of Animal Ecology, 5, 1-18.*

Although several of his classic papers on tests of the Lotka-Volterra models of predator-prey relationships were published elsewhere, this one is in a BES journal. These papers were seminal, not least because they raised questions about the applicability of the simple models which stimulated their development for much of the 20th century. Gauses' experiments using *Paramecium*, yeasts and mites, led to oscillations of predator and prey in which the prey was eventually eliminated. These were not analogous to those predicted by the models because they arose from the organisms interaction with the heterogeneity of the habitat; itself an important finding. Models have become much more sophisticated (see elsewhere in these accounts) but the occasions on which thorough experimental tests of them in the field or even laboratory as here, are rare, and consequently the links between theoretical ecology and studies of wild systems can remain elusive. Sometimes models can be accepted uncritically because they seem to describe reality but are very difficult to test experimentally. Gause led the way in an attempt to do so, and it is salutary that his work stimulated better modelling and more realistic experiments (e.g. see Shorrocks and Atkinson p.29) in classically iterative fashion.

John Whittaker

54

Mack, R. & Harper, J.L. (1977)
Interference in dune annuals: spatial pattern and neighbourhood effects. *Journal of Ecology, 65, 345-363.*

Back in 1977, plant population biology was a nascent subject, built from the borrowed parts of other disciplines. Harper published his foundational *Population Biology of Plants* that year and it is notable how much of the book came from agriculture, forestry and horticulture. The paper is a reminder that Harper was struggling to establish an independent discipline, shorn of zoocentric concepts like 'competition' (Harper preferring the term 'interference'). Mack & Harper is an experimental demonstration that 'density,' a central concept in population biology, is not well-suited to plants. As Mack and Harper put it, " 'density' is a very crude measure of the state of a population or the conditions met by the individuals. The individual plant does not react to the density of its population but to the activity of some of its neighbours." They describe experiments demonstrating that up to 69% of the variance in target plant weight is accounted for by the size, angular dispersion and distance of neighbours. Directly or indirectly, this result inspired many others to fit individual-based models to the growth and dynamics of plant populations - a technique that has become standard in plant population biology today.

Jonathan Silvertown

55

Southwood, T.R.E. (1961)
The number of insect species associated with various trees. *Journal of Animal Ecology, 30, 1-8.*

'*Macroecology*' is a non-experimental, statistical investigation of species' ecology and evolution, or in simple terms a search for patterns in nature, primarily achieved by mining existing large-scale data sets [Brown,J.H. *Macroecology*. University of Chicago Press (1995)]. Bafflingly, this study by Southwood, the first widely available paper to use what was undoubtedly a macroecological approach is not even cited by Brown. Southwood's question was: 'Why do some species of plants host more species of insects than others?' In 1960 he had attempted to answer the question for Hawaiian trees, and then applied the same ideas to UK trees and their associated insects in 1961. Using existing species-lists he argued that the number of insects associated with a tree is proportional to the tree's recent abundance, and offered a theoretical explanation based on 'encounter rates' over evolutionary time [for a succinct summary of his ideas see Southwood (1973 *Symposium of the Royal Entomological Society of London*, **6**, 3-30). By modern standards of statistical rigour these early, pioneering forays into macroecology can easily be criticised. What cannot be criticised is Southwood's vision for an approach to ecology that did not become fashionable for another 30 years.

John Lawton

56

Frankie, G.W., Baker, H.G. & Opler, P.A. (1974)
Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *Journal of Ecology, 62, 881-919.*

A major growth area in community ecology during the latter part of the 20thcentury involved investigation of the phenology and reproductive biology of tropical ecosystems, particularly in the Neotropics. Gordon Frankie, Herbert Baker and Paul Opler were among the early pioneers in this field, initiating detailed comparative studies of the phenology of tropical forests in Costa Rica. In this classic paper, which has been cited >600 times, they report on an exhaustive analysis of leafing, flowering and fruiting periodicities of 298 tree species at wet and dry forest sites. Significantly, and in contrast to most earlier work, the authors interpret the phenological patterns that they observed not only in terms of climatic factors, particularly the timing and duration of the wet and dry seasons, but also in the context of plant-animal interactions, especially pollen and seed dispersal agents. They make the important point that climatic triggers are most often best viewed as proximate factors eliciting phenological responses, but that the ultimate (adaptive) explanations for the timing of these events probably reside in beneficial plant-animal interactions associated with flowering and fruiting. Distinguishing between proximate and ultimate factors governing adaptive trait variation is today commonplace and lies at the heart of modern evolutionary ecology.

Spencer C.H. Barrett

57

Paine, R. T. (1980)
Food Webs: Linkage, Interaction Strength and Community Infrastructure. *Journal of Animal Ecology, 49, 666-685.*

Bob Paine delivered this paper as the 3rd Tansley Lecture so he could fly a few kites without fear, leaving a ripe field of intriguing ideas and concepts for exploration by the rest of us. Thanks, Bob. From empirical data collection, Bob showed that the vast majority of interactions in food webs are very weak, with only one or two strong interactions that keep aggressive competitors in check and allow weakly linked species to develop as co-evolved modules. This was the first plausible explanation for the lumpy structure of interaction webs that promoted stability in model ecosystems described earlier by May. It was exciting to see field work and theory coming together.

Furthermore, Bob Paine showed unequivocally that these strong interacters can only be identified through manipulative field experiments. Simply documenting who eats whom, or even quantifying energy moving between prey and predator will not reveal those linkages which are functionally important. In his food web there is insignificant energy moving along the sea urchin-kelp linkage, but remove the sea urchin and everything comes tumbling down. As testimony to the paper's inspirational effect, I spent the next 15 years repeating Bob's approach in an estuarine food web and found the same things: it didn't take Bob half as long!

Dave Raffaelli

58

Atkinson, W.D. and Shorrocks B. (1981)
Competition on a divided and ephemeral resource: A simulation model. *Journal of Animal Ecology, 50, 461-471.*

The question, "How do species coexist?" has taxed ecologists for centuries. Classical models state that stable coexistence is possible if the strength of intraspecific competition exceeds that of interspecific competition. But in what ecological scenarios could that occur? Motivated by *Drosophila* fruitflies exploiting patchy food resources, Atkinson & Shorrocks noted that clustering of species could provide opportunities for inferior competitors to grow in the absence of dominants. The dominants would (on average) find themselves fighting among themselves, elsewhere. To test this, Atkinson & Shorrocks developed one of the best-known early ecological examples of a simulation model. They exploited burgeoning computer processing power to simulate aggregated distributions of competing species across food patches, and measured duration of coexistence. Aggregation did indeed promote coexistence. Less robust was speculation that coexistence could emerge from random selection of patches by egg-laying females. This paper joins the list of 100 influential papers for three main reasons. First, it clarified the role of aggregation in promoting coexistence among species. Second, it promoted the use of simulation modelling as a new weapon in the armoury of ecological research. Third, its conclusions were not without controversy: debate surrounding the ecological mechanisms that promote aggregative coexistence rages on.

David Hodgson

59

Cornell, H.V. & Lawton, J.H. (1992)
Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *Journal of Animal Ecology, 61, 1-12.*

The relationship between the species richness of local assemblages and the species richness of the regional assemblages in which they are embedded is a fundamental ecological pattern. Regional richness must obviously equal or exceed local richness, but given that constraint a wide variety of relationships remain possible. This paper is significant in that it brought to wide attention the importance of understanding local-regional richness relationships; reviewed the theoretical evidence for the different forms these relationships might take; and established some of the core terminology to be used when discussing them (e.g. the distinction between Type I 'unsaturated' and Type II 'saturated' relationships). Importantly, it argued that local assemblages are typically unsaturated with species (residents do not inevitably exclude invaders), that Type I relationships are likely to be widespread, and that the principal direction of control is from regional to local species richness. These assertions have all subsequently been much debated, and the relative role of local and regional processes in shaping local species assemblages, and how this changes in time and space, remains contentious. In opening up this discussion this paper arguably gave a much needed boost to the development of the field of macroecology, which was established on the premise that regional ecological patterns and processes were fundamentally important, and that ecology needed to pay more attention to them.

Kevin Gaston

60

Anderson, R. M. (1991)

Populations and infectious diseases: ecology or epidemiology? *Journal of Animal Ecology, 60, 1-50.*

Not long ago, parasitism was ecology's Cinderella interaction. One could attend a British Ecological Society AGM, or read one of its journals, and count oneself lucky to be able to listen to one or two talks or find a parasite paper to read. Now those meetings have parasite ecology talks almost throughout (and the same is true, recently, at British Society for Parasitology meetings) and there are several parasite papers in each issue of most of the journals. To link the gradual evolution of any scientific discipline to one key publication can be as misleading as it is tempting. But there's a good case for doing this with Roy Anderson's 1991 Tansley Lecture. He and Bob May, in a series of papers from the mid-1970s, had given parasite ecology a quantitative edge and rigour that it had lacked, albeit often from a theoretical perspective. They had created a new discipline, ecological epidemiology, which the title of the paper itself announces. The title implies, too, the incorporation of infectious diseases into the ecological parasitology fold, which Anderson and May had done, in part, through their novel distinction between micro- and macroparasites. A new agenda had been set. Ecologists have been exploring it since at a rate that continues to accelerate.

Mike Begon

61

Hudson, P.J., Dobson, A.P. and Newborn, D. (1992)

Do parasites make prey vulnerable to predation? Red grouse and parasites. *Journal of Animal Ecology, 61, 681-692.*

This paper is an interesting mixture of observation, experiments and mathematical modelling focusing on one issue: the interaction between two natural enemies in their impact upon their host. This was published twenty years ago, relatively early in a series of studies on this theme, which teased apart the roles of macroparasites, predators, tick-borne pathogens and humans in their relative impacts on the hapless grouse, and how interactions between them modulate this impact. This particular choice is a representative of that series. Extensive survey data are used to establish a hypothesis which is then tested by a manipulative experiment. This approach is repeated in later years to remove parasites from large areas and so conclusively demonstrate that parasites can cause population cycles. The dynamical consequences of the phenomenon they have demonstrated (that more heavily parasitized grouse are more susceptible to predation) is then explored in a mathematical model, with some counter-intuitive outcomes. Under certain circumstances, increases in predation can lead to increases in the grouse population. The theoretical work builds on the classic Anderson and May host-parasite models of the late 1970s, illustrating how such models can be adapted to provide insights into specific systems while maintaining sufficient simplicity to retain analytical tractability.

Rosemary Hails

62

Turkington, R. & Harper, J.L. (1979)

The growth, distribution and neighbour relationships of Trifolium repens in a permanent pasture. IV. Fine-scale biotic differentiation. *Journal of Ecology, 67, 245-254.*

In 1975 Roy Turkington moved from Northern Ireland to Bangor to join John Harper's research group. His painstaking investigation resulted in four papers on the distribution and neighbour relationships of a single species (*Trifolium repens*) in a single permanent pasture. As a whole, the papers helped to initiate a more intimate approach to plant ecology which involved recording the plant's eye view of its neighbourhood. In adapting a plotless sampling approach [Yarranton (1966) *Journal of Ecology*, **54**, 229-237]. Roy showed that clover samples its neighbours non-randomly, being much more likely to contact certain species than their proportions in the community would suggest. The key message was that the human perspective (% cover) provides an inadequate estimate of the impact that one species might have on another in the plant community. The series culminated in my chosen paper which showed that clover ramets appeared to be adapted to their local biotic neighbourhood, growing better with neighbour species than with non-neighbours, suggesting a very fine scale of biotic differentiation, previously unexpected. This work inspired many others to follow the same approach.

Libby John

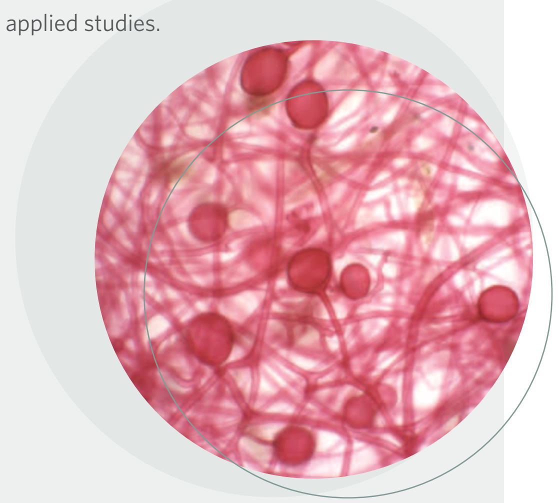
63

Newsham, K.K., Fitter, A.H. & Watkinson, A.D. (1995)

Arbuscular mycorrhiza protect an annual grass from pathogenic fungi in the field. *Journal of Ecology, 83, 991-1000.*

This paper broke the mould in two ways. First, it questioned the 'orthodox' view derived by extrapolation from many pot studies in the 1960s to 1980s, that the primary role played by arbuscular mycorrhizal fungi (AMF) in natural ecosystems is the enhancement of phosphate uptake, generally coupled to an increase in growth rate of the host plant. Second, it demonstrated unequivocally, that under field conditions the presence of these biotrophic symbionts could protect plants from attack by naturally occurring pathogenic fungi. It was thus visionary in the sense that, for the first time, it enabled us to recognise the multi-functional potential of the symbiosis. The work was firmly based upon an exemplary rigour of design and statistical analysis. This study has laid the foundation for a widespread recognition of the role of AMF in provision of systemic acquired resistance (SAR) to attacks by soil borne pathogens, in crop plants as well as in natural communities. Several current international collaborations (funded by major grants from the National Science Foundation and UK Research Councils) are a direct consequence of this study. The paper by Newsham et al. shows nicely how fundamental research can lead to a reorientation of applied studies.

David Read



64

Helgason, T., Merryweather, J.W., Dennison, J., Wilson, P., Young, J.P.W. & Fitter, A.H. (2002)

Selectivity and functional diversity in arbuscular mycorrhizas of co-occurring fungi and plants from a temperate deciduous woodland. *Journal of Ecology, 90, 371-384.*

Bugle Ajuga reptans one of the plants used in research provided by AH Fitter

There are approximately 1000 times as many species of vascular plants as there are described species of arbuscular mycorrhizal (AM) fungi. This disparity in numbers led to a traditional view that the fungi were not host specific and that the benefit conferred on a plant host by different fungal species was more or less the same. Helgason et al. (2002) isolated AM species from a woodland soil and tested the ability of each fungus to colonise and confer benefit on five co-occurring plant species. Fungi differed dramatically in their ability to colonise plants and in some cases failed to do so. Moreover, the effect on plant performance varied with each host-fungus combination. Thus, in any plant community there is likely to be a mosaic of fungal occurrence and plant growth, dependent upon which fungi happen to colonise the roots. This paper changed our view of AM-plant interactions by showing that the fungi exhibit host selectivity and functional diversity. Using a combination of molecular biology and good old-fashioned growth experiments, it challenged our view of mycorrhizas being generalists and made the important prediction that the number of AM species is considerably greater than that described at the time.

Alan Gange

65

Pearsall, W.H. (1920)
The aquatic vegetation of the English lakes. *Journal of Ecology, 8, 163-201.*

Pearsall became a prominent figure in mid-twentieth century nature conservation, partly through his famous book *Mountains and Moorlands* (Collins New Naturalist, 1950). But his professional life began in limnology, based on a childhood in the English Lake District and an interest fostered by his headmaster father, who helped in the fieldwork. During the decade of the First World War, when he was not in the army, he worked on the bigger English lakes, starting with vegetation succession (then a newish concept) in Esthwaite Water and eventually looking at underwater vegetation more widely. This paper is prominent for considering the determinants of submerged plant communities. Pearsall proposed that light determined the ultimate depth of colonisation, but the nature of the sediment largely fixed the species composition of the communities. Later he developed the ideas of (a) a continuum of lake ecosystems, rather than the strict lake types proposed by continental limnologists, and (b) the evolution of lake basins from a primitive oligotrophy to a silted eutrophy, as they filled with sediment. This 1920 paper provided many of the data on which he based these concepts, the first of which remains valid, the second of which provided the platform for a better understanding, and stimulated much work in palaeolimnology, which challenged it.

Brian Moss

66

Mortimer, C.H. (1941-1942)
The exchange of dissolved substances between mud and water in lakes. Parts 1-4. *Journal of Ecology, 29, 280-329 & 30,147-201.*

Sediments in lakes had been considered largely inert until C.H. Mortimer's paper established the important chemical interactions that occur at the interface of the sediment and water and greatly influence the processes determining nutrient cycling and productivity in lakes. A citation classic (around one thousand citations) it was one of the first truly biogeochemical papers and established a sequence of reduction/oxidation reactions by which once oxygen is exhausted, sediment bacteria begin to convert nitrate to nitrogen, oxidised iron and manganese to their reduced forms and sulphate to sulphide. Mortimer had no way of measuring methane so others later elaborated this final step in the sequence, though Mortimer was aware of it. The sequence has general relevance in wetlands, peats and marine sediments as well as in lakes and incidentally in the paper, Mortimer also introduced the use of depth-time diagrams and developed a method for measuring redox potential. All three achievements are absolutely fundamental to modern work (in regional limnology, climate change and eutrophication), which frequently uses and repeats them without reference to Mortimer, whose findings have become part of the received wisdom.

Brian Moss

67

Lund, J.W.G. (1949-1950)
Studies on Asterionella: *Parts I & II. Journal of Ecology, 37, 389-419 & 38, 1-14.*

Long-term data sets are now immensely valuable, not least for assessing the effects of climate change. One of the first such sets began in 1932 when regular chemical analyses and counts of the phytoplankton populations began on some of the Cumbrian Lakes in the Windermere Basin. Such monitoring, with coupled experiments, allows interpretation of what determines the population dynamics of individual species. John Lund standardised the procedures for monitoring in 1945 and was the first to demonstrate the value of such an approach with his two-part paper on the diatom, *Asterionella formosa*. Using the data set Lund was also able to explain the wax and wane of other diatoms, small flagellates and desmids, but his abiding contribution, widely copied, was to demonstrate the value of long-term data, coupled with experiments and bioassays, to start explaining precisely the population ecology of particular species and to lay the basis for what is now known as the Plankton Ecology Group (PEG) Model, which is used as a yardstick for explaining the behaviour of plankton world-wide. The continued monitoring of the Cumbrian lakes still provides significant insights into plankton ecology and great value in informing sensible management of lakes and reservoirs.

Brian Moss

68

Hynes, H.B.N. (1950)
The food of fresh-water sticklebacks (Gasterosteus aculeatus and Pygosteus pungitius), with a review of methods used in studies of the food of fishes. *Journal of Animal Ecology, 19, 36-58.*

This study is composed of three parts, an initial review of the methods then used to assess the diets of freshwater fish, followed by an extensive account of the diets of three-spined (*Gasterosteus aculeatus*) and nine-spined (now *Pungitius pungitius*) sticklebacks at a number of locations, and completed by an examination of the feeding relationships of these two species together with roach and sand goby at a single location. The latter part is a rather limited study specific to one somewhat unusual location, but the first and second components have a much wider applicability and probably account for the work's high citation rate in almost equal measure. The review of diet descriptors covers what were to become known as the frequency of occurrence, numerical, gravimetric and volumetric methods, but most importantly it also reviewed the 'hybrid' points method originally proposed by G.H. Swynnerton & E.B.Worthington [*Journal of Animal Ecology* (1940) **9**, 183-187] in a seldom-cited study of the diet of fish in Haweswater, U.K. For some reason, Hyne's description of the points method became the one to cite and reference to it may still be found in a vast range of diet studies across a range of consumer taxa. The subsequent popularity of the three-spined stickleback amongst behavioural and ecological researchers undoubtedly also contributed to the paper's subsequent citations.

Ian J Winfield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Le Cren, E.D. (1951)
The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (Perca fluviatilis). *Journal of Animal Ecology, 20, 201-219.*

Following an initial consideration of the mathematics underlying relationships between the lengths and weights of individual fish and its indication of their individual conditions, is an analysis of an extensive dataset of this type for perch (*Perca fluviatilis*) in Windermere, U.K., and then a study of seasonal variation in gonad weight and condition in this population. A number of features of this work have combined to make it so highly cited. First, the initial mathematical consideration of length-weight relationships in fish was far ahead of its time and quickly found an appreciative and large audience amongst fish ecologists and fisheries scientists alike. Second, this work was one of the early papers produced by what was to become a long-term study on perch population biology in Windermere which has continued to the present day. As such, this paper was inevitably cited by a number of subsequent papers from the Windermere stable and also likely benefitted from the publicity around the research programme as a whole. Third, the final component of the study on seasonal variations in gonad weight and individual condition was also extremely novel at the time and has become almost a standard way in which such fish data are analysed and presented.

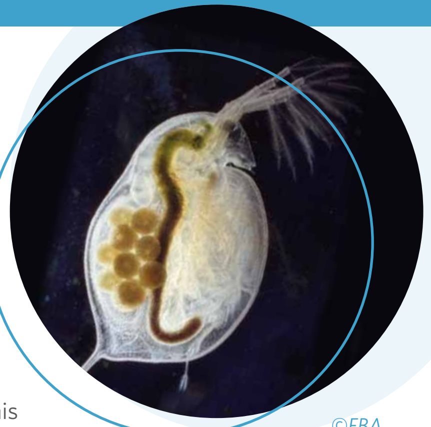
Ian J Winfield

70

Elliott, J.M. (1976)
Energetics of feeding, metabolism and growth of brown trout (Salmo trutta L.) in relation to body weight, water temperature and ration size. *Journal of Animal Ecology, 45, 923-948.*

This landmark paper analysed the results of laboratory experiments by the author on the growth of brown trout in relation to temperature and food availability. The experiments involved detailed measurements of food intake and growth of individually-housed fish of a broad range of body sizes when kept at temperatures covering most of the natural range encountered by wild trout. This paper used the data from those earlier studies to construct a series of equations that allowed prediction of growth and energy budgets of trout under a broad range of environmental conditions. In addition to quantifying the causes of variation in metabolic costs, these equations revealed the ecological conditions under which growth rate was maximised, and highlighted the fact that both growth rate and growth efficiency were maximised at intermediate temperatures. These quantitative models for consumption rates, growth rates and energy budgets have repeatedly proved to be very accurate when tested using trout taken from populations drawn from the wide geographic range of the species. The influence of the models has gone far beyond the sphere of ecological energetics, since they have been used repeatedly by the aquaculture industry to predict growth performance of farmed fish under differing culture conditions.

Pat Monaghan



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71

Lampert, W. (1989)
The adaptive significance of diel vertical migration of zooplankton.
Functional Ecology, 3, 21-27.

In this succinct essay review Winfried Lampert helped revolutionise understanding of how the zooplankton functions. Zooplankters had long been known to move up and down the water columns of lakes and the ocean, usually upwards at night and down by day. Initial explanations were broadly that this behaviour was energy-efficient, providing food in the upper layers of warm water at the expense of increased respiration for part of the cycle, but taking the animals to cooler layers for later assimilation of the food, and growth. It would however be immaterial whether the animals were at depth by day or by night. Explanations for this then focussed on quality of the food, arguing that by the end of the daylight the algae would have acquired better food quality, through accumulated stores that the zooplankters might exploit best after sundown. Lampert's contribution, having reviewed literature that showed that vertical migration did not result in increased productivity and growth of the populations, was to demonstrate that the behaviour reduced the risk of predation by fish and was, on balance, advantageous. As a result, a major focus of plankton ecologists is now on the integration of work on food quality and production, predation, and the evolution of traits that influence grazing and predation risk.

Brian Moss

72

Southwood, T. R. E. (1977)
Habitat, the templet for ecological strategies?
Journal of Animal Ecology, 46, 337-365.

Southwood's Presidential Address to the British Ecological Society remains highly cited and influential. Southwood asks whether the characteristics of a species' habitat (expressed in terms of its variability in space and time) are the template shaping the evolution of life history strategies. His ambitious goal was to develop an ecological equivalent of the Periodic Table, providing a theoretical framework for understanding interspecific variation in species' life-history strategies. Ecologists were well aware of evolutionary trade-offs shaping life-histories and the important role of their biotic and abiotic environment. MacArthur and Wilson had introduced the concept of *r* and *K* selection, which recognised a spectrum of life history strategies depending on levels of competition. Southwood makes a compelling case for the shaping role of habitat characteristics for individual species and ultimately for whole communities. He stresses that not all species in the same habitat will exhibit the same strategies, not least because the idiosyncrasies of different resources will select for different characteristics in the co-occurring species exploiting them. Southwood includes simple graphical and mathematical arguments, supported by case studies. Many of his examples involve insects, reflecting his deep entomological knowledge. In the same year, an equally influential paper by J.P.Grime [*The American Naturalist* (1977) **111**, 1169-1194] provided parallel arguments, but with a focus on plant strategies.

Owen Lewis

73

Stearns, S.C. (1989)
Trade-offs in life-history evolution. *Functional Ecology, 3, 259–268.*

Stearns conceptualized the idea of correlated variation among traits, specifically when a beneficial change in one trait is linked to a detrimental change in another in relation to fitness gain. The idea of trade-offs is so powerful because in their absence, most traits would be bounded just by design or shared history. Trade-offs open opportunities for evolution of phenotypic integration in complex anatomical structures or life-history variables. Stearns advocated an integrative analysis of trade-offs, with measurement at different levels (genotype, phenotype; from individual to population level, i.e., inter-generational trade-offs). A persistent challenge is the distinction between immediate effects, i.e., those emerging from the genetic variance-covariance matrix, and past constraints, i.e., emerging from negative evolutionary covariance among traits within a specific radiation. Stearns's theoretical framework addressed these multiple levels of understanding. He provided an insightful analysis of the genotypic/phenotypic interface for trade-offs like age vs size at maturity and reproductive investment vs survival, and then discussed specific methods for measurement and quantification. Given the pervasive influence of genotype x environment interactions it is surprising that we often still discuss tradeoffs as invariant properties. By dissecting the different levels at which tradeoffs operate, Stearns offered insightful guidelines for future research.

Pedro Jordano

74

Davies, N.B. & Brooke, M. de L. (1989)
An experimental study of co-evolution between the cuckoo, Cuculus canorus, and its hosts II. Host egg markings, chick discrimination and general discussion.
Journal of Animal Ecology, 58, 225-236.

Individual organisms almost universally interact with individuals of other species, either as predator, prey, host, parasite, competitor or mutual benefactor. Coevolution is, therefore, a widespread and common phenomenon, and is fundamental to our understanding of how evolutionary processes work. The conflict between avian brood parasites, particularly cuckoos, and their hosts has become a classic example of coevolution. Using model eggs experimentally placed into the nests of a range of bird species, Davies and Brooke found evidence that the risk of cuckoldry has played an important role in the evolution of discrimination behaviour of the hosts. Because host species have so much to lose by taking a cuckoo into their nest, there has been selection for hosts to be able to distinguish foreign eggs from their own and reject them. On the other side of the conflict, cuckoos have been under selection pressure to match the appearance of their eggs with those of their host species. Davies and Brooke showed how fundamental and important questions could be answered using good fieldcraft and deceptively simple experiments in the field.

Ian Hartley

75

Ghalambor, C.K., McKay, J.K., Carroll S.P. & Reznick, D.N. (2005)

Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Functional Ecology, 21, 394-407.*

The capacity of organisms to accommodate their form and function to changing environments is called phenotypic plasticity, a concept not well integrated into the Neo-Darwinian synthesis but gaining increasing recognition and interest. Phenotypic plasticity is at the core of rapidly expanding areas such as epigenetics and has become a key concept in understanding species responses to global change. An implicit assumption in many studies is that a plastic phenotypic change is beneficial, i.e. increases fitness of the individual organism capable of such adjustment or change in response to the environment. However, as Ghalambor et al. remind us, plasticity can be not only positive, but neutral and even negative for fitness. The paper makes a sound contribution to the situations were plasticity is adaptive, and revises scenarios where plasticity prevents or allows evolution by directional selection. The explicit recognition of the frequent case that plastic adjustments do not lead to perfectly optimal phenotypes is one of the several merits of this revision, in addition to the brilliant explanation of when plasticity is or can be adaptive. The paper has significant limitations, e.g. in not emphasizing that what is maladaptive today could be adaptive tomorrow (see web version), but reading it remains an inspiring experience.

Fernando Valladares

76

Stephens, P.A., Buskirk, S.W., Hayward, G.D. and Martinez del Rio, C. (2005)

Information theory and hypothesis testing: a call for pluralism. *Journal of Applied Ecology, 42, 4-12.*

Ecologists work with noisy systems, and require statistics to detect signal, estimate parameters and infer process. Yet, ecology often struggles to keep up with new statistical paradigms. A generation of ecologists has been taught to simplify complex models, stepwise, to either support the null hypothesis or reject it in favour of an interesting ecological signal. But should we? At each step, this approach asks, "What is the probability of collecting such extreme (or even more extreme) data, given that no signal exists?" The 'information theoretic' approach instead asks "What is the relative likelihood of the data given a defined set of rival hypotheses?" Instead of stepwise-rejecting a series of alternative hypotheses, thereby risking either ignorance or false attribution of significance, we can instead ask which hypothesis is most likely, and weight ecological signals by the relative likelihoods of models that contain them. Stephens *et al*. reassured us that classical falsificationist tests work for well-designed experiments that manipulate few explanatory variables. Ecologists working with survey data or multiple hypotheses should embrace information theory instead. This paper helped to transform the statistical paradigm in ecology, meanwhile intensifying debate surrounding 'what kind of statistics' we should do. Meanwhile, the Bayesian revolution has begun…

David Hodgson

77

Arrhenius, O. (1921)

Species and area. ***Journal of Ecology, 9, 95-99.***

The Swedish biochemist and botanist Olof W. Arrhenius (1895-1977) published in 1921 in the *Journal of Ecology* (building on work published in Sweden in 1920) the first mathematical formulation of the species-area relationship, based on empirical studies of a suite of plant communities from the Stockholm region. Hereby, he provided a formal description of one of the most consistent ecological patterns, namely the increase in species number with increasing area, describing it as a power function. This relationship, and not just the general form of it but specifically Arrhenius' (1921) formula, constitutes a key basis for theory development in island biogeography, ecology and conservation biology, notably in the highly influential equilibrium theory of island biogeography. While so fundamental and widely recognized that it may be the 'closest thing to a rule in ecology' [Lomolino (2000) *Journal of Biogeography*, **27**, 17-26], the general form of the species-area relationship, or vice versa its variability, the underlying drivers as well as dynamic implications remain subject to debate and an active research area - and still with consistent reference to Arrhenius' 1921 article.

Jens-Christian Svenning

78

Fisher, R.A., Corbet, A.S. & Williams, C.B. (1943)

The relation between the number of species and the number of individuals in a random sample of an animal population. ***Journal of Animal Ecology, 12, 42-58.***

Fisher, Corbet & Williams (1943) is a classic in the fields of biodiversity research and macroecology, written decades before these terms were invented. Empiricist A. Steven Corbet and 'C.B.' Williams of insect migration fame combined with the brilliant statistician and geneticist Ronald A. Fisher to generate the first detailed understanding of the frequencies of rare and common species in biological communities. The paper represents an impressive combination of empirical data (Lepidoptera samples from Malaya and England) and mathematical analysis that remains a model for ecology today. Fisher's alpha, derived from his logarithmic series, described the steepness of the curve of the number of species observed as a function of the log of the number of individuals sampled – it provided the first metric of the species-richness of biological communities independent of sample size. This directly stimulated the huge literature on the measurement of biological diversity across the world. More fundamentally, their realisation that predictable patterns of rare and common species within biological communities established multi-species community ecology as a 'hard' science. The paper represented the first fundamental analysis of rarity, contributing to Hutchinson's ideas about niches, Preston's analysis of rarity, and MacArthur, Whittaker, Hubbell and others' ideas that have led to the establishment of modern large-scale ecology, biodiversity research and macroecology. An amazing paper!

Chris D Thomas

79

Elton, C. (1949)

Population interspersion: an essay on animal community patterns. ***Journal of Ecology, 37, 1-23.***

Charles Elton's most important works include *Animal Ecology* (1927) and *Voles, Mice and Lemmings. Problems in Population Dynamics* (1942), but many of his papers were also highly influential. Elton's Presidential Address to the British Ecological Society on 7 January 1949 deserves to be read more widely by later generations of ecologists. In this paper, Elton discusses minor habitats, such as individual plants, both living, dead and decaying, plant and animal secretions and excretions, animal artifacts, and so forth. Elton was frustrated by the context of ecological processes being lost when ecologists ignored information about minor habitats. The real hidden gem in this paper is Elton's discussion of the population dynamic consequences of the spatial distribution of species amongst minor habitats in the wider landscape. He concludes that "theories about population changes and interaction, which are nearly all based upon conceptions of mean density, must learn to take account of the fact that populations are split up into centres of action". He is much ahead of his time in realizing how spatial aggregation of species may influence their interactions and chances of coexistence, and how spatial patchiness may be generated by the interactions of plants and animals themselves.

Ilkka Hanski

80

Lloyd, M. (1967)

Mean Crowding. ***Journal of Animal Ecology, 36, 1-30.***

Lloyd's paper: 'Mean Crowding' attempted to relate the counts of individual animals in a sample to their actual experience of crowding. Lloyd's index was derived purely from the sample variance and mean of a set of counts. It equated spatial non-randomness with deviations from the Poisson distribution, an idea originating in 1922. Spatial non-randomness (variously termed aggregation, heterogeneity, clustering or patchiness) cannot be well described by a variance-mean relationship because the only inference possible relates to some scale smaller than the units in which the counts were sampled. Crucially, indices derived from such relationships (others include Taylor's power-law *b;* Iwao's quadratic; and the negative binomial parameter k) disregard any spatial information concerning the location of where samples were counted and cannot infer pattern at the scale of the sample units or higher. It is therefore surprising that Lloyd's paper has been cited 900 times, particularly since his index is identical to one published by Morisita in 1959. The study of pattern utilising all the spatial information in the sample was carried forward by four developments made in the 1990s: the metapopulation models; the geostatistics approach; SADIE analyses; and the advent of spatio-temporal statistical mixed model analyses; none relied on Lloyd's ideas.

Joe Perry

81

Taylor, L.R., Woiwod, I.P. & Perry, J.N. (1978)

The density-dependence of spatial behaviour and the rarity of randomness. ***Journal of Animal Ecology, 47, 383-406.***

This is one of a series of contributions published by various combinations of the authors in *Journal of Animal Ecology*, in which they explore the spatial and temporal patterns of variation in the densities of species. This paper documents how the aggregation of the individuals of a species, and hence the spatial variance in their density, changes with that density. Arguably, this is one of the most foundational issues in population ecology, although it clearly excites some researchers in the field far more than it does others. Several features of this paper make it particularly notable. First, and arguably presaging the current era of meta-analyses, it draws together a remarkable body of data, comprising 156 separate data sets, 3840 samples, more than 200,000 sample units, and an overall total of about 109 individuals. Second, it addresses a broad range of spatial scales, from what we might term the microecological (ciliates on the surface of a flatworm) to the emphatically macroecological (humans across the U.S.). Third, using these data the paper convincingly establishes the generality of scaling of aggregation, that this is well captured by Taylor's power law (a power relationship between spatial variance and mean density), and the rarity of random spatial distributions of individuals at all but the lowest densities.

Kevin Gaston

82

Wiens, J.A. (1989)

Spatial scaling in ecology. ***Functional Ecology, 3, 385-397.***

Wiens pointed out that two ecologists might get different answers to the same question if they happen to approach the problem at different scales. He gives several cases of this: for example a physiologist will tell you that stomatal mechanisms regulate transpiration; whereas at the landscape scale, because of the feedback from the planetary boundary layer, the size of the stomatal pores does not matter as much as the physiologist would have predicted; rather, the water use at a regional scale is partly controlled by climatological variables acting at a landscape scale. When the ecologist ventures into the field with a 1-metre square quadrat, the size of the quadrat is often determined by the convenience of carrying the sample unit, and is not usually related to the scale of pattern of the vegetation. However, the answers obtained may turn out to be strongly scale-dependent. The paper by Weins was one of the first to point this out, and it appears to have influenced many researchers who cited the paper in the 1990s.

John Grace

83

Hanski, I. (1994)

A practical model of metapopulation dynamics. *Journal of Animal Ecology, 63, 151-162.*

Two conceptually and mathematically simple models, MacArthur & Wilson's (1967) theory of island biogeography and Levins' (1969) metapopulation model, stimulated much interest in what we now call spatial ecology at the end of the 1960's. These two models highlighted the effects of island area and isolation on the number of species occurring on islands (or habitat fragments) at equilibrium (the island model), and the viability of species living in networks of habitat fragments (the metapopulation model). However, the two models remained unconnected and had their limitations. The island model assumed a large mainland population that is the only source of colonization, and the Levins model assumed an infinite number of identical habitat fragments with equal connectivity to each other. The conceptual contribution made by Hanski (1994) was to show how the Levins' metapopulation model could be extended to a finite network of habitat fragments with dissimilar areas and isolations (spatial connectivities), essentially merging the two models. Furthermore, Hanski (1994) showed how the model parameters could be estimated with empirical data, paving the way to numerous applications in conservation biology in the coming decades. The approach pioneered by Hanski has subsequently been elaborated in more complex models that have provided further insight into the dynamics of species inhabiting fragmented landscapes.

Michael Hassell

84

Gaston, K.J., Blackburn, T.M. & Lawton, J.H. (1977)

Interspecific abundance range size relationships: An appraisal of mechanisms. *Journal of Animal Ecology, 66, 579-601.*

It has been said that to produce a citation classic one must write a very good or a very bad manuscript. This paper most certainly falls into the former category. It was a landmark of its time, by providing a comprehensive literature review and a series of testable hypotheses. These hypotheses revolve around the central problem of why species that are abundant locally tend to have wide ranges, and vice versa, leading to positive abundance – range size relations. The paper begins with a quote from Darwin who was aware of the problem, but 150 years later, we are still unsure as to the reason why the relations exist. This paper was important because it produced a formal set of hypotheses that could be tested. Two of the hypotheses, namely that sampling artefacts are responsible, are dismissed, leaving six biological explanations, involving position in the range, resource use and availability, habitat availability, metapopulation dynamics and density-dependent growth and death rates. Good science proceeds by the testing of hypotheses and this paper is an excellent example of how to progress science and write a potential citation classic at the same time.

Alan Gange

85

Committee appointed by Council on 26 May 1942 (1944)

Nature conservation and nature reserves. Journal of Ecology, 32, 45-82; *Journal of Animal Ecology, 13, 1-25.*

During the darkest days of World War II in 1942 the BES Council established a committee chaired by Arthur Tansley 'to consider and report on the whole question of the conservation of nature in Britain', in response and support to a Government-supported Nature Reserves Investigation Committee (NRIC), set up to prepare for the post-war situation. The BES Committee's Report (probably drafted by Tansley himself) was (unusually) published in both BES journals. The case for establishing a reserve was seen to be research, public enjoyment and education. The Report backed the NRIC in asking that 'the Government should take full responsibility for the conservation of native wild life, both plant and animal' by establishing a National Wild Life Service responsible not only for the management of nature reserves, but for 'continuous research on the problems of conservation and control, whether within or outside the reserves'. The result was the setting up in 1949 of the Nature Conservancy, and indirectly contributed to the enormous growth and interest in biological conservation in succeeding decades.

R J (Sam) Berry

86

Foster, D.R. (1992)

Land use history (1730-1990) and vegetation dynamics in central New-England USA. *Journal of Ecology, 80, 753-772.*

Foster reports a detailed study of changes in land use history and vegetation composition over a 250-yr period in central Massachusetts (USA). For North America the Foster paper stands out for its thoroughness, detail, and for its extended time interval. A key feature is the 380-ha study tract: small enough to be studied in detail, but large enough to be representative of the township, county, and region. There are three principal findings. Firstly, the study tract changed dramatically over the 250 years from being entirely forested (save for a bit of marsh) to being more than 80% open land in 1840-50 to being overwhelmingly forested again today following abandonment of agricultural lands. Secondly, patterns of land ownership varied in turnover rate and size of individual holdings. A particularly elegant series of figures documents at 10-yr intervals how the study tract went from 25 land owners in 1760 to 13 owners in 1840 to 2 in 1900 (by 1910 Harvard University owned the land). Thirdly, the spatial patterns of land use types were best explained by soil drainage and proximity to farm houses and town roads. The Foster paper serves as a model for the rewards of extracting and summarizing historical land use records from other locales.

Peter L Marks

87

Turner, I.M. (1996)

Species loss in fragments of tropical rain forest: a review of the evidence. *Journal of Applied Ecology, 33, 200-209.*

The loss of species is one of the major concerns of the educated people throughout the world. In the tropics we have the opportunity to preserve fragments of the original ecosystems, but will these fragments actually preserve the diversity they started with? Turner's paper shows that in nearly all cases tropical rain forest fragmentation has led to a local loss of species, both for animals and plants. In 1996, when the review was published, Turner found only 28 papers, most were from the Biological Dynamics of Forest Fragments project (BDFFP) in Amazonian Brazil. Since then the field has grown dramatically. In August 2012 a search in the Web of Knowledge for fragment* AND forest* AND tropic* returned 4209 papers. . In 1996 the BDFFP dominated the scene and still does - 542 publications by 2010. However, a large new project, the Stability of Altered Forest Ecosystems (SAFE) in Borneo, is likely to produce a lot of interesting new insights into the effects of fragmentation. Turner's paper on the fate of forest fragments was a timely review of a field that will continue to be important for the foreseeable future.

Edmund Tanner

88

Baker, H.G. (1948)
Stages in invasion and replacement demonstrated by species of Melandrium. *Journal of Ecology, 36, 96-119.*

Reproductive isolation is often weakly developed in plant species resulting in episodes of hybridization. Recent studies on the ecological and genetic consequences of hybridization have provided novel insights into plant invasions, and the extent to which the infusion of alien genes into the gene pool of native taxa leads to a loss in species identity has become a key issue. An early effort to examine this problem by the renowned evolutionary ecologist Herbert G. Baker was the topic of his Ph.D. thesis at the University of London. By sampling populations of *Silene dioica (Melandrium dioicum)* and *Silene latifolia (Melandrium album)* from selected regions of the UK, and investigating patterns of morphological variation, Baker recognized four chronological stages in the invasion and replacement of one species by another. His work indicated that the destruction of woodlands by agriculture and urbanization favoured the spread of *S. latifolia* bringing it into contact with *S. dioica*. Pure *S. dioica* populations were often difficult to find in some areas owing to extensive hybridization. Today *Silene* is a classic model system in ecological genetics [*Heredity* (2009) **103**, 5-14] and molecular markers could be profitably used to investigate Baker's predictions concerning future interactions between the two species.

Spencer C H Barrett

89

Blossey, B. & Notzold, R. (1995)
Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. *Journal of Ecology, 83, 887-889.*

Blossey & Notzold (1995) proposed that if an alien plant escapes some or all of its native herbivores, resources spent on defence might be to some extent 'wasted', and natural selection would reallocate them to increased growth or reproduction. Coming early in the explosive growth of invasion biology, and making the simple, relatively easily tested predictions that (a) under identical conditions, plants from the introduced range will outperform those from the native range, and (b) specialist herbivores will perform better on introduced plants, the Evolution of Increased Competitive Ability (EICA) hypothesis has been a major success, with over 500 citations at the time of writing. Not that all those tests have been positive; indeed support for the hypothesis has been decidedly mixed, not least because support for the underlying idea that recently introduced plants face fewer enemies is also rather equivocal. But an idea doesn't necessarily have to be right to be important, and the enduring appeal of this very brief, 3-page Forum paper illustrates the value of concisely stating a new hypothesis and especially, I suspect, of giving it a memorable name and acronym.

Ken Thompson

90

Davis, M.A., Grime, J.P. & Thompson, K. (2000)
Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology, 88, 528-534.*

'Forum' papers were introduced into the *Journal of Ecology* to present new ideas and stimulate scientific debate. Davis et al. have amply met those expectations; their paper has already been cited 994 times, notwithstanding its relatively recent publication. Invasive species are acknowledged as one of the greatest threats to biodiversity, as the global homogenization of communities progresses; yet we have had little systematic understanding of what makes a plant community susceptible to invasion. This paper provided a concise theoretical framework: it proposed that a plant community becomes more invasible whenever there is an increase in the amount of unused resources. Either reduced resource uptake or greater resource supply will increase invasibility, which thus may fluctuate over time and is not necessarily an inherent attribute of communities. This idea is illustrated by patterns of invasion resulting from a common inoculum of 58 species on a two-dimensional experimental matrix, comprising gradients of fertility and disturbance. However, resource enrichment or release must coincide with the availability of propagules, explaining the elusive, episodic, nature of invasions. The paper makes seven testable predictions, based on fluctuating resource availability - a stimulus to the development of invasion ecology from a diffuse, anecdotal subject to a much-needed predictive science.

Tony Davy

91

Bradshaw, A.D. (1983)
The reconstruction of ecosystems: Presidential Address to the British Ecological Society, December 1982. *Journal of Applied Ecology, 20, 1-17.*

Tony Bradshaw was one of the greatest influences in the establishment of the new science of restoration ecology. The selection pressures of metal-contaminated sites had provided a field laboratory for studies of evolution and ecological genetics, for which he was already famous, when he began to promote the idea that ecologists should attend to the repair of industrial dereliction and then the reconstruction of ecosystems. This Presidential Address provided a compelling, fluent argument for ecological restoration, drawing particularly on his extensive experience with the reclamation of heavy-metal, colliery and china-clay wastes. Soil takes centre-stage, especially the amelioration of toxicities, nutrient deficiencies and adverse water relations. Tony recognized that such work afforded unique insights into natural colonization and successional processes, blurring the traditional distinction between 'pure' and 'applied' ecology. He highlighted the importance of facilitation and the necessity to amass sufficient nutrient capital as a prerequisite for ecosystem development. Reconstruction was conceived essentially as employing ecological understanding to accelerate or enable natural processes. He believed that the ability to build a system from its components was a better test of understanding than any analytical dismantling, however scientific. The paper embodies a positive, forward-looking message for tackling our daunting environmental problems.

Tony Davy

92

Bobbink, R., Roelofs, J.G.M. & Hornung, M. (1998)
The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. *Journal of Ecology, 86, 717-738.*

Dramatic increases in atmospheric nitrogen deposition in Europe during the last few decades of the 20th Century inevitably led to interest in its possible ecological effects. By the late 1990's a considerable number of studies was being undertaken in semi-natural ecosystems across Europe, and a review of this work was timely, not least because of the possible effects on biodiversity. In this paper the authors reviewed the evidence that atmospheric deposition leads to the accumulation of nitrogen in ecosystems, its effects on nitrogen availability and plant growth and competition, including the potential increased susceptibility to stress factors such as frost and drought, and effects mediated by increased soil acidification. It also considered the potential involvement of pathogens and herbivores in vegetation change induced by atmospheric nitrogen, most notably the role of the chrysomelid heather beetle (*Lochmaea suturalis*) in the conversion of Dutch heathlands into grasslands. The authors brought together evidence of effects in a wide range of terrestrial ecosystems, but also too in soft water lakes. They highlighted the fact that in general nitrogen deposition leads to loss of biodiversity, and that nitrogen emissions must be controlled to limit this effect. European research in this field led the world, and the importance of emissions control is now recognised worldwide.

John A Lee

93

Ratcliffe, D.A. (1970)
Changes attributable to pesticides in egg breakage frequency and eggshell thickness in some British birds. *Journal of Applied Ecology, 7, 67-115.*

The publication of *Silent Spring* in 1962 first raised public concern over pesticides but it was the rigorous scientific work of Derek Ratcliffe throughout the 1960s, culminating in this paper in 1970, that provided the evidence that changed the policy, and thus changed the world. Ratcliffe meticulously compared the weight and thickness of contemporary eggshells with those collected from previous decades. He discovered that shells collected from the late 1940s onwards were thinned in many different species, and that the timing of the thinning matched the introduction and widespread agricultural use of organochlorine pesticides. Ratcliffe's initial findings were published in Nature but the *1970 Journal of Applied Ecology* paper set out, over 50 pages, a detailed analysis that covered a wide range of species and brought together field observation, laboratory study, novel mathematical indices and statistical probability. In perceiving, then understanding and then explaining, the link between environmental pollution and reductions in egg weight, breeding failure and population decline, Ratcliffe was forging the science of evidence-based environmentalism. His science shifted national policy. National concerns in the UK linked with those in the US, and became an international campaign. The European Union banned dieldrin from agricultural use in 1981 and DDT in 1986.

Tom Tew

94

Green R.E., Newton I., Schultz S., Cunningham A. A., Gilbert M., Pain D. J. & Prakash V. (2004).
Diclofenac poisoning as a cause of vulture population declines across the Indian subcontinent. ***Journal of Applied Ecology, 41, 793–800.***

In the 1990s vultures began dropping from their perches across the Indian subcontinent. It took a few years to find a common element in the deaths of otherwise healthy birds. Each had suffered from visceral gout followed by kidney failure and each contained residues of diclofenac, a nonsteroidal anti-inflammatory drug developed for human use but lately introduced as a veterinary medicine in Pakistan and India. Green and colleagues used a simulation model of vulture demography to determine whether the relatively small numbers of dead ungulates that had been treated with diclofenac were sufficient to account for the vulture population crashes. Their models were based on vulture survey data and knowledge of demographic rates. Vultures vary in feeding frequency, so they ran models with intervals between feeding bouts of 2, 3 and 4 days. Their specific objective was to estimate the proportion of ungulate carcasses that would need to contain lethal doses of diclofenac to cause the observed population declines. The answer (between 1 in 130 and 1 in 760) was similar to the proportions observed among dead or dying ungulates in the wild and the researchers made an urgent call for action to prevent future diclofenac exposure.

Colin R Townsend

95

Chamberlain, D.E., Fuller, R.J., Bunce, R.G.H., Duckworth, J.C. & Shrubb, M.(2000)
Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. ***Journal of Applied Ecology, 37, 771-788.***

The widespread, and dramatic, declines of farmland birds have been a key conservation science issue in Europe for almost 40 years. This paper represented a step-change in the strength of evidence linking these declines to agricultural intensification. It drew together a vast array of long term (1962-1996) data sets on birds and habitats in England and Wales; 31 variables relating to agricultural change in arable and livestock sectors and population trends for 29 bird species, and demonstrated a remarkable match between the two. The rate of change in bird populations mirrored that of agricultural change with a six year time lag, a delay that would be expected if the relationship is a causal one driven by indirect mechanisms such as food reduction. The findings were a key part of the evidence that led the British Government, in 2002, to pledge to reverse the decline in farmland birds -initiating a wealth of research (and policy) to develop effective agri-environment options. The study also showed that effects of land use change on bird populations may involve several interacting factors, driving population declines, suggesting broad-scale agricultural extensification may afford the greatest benefits for bird populations

Juliet Vickery

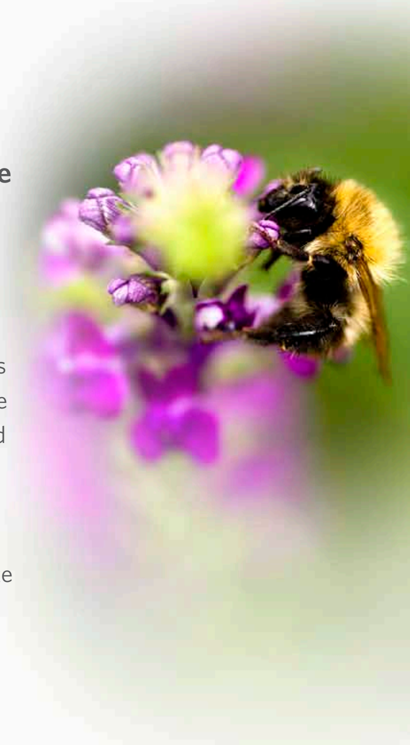
96

Kleijn, D. & Sutherland, W.J. (2003)
How effective are European agri-environment schemes in conserving and promoting biodiversity? ***Journal of Applied Ecology, 40, 947-969.***

This paper was one of the first to question the effectiveness of agri-environment schemes to conserve biodiversity. Although other authors had published research on agri-environment schemes only a handful of papers had explicitly addressed the policy of encouraging farmers to protect and enhance the agricultural environment since this legislation was adopted in 1992 under the European Union's Common Agricultural Policy (CAP). Following the 2003 paper, research on this topic has increased sharply. The authors described a 'lack of robust evaluation studies' in their paper, which no doubt sparked and increased research on this topic, including research aimed at improving the effectiveness of agri-environment schemes.

Not only has Kleijn and Sutherland's paper had an influence on research but it also stands out as being particularly relevant to policy. The paper was written in the context of EU agricultural policy: both the costs of the CAP and consumer concerns about intensive agriculture are highlighted in the introduction. The paper continues to be heavily cited in both ecological journals and the policy literature.

Allan D Watt



97

Carvell, C., Meek, W. R., Pywell, R. F., Goulson, D. & Nowakowski, M. (2007)
Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. ***Journal of Applied Ecology, 44, 29-40.***

The ideal when studying applied problems is to provide a management solution, implement that solution and then test its efficacy under field conditions. The majority of studies fall short of this, usually stopping before offering a management solution. An exception to this is Carvell et al. (2007) where the co-authors are government scientists, a university academic and a practitioner. They test the management recommendations from a number of short-term, single site studies using a large-scale field experiment. The experiment tests the attractiveness to bumblebees of six types of field margin. Implemented on six farms spread across central and eastern England and sampled numerous times over three years. The end result is a very large dataset which was used to assess the forage value of the margins for bees. It is not perfect (they could have sampled flower visitors other than bees) but the paper represents a quantum shift in our approach to testing the efficacy of agri-environmental schemes.As well as citing this paper frequently in my research I use it in my undergraduate lectures, presenting the field experiment first and then watching the farmer- training DVD which is presented by one of the co-authors. This way, students can see both excellent science and real impact on the farm.

Jane Memmott

98

Ticktin, T. (2004)
The ecological implications of harvesting non-timber forest products. ***Journal of Applied Ecology, 41, 11-21.***

Non-timber forest products (NTFPs) provide important livelihoods benefits for millions of forest-dependent people, and can deliver conservation benefits if they incentivise communities and governments to protect standing forest. However, there could be ecological consequences of harvesting these products, particularly if extraction rates are not sustainable or the extracted species have key ecological roles. Prior to the article of Ticktin (2004), our knowledge of the ecological consequences of NTFP extraction was disparate, and spread out across many different case studies. Ticktin made an important advance by systematically reviewing the conclusions of 70 different studies from across the world. Although he shows that many NTFP are extracted unsustainably, the good news is that some management techniques can be effective at reducing the negative impacts of harvesting. These include enrichment planting, shade management, and focussing on non-lethal harvesting activities that do not affect the population of adult stems (such as the harvesting of bark, fruits, latex and resins). The results highlight the importance of considering a species life-history when developing management plans, and considering the importance of spatial scale. Ticktin also demonstrates the need for researchers to work more closely with resource users when investigating the ecological consequences of NTFP harvesting.

Jos Barlow

99

Caughley, G. (1994)
Directions in conservation biology. ***Journal of Animal Ecology, 63, 215-244.***

In 1994 conservation biology was still a new science. The prevailing paradigm was derived from theoretical population biology, examining largely stochastic demographic and genetic factors that might drive extinction in small populations with long run stable population sizes. Caughley's criticism was that this treats an effect (smallness) as if it is a cause, and analyses persistence in small populations where nothing unusual happens. He highlighted an alternative, more useful paradigm for conservation – the declining population. Conservation priorities largely result from deterministic processes (attributable to people) that are reducing the size of populations, and driving them towards extinction. The priority then is the diagnosis of the causes of the declines, ways and means to intervene, and the likely outcomes from alternative interventions. Caughley concluded that the declining-population paradigm urgently needed more theory and the small-population paradigm needed more practice. This paper has had lasting consequences. Conservation biology now explicitly addresses both paradigms. It also brought tools and skills from unfashionable wildlife management into fashionable conservation biology, influencing conservation practice for the better. Sadly, Graeme Caughley died in 1994, very shortly after this paper was published and an obituary was also published in the *Journal of Animal Ecology* of that year.

Georgina Mace

100

Sutherland, W.J. and 38 others (2006)
The identification of 100 ecological questions of high policy relevance in the UK.
Journal of Applied Ecology, 43, 617-627.

This paper is a landmark in bringing together the (primarily) academic ecological research community and a key group of users of research – land-use policy makers and advisors. Its importance lies not just in the questions produced (most are still relevant), but in the approach adopted and the dialogue created. The spread of questions illustrates the policy need to address broad general themes. Many of the questions do not have straightforward answers but will ultimately involve judgements: for example 'where should new woodlands be located?' depends on what sort of woodland, which in turn depends on what it is to be used for. This may take the researcher into unfamiliar territory. The paper notes that the "scientist cannot remain distinct from the policy process in providing the evidence base"; there must be on-going discussions from the initial identification of the question, through to the presentation of the results including the limitations and uncertainties involved. Not all researchers will be happy with this idea, preferring to see research as something "untainted" by the messy things that policy involves (competing interests, human values, politics). However if you want your research to contribute to scoring goals, you have to be playing the game.

Keith Kirby

04 Winter moth provided by David Green

09 Winter moth provided by David Green (top image)

Pair of winter moths by Keith Tailby (bottom image)

10 Great tit nest provided by Professor Chris Perrins LVO FRS

12 Venturia Canescens Icheumonidae provided by Professor Michael Hassell CBE FRS

13 Scottish heathland provided by Dr Rob Brooker

15 Bellamy's bank, miller's Dale, Derbyshire one of the original research sites provided by Professor Ken Thompson

16 Seeds of a range of British grass species provided by Professor Ken Thompson

18 Picture of Sassendal, Svalbard with students on a UNIS Arctic Biology field course, provided by Professor Ian Hodkinson

19 Scottish mountain vegetation provided by Professor Robin Pakeman

21 Woodland canopy provided by Dr Keith Kirby

23 Leaf litter experiment provided by Dr Keith Kirby

24 Maize plant provided by Dr Alan Chilimba, Director of the Lunyangwa Research Station, Mzuzu, Malawi

29 Predator cages for gobies provided by Professor David Raffaelli

31 Bugle Ajuga reptans one of the plants used in research provided by Professor Alastair Fitter CBE FRS (top image)

Vulpia ciliate provided by Professor Alastair Fitter CBE FRS

Mycorrhizal hyphae provided by Dr Angela Hodge

33 Perch provided by the Freshwater Biological Association

34 Zooplankton provided by the Freshwater Biological Association

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