

Conference Commentary

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The past few years have seen a burst of conferences on plant population biology. Many of these conferences, like the present one, have been directly concerned with the interactions between ecology, genetics and physiology. There is clearly a widely felt urgency to find interfaces, bridge them, and thereby to integrate different disciplines and to exchange ideas. The expected products of this integration are creativity and new directions. There is no question that plant population biology is now a vigorous area of inquiry. So where does this need for new directions come from? Is it simply a natural manifestation of the vigour of a growing area, or, as some cynics might say, has the firework fizzled and is it in need of new spark and inspiration? As I sit here a few months after the conference, reading the transcript of the final discussion and reflecting back on the papers, I think the answer is all and more of the above. Indeed, since many of the comments made in the concluding discussion reflected both the history and the current crises in the subject, it seems appropriate to summarize some of that discussion here.

A historical perspective was provided by Pierre-Henri Gouyon. As a student ten years ago he felt excited by the arrival of plant population ecology. Its arrival in France was as in other countries of Europe, and as in the United States. It came (it must be said, its incarnate form was John Harper!), it was seen, and it certainly conquered an ecology rather moribund with the excesses of descriptive phytosociology and "multi-factor ecology." The latter was an autecology based on the assumption that if only we could measure all the environmental factors impinging on every species we would then understand their ecology and distribution. Plant population ecology promised a more dynamic view dealing with process, it was placed in a Darwinian context and integrated with evolution, and its Harperian origins gave it a thoroughly experimental tradition. The success of this invasion was alluded to by a number of speakers during the final discussion.

Pierre-Henri Gouyon told us that in France "now Population Biology exists; even in the same corridor you can find geneticists, physiologists, ecologists, together, even not fighting, even discussing!". Mike Hayward also told us we should be encouraged that ecologists and physiologists are now getting together and looking at common problems. Other speakers were more pessimistic, more yearning for direction and unity. Pierre Jacquard felt that we had been given a tool, demography, but not a science, and that our pride in being able to measure more things than zoologists may be leading us into a new descriptive phase. He feared continued progress might be in the direction of measuring smaller and smaller plant parts! George Williams also remained perplexed: "One of the things that struck me first at the Population Biology Conference in Waageningen and continues to puzzle me now is what is the central theme of population biology, what is the question that is being asked by population biologists"... there seems to be no unification or even any way to get at unification."

When Pierre Jacquard surmised that "perhaps some of our defects are the result of past successes" I think he went a long way towards explaining the source of the disquiet expressed by many speakers. Plant population biology conquered precisely because John Harper showed us how it could be done, and how it could be done in an exciting way. The subject was not born because there was some pre-ordained issue to be solved (cf. the development of population genetics as a means of reconciling Mendelian processes with evolutionary change), nor did it have a strong theoretical base. Its self-thinning laws were empirically derived; the competition theory of De Wit was a gem, but borrowed more from the physical chemist than from the plant physiologist; and while a vast theoretical literature existed in animal ecology and population genetics, these were two separate strange and alien ponds, in which few botanists had the tools or the courage to fish. Could it have been otherwise? During the discussion Jim Cullen, confessing to being a zoologist watching from the sidelines of the meeting, pointed out that a unifying force in animal population biology had historically been the question of what regulates populations. This question had its source in a powerful theory of population regulation and in real-world contrasts such as the subtly synchronized cycles of Lynx and Hare versus the

wildly chaotic cycles of Australian insects. The question of population regulation has persisted in animal ecology, perhaps no longer with the full force of the density-dependent/independent battle, but nevertheless with sufficient intensity to generate sophisticated approaches to population dynamics, and to theoretical and empirical determination of community structure. In contrast we have almost no theories of plant population dynamics. This is true at both the conceptual and at the mathematical model building level. Thus not only do we hardly know or even discuss, beyond decrying Lotka-Volterra models, which if any population models are valid for plants, but it seems not to be an issue whether density dependence occurs, whether metapopulation concepts are useful, or how component dynamics affect community process. In the discussion Steve Kelley reminded us that "What you see is dependent on your theory and if the theory is not developed to any degree of sophistication, you end up doing a lot of unproductive research." While I strongly support an eclectic approach to all science and therefore would not exhort everyone to go out and do theory, there is a need for such theory to balance the historically empirical basis of the discipline.

The difficulties of integrating physiological, ecological, and genetic approaches do not simply stem from the absence of common questions. Often, highly conflicting paradigms form the fabric of the different disciplines. For example, I have argued that explaining the distribution of a species is not an ecological but a genetic question. This is perhaps an extreme view, but it stems from the notion that any explanation should account for evolutionary failure and for why a population does not evolve beyond its existing limits. So many current explanations are purely ecological and wedded to the assumption that to explain distribution one only has to find physiological tolerance limits. Evolutionary issues are therefore by-passed and integrative approaches delayed.

Another somewhat related problem came up in discussion. It was pointed out by Pierre-Henri Gouyon that evolutionary biology is in a crisis. "One of the best signs of a crisis in any field is when a scientist begins to question its fundamental concepts: thus adaptation has been questioned as a useful concept simultaneously by Gould and

Lewontin, and by Harper"... "We are in an active destructive phase." As I mentioned during discussion, this is a serious point of inhibition between physiological ecology and evolutionary ecology. Physiological ecologists assume the paradigm of adaptation, assume populations are different in a way that is adaptive. In contrast, evolutionists are seriously trying to destroy the concept of adaptation or at least get by without it. It is no wonder communication is at times difficult!

During the discussion I outlined a hierarchy of types of interactions that can occur between disciplines. We can interact socially. We can use each other's techniques. We can work on the same species. Or we can ask shared questions. (Appropriately, at this point during the conference, a clap of thunder was heard as a Mediterranean storm passed overhead.) Asking shared questions is the hardest but also potentially the most valuable way to interact. One thinks of a chemist and biologist (with a little borrowing from an X-ray crystallographer) combining to resolve the structure of DNA. Nearer to home, one thinks of geneticists combining with ecologists in the early seventies to merge models of selection with models of population growth and so formally integrate theoretical population ecology and theoretical population genetics. However such instances are in my opinion very rare. Certainly this conference produced no agreed upon question. I personally shared beer, shared ideas on techniques, and enjoyed listening to others describe studies with some of my past, present, and perhaps future research organisms! Indeed, much of science proceeds more by insights that come from these modest hybridizations, rather than by some saltation, some interdisciplinary allopolyploid, that sends us back to our laboratories clutching a golden question.

The second focus of the conference was to examine the role of gene flow and dispersal in the population biology of plants. One outcome of the papers and the ensuing discussions was that, by the end of the conference, we were all very hesitant to use the word "population." Although this surprised me at the time, I now think that this was to be expected. The term "population" is not only used differently by ecologists and geneticists, but the use of summary population statistics (such as neighborhood area, or gene frequency) obscures the complexity

of pollen and seed dispersal events. These events may have consequences for the fitness of individuals, they may therefore themselves be the objects of selection, and they will affect genetic structure and propensity for differentiation. A focus on dispersal events also takes us out of the conventional view of populations as isolated units having only an internal dynamic and leads us to consider the broader scale of inter-population dynamics.

Another clear impression that I was left with after the second part of the conference was that the documentation of genetic variability should no longer occupy the center stage when we consider factors determining the rate and direction of evolution. Demographic structure could be all important. For example, a few large established individuals in a perennial population could be seen as a gerontocracy making disproportionate genetic contribution and so preventing or slowing evolutionary change. We are all aware of the homogenizing effects of gene flow, but evidence was presented of such effects among fig "populations" over distances that we think of as being geographic in dimension. And genetic correlations were shown to play a crucial role in selection response for life-history traits in natural populations. Certainly many factors, and not just simply the "raw amount" of variation, influence evolutionary rates and directions. Moreover, in their eagerness to measure genetic variation, population geneticists have perhaps forgotten that most of the traits of importance to the physiologist and ecologist show continuous variation. Variation in such traits cannot be easily quantified in terms of specific allelic frequencies at specific loci. These characters are therefore of little use for measuring levels of variation in a way that permits "character-free," unbiased comparisons across taxa. This concern with genes that are clearly identifiable electrophoretically or as overt polymorphisms could explain in large measure the lack of interactions between ecological physiological and genetic approaches that were alluded to earlier. Recent theories of evolution of quantitative traits will give population geneticists tools for studying ecologically and physiologically relevant traits. Conversely, the ecologist and physiologist will see genetic techniques as accessible, and if still not easy to master, at least not leading them down a seemingly endless

avenue of population statistics. Thus a view of evolution more firmly based in ecology and quantitative genetics may well bring about the integration we seek.

It remains for me to again thank the organizers of this symposium. Georges Valdeyron and Pierre Jacquard were largely responsible for much of the initial planning and conceptualization. Georges Valdeyron also planned a memorable field trip into the countryside of the Montpellier area, which included field sites, castles, a meal (or should I say feast), and an organ concert in the Romanesque Abbey of St. Guilhem-le-Desert. Rosalyne Lumaret impeccably handled the registration and general organization of the conference. Georges Heim did much of the editorial leg-work, and with Pierre Jacquard, coped with author-reviewer interactions. We thank them, the authors, and the participants, for a memorable meeting.

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