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Lessons from a Life in Time and Space

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Abstract

A research career investigating epidemiological and evolutionary patterns in both natural and crop host–pathogen systems emphasizes the need for flexibility in thinking and a willingness to adopt ideas from a wide diversity of subdisciplines. Here, I reflect on the pivotal issues, research areas, and interactions, including the role of science management, that shaped my career in the hope of demonstrating that career paths and collaborations in science can be as diverse and unpredictable as the natural world in which we study our organisms of choice.

INTRODUCTION

I have been incredibly privileged to make my career during a momentous period in the history of the biological sciences. During this time, many distinct strands of inquiry slowly merged or gained considerable richness through the acquisition of ideas, techniques, or approaches that previously did not exist or were part of a discipline that was seen as separate or even foreign. In looking back on my career, there were a number of touch-points, concepts, and interactions that help sum up my experiences. I hope in their telling I will encourage current and future generations of scientists to be ever alert to interesting ideas no matter their origin, to work collaboratively, and to never forget that "nothing in biology makes sense except in the light of evolution" (36, p. 125).

MENTORS, COLLEAGUES, AND HEROES

Colleagues, mentors, and heroes were all vital components in my development as a scientist—my career and life in general have undoubtedly been blessed by crossing paths or walking alongside a remarkable array of generous-minded people. Some I have come to know intimately, and our mutual interests transcend our scientific ones; others remain more distant but through their insights, skills, and general humanity still provide a spur driving our mutual interests in addressing what, why, how, and when?

Mentors

I find the modern administrative concept that mentors can be organized and implemented in the same way as other routine training processes to be a symptom of the belief that science is just another business that can be organized along the lines of whatever management model is dominant at the time. To me, mentors differ from colleagues who provide helpful advice that speeds settling into a new laboratory or work environment. Mentors are people who see an indefinable quality in an individual and, of their own volition, provide guidance borne of experience to develop the recipient's potential.

While I failed to realize it at the time, my first mentor in biology was my father. A charmed childhood lived first in the tropics (especially the Caribbean), then in the north of England (where the North Yorkshire moors and dales were my playground), and, finally, in southeastern Australia stimulated and encouraged my curiosity about the natural world. Although I failed to follow my father into marine biology, from the very start of an herbarium collection [my first specimen was hemp agrimony (*Eupatorium cannabinum*) collected in Plessey Woods, Northumberland on August 8, 1958] his gentle encouragement and assistance, in addition to my ever-expanding collection, imbued me with a strong knowledge of the northern European flora that later, in Australia, proved to be a powerful aid in weed biology studies. It was in England that I had my first encounter with parasites (albeit semi and wholly parasitic plants such as *Rhinanthus minor* and *Lathraea squamaria*) and initiated an interest that rapidly transferred to fungal pathogens when I began my first independent research project at the end of my undergraduate training.

In the years since then, I have greatly benefitted from the generous support of several diverse protagonists. My graduate supervisor, Graham Chilvers (Australian National University), fostered my early interests in pathology and drew me away from a constrained, unitarian disciplinary view by emphasizing the value of boundary crossing and borrowing and testing concepts from one field in another. John Harper's (University College of North Wales) constant challenging sharpened my thinking as well as my desire to get ecologists to recognize the ubiquitous nature of pathogens as an important force shaping the structure of wild plant populations and communities. Finally, Irvine Watson (University of Sydney) shared his knowledge of the early history of cereal rust research in Australia and the work of E.C. Stakman at Minnesota, firing an interest in rust fungi that still rages today. For me, a highlight that sprang from Irvine's support was a period in 1983 as a Fulbright Scholar with Alan Roelfs at the USDA Cereal Rust Laboratory in St. Paul (28, 29). Together, these influences pushed me to the realization that pathogens provide wonderful opportunities to witness evolutionary change and its broader downstream consequences play out over manageable periods of time.

To my lasting advantage, my mentors have all been very different. Indeed, in the latter part of my career, my mentors (Otto Frankel and Jim Peacock) had little in-depth knowledge of my scientific interests but saw in me management capabilities of which I was unaware. To them, I owe my deep interest in whole-of-agriculture issues and the fun I now have in serving various industries on management boards and committees.

Colleagues

Identifying specific colleagues who have influenced my career is fraught with the danger of hurting those not mentioned (although not forgotten or unappreciated). Indeed, there would be few who did not affect my outlook or influence the way I looked at problems throughout my career. However, almost inevitably, it is easier to identify influences that introduced a new approach or way of thinking than ones that reinforced existing directions. When I joined Commonwealth Scientific and Industrial Research Organization (CSIRO) in the late 1970s, my hitherto largely demographic and epidemiological focus expanded to include a population genetics approach, thanks to the welcome and encouragement I received from Don Marshall and Tony Brown (the resident plant population geneticists). Don's encouragement provided the impetus to apply isozyme technology to rust fungi and led to a stimulating and productive collaboration with the staff at the University of Sydney's Plant Breeding Institute at Castle Hill (23, 27). At the same time, I was able to complement Don and Tony's interests in the conservation of the genetic resources of a swathe of Australian endemic species of *Glycine* by adding detailed analyses of population-level variation in resistance to *Phakopsora pachyrhizi* (soybean rust) (15, 16, 24).

More recently, the potential opportunities that arise through the meeting of like-minded scientists across the globe led to two of my longest and most productive associations. Peter Thrall joined me in 1996 at what was probably the lowest ebb of activity in the *Linum marginale–Melampsora lini* study started by Andy Jarosz and myself ten years earlier. Our complementary skills and joint enthusiasm for getting out of the office reinvigorated the core of the project that then went on to produce 20 more publications, including those that provide clear evidence of evolution in both resistance and infectivity.

Perhaps the greatest bit of serendipity in my career started with considerable disappointment. A late 1980s sabbatical to the United Kingdom fell through, but before I had time to be resigned to missing out on some new stimulation, out of the blue I received an invitation to spend a summer in northern Sweden. Without a doubt, my decision to take up the invitation was one of the best in my life. Twenty-nine years on from my first visit in 1990, I still make an annual pilgrimage to the Skeppsvik archipelago to meet with Lars Ericson and collect another year of epidemiological data. I am greatly honored that my ongoing links with Sweden were marked by an honorary degree from Umeå University and foreign membership in the Royal Swedish Academy of Sciences. The establishment of the *Filipendula ulmaria–Triphragmium ulmariae* study (18) came at just the time I was exercising my mind about the consequences of time and space. It could not have been a more fortuitous turn of events.

Heroes

For me, these are a few scientific colossi from the past or present who laid down enduring principles that formed a central part of my research over most of my career. E.C. Stakman's adage that "plant diseases are shifty enemies" has proven correct time and time again. This insight is just as relevant 75 years later, and we would do well to remember it as molecular approaches are increasingly promoted as enduring solutions to disease control. It is not often that one gets a permanent reminder of our discipline's leaders, so it was with great pride that in 2003 I received the E.C. Stakman Award from the University of Minnesota for research leading to an understanding of the role of plant diseases as evolutionary forces shaping plant communities. The gene-for-gene theory contributed by H.H. Flor has been another powerful engine driving much of plant pathology. For me, it has been an integral part of my thinking about evolutionary trajectories of host and pathogen populations in wild communities.

Bottom Line

Supporting others and receiving support are hugely empowering activities. They carried me through dark times when nothing seemed to be going right and greatly enriched periods of progress and success. Knowing and interacting with colleagues around the world on multiple levels are truly invaluable features of science that make us citizens of the world.

RECONNAISSANCE IS NEVER WASTED

The message that reconnaissance is never wasted was drummed into me by my first technical support officer, Bob Herriot, an ex-farmer/soldier who had served in North Africa, Lebanon, and the Pacific Islands during various World War II campaigns. As a young postdoc, my enthusiasm and drive to succeed (and secure an ongoing position) gave me a feeling that unless I was actively setting up, measuring, or analyzing experiments, I was wasting time. Early field trips with Bob in the late 1970s when I was pursuing interests in the biological control of weeds (19) and the *P. pachyrhizi–Glycine* spp. pathosystem (24, 25) quickly disabused me of this view and reinforced the need for patience and observation. Many days traveling around southern New South Wales helped me develop a keen eye for pathological conditions observed while tramping through paddocks or bushland, contemplating a view with a coffee in hand and a mate by my side, or observing crops from a fast-moving car (auto botany). Years later, these and subsequent trips served as important sources of material for studying the phylogenetic relationships in rust fungi (64, 68) and were the inspiration for a long-term study of the *Cakile maritima–Alternaria brassicicola* association along coastal beaches (61) and many other activities.

Indeed, on one of our last field trips together, Bob and I followed up on an observation made by another technical officer working on the impact of rabbit grazing in the Kosciusko National Park. One day, knowing my interest in disease, Andrew Slee dropped a specimen of *L. marginale* infected with a few pustules of *M. lini* onto my desk with the general statement that there were a few infected plants at a particular place near Kiandra. Early in the summer of 1981, we visited the site and roughly assessed the severity of disease on 50 plants and took a few samples of rust. The rust was subsequently stored at 5°C, and my notes were consigned to a filing cabinet, as I was already fully occupied with other studies. Almost five years later, those notes served to identify the main site at which Andy Jarosz and I set up the beginning of a long-term host demographic, pathogen epidemiological study (20, 41, 56) that proved to be the foundation of a highly successful 30-year study of the temporal and spatial evolutionary dynamics of the *L. marginale–M. lini* wild host–pathogen association. In an analogous way, herbarium records can provide valuable insight into the geographic range of populations of both host plants and their pathogens, as has been demonstrated in a number of host–pathogen associations, including those involving the incidence of *Anthracoidea blanda* and *Puccinia caricina* on *Carex blanda* (2) and *Microbotryum violaceum* on *Silene* species (6).

Clearly, there is always a fine balance between procrastination and precipitate action. However, storing observations in the memory bank makes for a better understanding of the natural world. Although excess procrastination prevents progress, jumping in too early can equally lead to unnecessary frustration and heartburn when experiments do not work out.

OTHER DISCIPLINES DO FASCINATING STUFF

One of the biggest dangers in a scientific career is becoming too specialized. The balance between becoming a world expert in a highly specialized area and maintaining breadth is often difficult to strike as funding, promotion, and publishing prospects all come into play. Yet as R.J. Cook pointed out "Plant pathology…is one of the least specialized and most diverse fields in all of life sciences…our ranks are really a mixture of biochemists, geneticists, ecologists, microbiologists, soil scientists, ecologists, botanists, physiologists, even chemists, physicists and engineers" (34, p. 19). To this list, I would add evolutionary biologists. Although plant pathology embraces a very wide range of disciplines, the most exciting and challenging aspects of pathology are those that require a working knowledge of multiple disciplines; for me, melding epidemiological, ecological, and genetic considerations has had constant appeal but is an intersection that can still gain much from many other areas. Coming to plant pathology and epidemiology from a plant ecological background, I have always found it rewarding to look over the fence at the development of ideas in epidemiological and coevolutionary studies. Thus, studies involving human and animal disease epidemiology and control (4), insect–plant associations (57), bacteria–phage associations (47), ornithology (40), *Daphnia*–metazoan infections (37, 38), and the impact of parasites on free-living island populations of Soay sheep (33) have all given me food for thought. Indeed, if nothing else, delving into other disciplines can uncover examples and studies that support hypotheses or guide the development of new approaches. For example, although invasive pathogen outbreaks demonstrate the potential effect of pathogens in shaping naïve plant populations, the number of studies that clearly demonstrate that endemic pathogens play a role in plant population and community structure is very limited (22). However, by looking beyond phytopathology's traditional literature base, I have found valuable gems involving snow blights affecting plant community transition zones (8) as well as foliar and soilborne diseases affecting grassland composition (3, 14). Much interesting work is also buried in the gray literature (this is particularly the case for many forestry-based studies) or in languages other than English.

DISEASES ARE SHIFTY ENEMIES

E.C. Stakman was undoubtedly correct when he stated, "Diseases are shifty enemies" (55). Although over the years I have tended to substitute pathogens or, more specifically, rusts for diseases, there is no doubting the amazing and daunting ability of most pathogens to twist and turn, providing false optimism to researchers, breeders, agronomists, and farmers whenever humankind appears to get the upper hand. Time and again, pathogens have shown evolutionary lability by bouncing back from human-imposed controls through changes in their susceptibility to fungicides, their ability to overcome resistance genes (particularly pathotype-specific ones), and in their environmental envelope. This near-ceaseless flexibility and its implications and consequences for the rapidity at which fungal evolution can occur intrigued me early in my career. Here was a set of organisms in which I could hope to see and document evolutionary change at the population level within my own short attention span.

In this regard, I found rusts particularly interesting, an interest fired by opportunities to study the population structure of wheat stem rust (*Puccinia graminis* f.sp. *tritici*) in two very different environments. In Australia, migration and mutation are the only sources of variation, with occasional long-distance dispersal events from southern Africa (66) providing an injection of genetic variation that led to the development of a new lineage of pathotypes arising sequentially through simple one- or two-step mutations in infectivity. Using isozymes, we were able to confirm the distinctiveness of different lineages, the essentially clonal nature of lineages and even the occurrence of somatic hybridization events that led to the development of a distinctly Australian combination (23, 27). Although the hybrid that formed between races 126–5, 6, 7, 11 and 21–0 remained constrained to attacking wheat, we were able to show that a particular rust attacking barley in Australia was a hybrid between *P. graminis tritici* and *P. graminis secalis* (26). These studies underpinned a successful Fulbright scholarship application and in March 1983 my family and I went to the St. Paul campus of the University of Minnesota where I spent a fabulous eight months working with Jim Groth (Department of Plant Pathology) and Alan Roelfs (USDA, Cereal Rust Laboratory) on the laboratory's great collection of stem rust isolates from the asexual Great Plains population and its contrasting sexual population collected in the Washington–Oregon area (28, 29).

This work reinforced in me the undoubted importance of the sexual cycle in generating huge levels of variation. It sparked an ongoing interest in the complexity of rust life cycles and the ecological and epidemiological differences that occur among autoecious and heteroecious rusts, the role of different spore stages, and the evolutionary changes resulting in various forms of microcyclic rusts. In the early 2000s, that interest saw a short blooming in the use of a limited set of molecular markers to examine evolutionary relationships among the Pucciniaceae (64, 65) and broader Puccinales (68). In this regard, an ongoing regret of mine has been an inability to follow up on my interest in the wider evolution of *M. lini*. In the endemic Australian interaction between *M. lini* and *L. marginale*, marked differences in pathogenicity profiles were demonstrated between eastern and western Australian populations of the pathogen (32) and marked amplified fragment length polymorphism (AFLP) differences were found between metapopulations occurring in the plains and mountain regions of eastern Australia (9, 10). To my regret, I have never been able to look in more detail at potential speciation of *M. lini* on a global scale, where relatives of indeterminate phylogenetic distance occur in North America (54) and Eurasia on more than 30 *Linum* or closely related genera (e.g., *Hesperolinon*). I feel certain such a study, although potentially difficult because of quarantine restrictions and challenging collecting environments in the Caucasuses, would provide interesting insights into the divergence of closely related host–pathogen evolutionary paths. Although a move to scientific management prevented me from exploring the evolutionary phylogeny of *M. lini* in greater detail, I still marvel at the complexity of rust pathogen life cycles and wonder about the extent to which closely related rusts with a common aecial host but quite diverse telial hosts might exchange genetic material from time to time.

Determining the various mechanisms whereby variations are generated in different species is always intellectually satisfying but is only a first step to understanding their relative roles in the interplay of host and pathogen populations in space and time that are the basis of coevolutionary trajectories.

TIME AND SPACE MATTER: EVOLUTION IN THE REAL WORLD

Putting sources of variation into the real-world context of a crop or wild plant–pathogen system raises issues of time and space that simultaneously involve a challenge and a joy. A challenge because of the difficulty in assessing the role of time and space at the core of the epidemiological and genetic dynamics of host–pathogen interactions. A joy because, for a field biologist, there is no greater pleasure than being in the field. In many ways, the temporal component of evolutionary and epidemiological studies is the hardest to satisfy. Certainly, studies over a few years (1–3 years) are commonplace, but it is increasingly apparent that much longer-term assessments stretching over decades provide a totally different level of understanding with regard to some fundamental parameters, e.g., threshold sizes, extinction and recolonization rates, epidemic amplitudes, and periodicity.

Early in my studies of the evolutionary trajectory of natural host–pathogen associations, I thought (or perhaps just hoped) that space—in the form of multiple different local host–pathogen populations, with each potentially at different points along the evolutionary spiral—would provide a reasonable surrogate for following demographic, epidemiological, and genetic patterns through time. However, rather than being simple two-dimensional jigsaws of interactions, host–pathogen associations are complex three-dimensional interactions in which change through time is a vital component (52, 53). Indeed, it is not unreasonable to argue that natural host–pathogen associations are overlapping sets of two interacting metapopulation associations, with one involving changes within and among local pathogen populations and the other involving local host populations, between which linkages are driven by selection for viability and fecundity, leading to changes in resistance and pathogenicity.

Over my career, I have been lucky enough to have been involved in four such long-term studies ranging in length from 5 to 35 years (and still counting). In Australia, the long-running *M. lini–L. marginale* study of host and pathogen demography, epidemiology, and population structure is the most comprehensive in terms of genetic considerations but, because of variable resourcing, is temporally patchy in the number of populations monitored and genetic data gathered. Despite this, over the 30-year span of this study we were able to gather compelling data supporting long-term epidemiological patterns (42, 56), host and pathogen fitness effects (42, 59), variation in resistance and infectivity within and among populations (20, 21), marked differences in genetic structures between different host–pathogen metapopulations (10, 31), local adaptation (60), and coevolutionary tracking in host and pathogen populations (62, 63). A very different study in Australia involved the necrotrophic pathogen *A. brassicicola* attacking an introduced seashore plant, *C. maritima*. Here, in contrast to my other long-term studies that assessed pathogen activity once yearly, Peter Thrall and I followed the rise and fall of epidemics at six-week intervals for five years. At that point, because of other pressures on time, we wound up the monitoring program after the forty-second survey, perhaps not sure what the question was but secure in the knowledge that 42 was the answer (1). Host demographic and pathogen epidemiological patterns were followed on a total of 60-plus beach populations distributed into three contiguous metapopulation groups growing on the New South Wales south coast. Variability among population sites in size, exposure, and substrate underpinned differences in epidemic behavior and pathogen aggressiveness among the individual local host–pathogen associations (58), whereas each of the metapopulations performed slightly differently from each other (61; J. Papaïx, P.H. Thrall, L.G. Barrett, J.J. Burdon, unpublished data).

As mentioned above, perhaps the greatest piece of serendipity in my career was the opportunity to spend a summer in northern Sweden. The summer of 1990 was the start of a great enduring collaboration and friendship with Lars Ericson that focused on understanding the epidemiological dynamics of a natural host–pathogen metapopulation occurring on the Skeppsvik archipelago of approximately 50 islands in the Bothnian Gulf. We now have 29 consecutive years of data covering the incidence, prevalence, and severity of the rust pathogen *T. ulmariae* in more than 230 local *F. ulmaria* populations scattered across those islands. With this large data set, we have been able to show host fitness effects and resistance variation (39) as well as document how the pattern of pathogen activity has varied spatially. Disease levels were higher in some areas than others in some years but showed different patterns in other years as survival, extinction, and recolonization processes changed over time and space (52, 53). During the first ~10 years (1990–2000), pathogen extinction and recolonization in this system were reasonably predictable. However, the climate of northern Scandinavia is steadily warming (7, 11), and with the advantage of a longer temporal perspective we recently demonstrated a clear link between warming summer temperatures (which have risen by approximately 1°C since the start of the study) and increasing levels of pathogen extinction during the following winter period (69). As always, the exciting question is what will happen over the next years as climatic patterns continue to change.

There are few other long-term studies of nonagricultural host–pathogen associations (but see 5, 30), but it would be very remiss of me if I failed to acknowledge an amazingly large and ongoing study of the interaction between the host plant *Plantago lanceolata* and its powdery mildew pathogen (*Podosphaera plantaginis*), which encompasses ~4,000 separate populations spread over many islands and fields in the Åland archipelago of southern Finland. This magnificent study involves demographic and epidemiological baselines against which many insightful experiments have uncovered strong evidence for coevolutionary interactions between host and pathogen (44, 46, 50, 51).

There is no doubt that in plant pathology the "need for work in the field has not lessened" (67, p. 18). Furthermore, in many areas there is simply no substitute for long-term field studies because evolution occurs in the real, heterogeneous world with all its surprises and unpredictable fluctuations. Equally important though is to acknowledge that a deeper understanding is gained when such studies are tightly linked with a comprehensive laboratory-based program using the most modern molecular approaches.

DISEASE CONTROL THROUGH ECOLOGICAL AND EVOLUTIONARY THINKING

Despite a century or more of intensive efforts by plant pathologists and breeders, disease caused by a wide array of fungi, oomycetes, bacteria, viruses, and nematodes still inflicts significant production losses. Step-by-step incorporation of individual resistance genes has had success in protecting many crops but, almost inevitably, that success is followed by the appearance of new fungal pathotypes able to overcome that resistance, i.e., the "man-guided evolution in plant rusts" (43, p. 357) so apparent in wheat grown in the 1950s and 1960s. Although the rate at which resistance genes have been overcome has been reduced by tactics as simple as deploying gene pyramids containing multiple resistance genes, there is little reason to doubt the power of pathogens to respond to evolutionary selective pressures. Certainly, modern molecular technologies have opened up opportunities for novel approaches and raised hopes that resistance based on nonhost interactions (12), *R*-gene transfer from wild relatives (45), altered host susceptibility factors (13), or the use of specific pathogen *R*-gene effectors that are important for pathogen infectivity (35) may prove more durable or at least provide a greater diversity of genes to use in pyramiding. However, this first wave of benefits continues to rely on the same field deployment approaches—genetically uniform, high-density stands—that in the past have proven to severely underestimate the epidemiological power and evolutionary responsiveness of pathogens. This continuation of a brute-force approach that maintains strong directional selection on the pathogen worries me. I have great faith that the force of evolution will generate solutions for pathogens that will allow them to bounce back from such controls as long as we continue to use them in a way that reflects convenience for their fit to modern farming systems rather than taking a more sustainable, evolutionary approach that aims to present pathogens with a more variable environment in which disruptive selection is the norm. Approaches focused on presenting pathogens with shifting selection targets in which every transmission event has a high probability of resulting in a less than optimal fit of pathogen strain to host genotype is likely to lead to pathogen population structures of greater diversity but lower average infectivity and reduced population size and evolutionary potential (17, 48, 49, 70).

To achieve sustainable disease management requires a shift in mindset away from a sole focus on yield and productivity to a broader integration of productivity with underlying ecological, economic, and environmental dimensions. Multidisciplinary collaboration is critical for the development of effective sustainable disease management strategies. Evolutionary plant pathologists and geneticists need to play a major role in designing management practices that maximize host plant defense while simultaneously minimizing opportunities for pathogens to evolve. Most importantly, the approaches used must be adaptive (71). To be effective and durable, sustainable disease management must tackle the practices and social constraints that currently make adoption of a comprehensive suite of control measures based on ecoevolutionary principles difficult. To ensure greater stability of production systems, we must be smarter in the ways we integrate the use of genetics and pesticides into the agronomy and production dynamics of all farming systems.

THE DARK SIDE IS NOT ALWAYS DARK

Throughout my career, most of my colleagues have had ambivalent feelings about administration and management, certainly with respect to being drawn into management oneself. In this regard, I was no different. All I saw was a process fraught with frustration, compromise, and huge impositions on time better spent in pursuing scientific questions. How wrong I was!

When I first joined the CSIRO after two years of postdoctoral study in Wales, it had a university feel about it, just without undergraduate students or teaching. Although annual reports were required, the research staff were essentially free to pursue their own interests. Over the next few decades, political pressure (from the government that provided most of the funding) demanded and received increasing focus on the "industrial" in CSIRO's name and an expectation that research would be more aligned with industry needs. By the time I fell into more senior management roles in the mid-1990s, this, combined with a steadily tightening funding environment, led to somewhat less individual autonomy and increased the shaping of individuals into groups with common aims. I am sure that I railed against this change as much as many of my colleagues, but reasonably quickly I could see the advantages to research and its application. Moving into senior management brought contact with industry funding bodies (and their boards, all with a healthy mix of producers, scientists, and individuals with governance, legal, and commercial skills) and private business, including both national and multinational life science companies. Seeing the research and production world through their eyes was a great learning experience and one that I only wish I had experienced a little earlier in my career.

Trying to retrace the earlier steps in my career was not very successful. After nine years in charge of a major component of CSIRO (CSIRO Plant Industry), I stepped down with the intention of seamlessly slipping back into my former research role. The idea was far simpler than the reality: Technology had moved on, funding was limited, and, truth be told, I did not want to give up my involvement in the broader framing of agricultural industry processes. Thus, I now have what I regard as an almost perfect life structure: a mix of scientific writing, ongoing epidemiological studies in established metapopulation systems, and membership on a number of boards, panels, and committees that are influencing the direction of Australian agriculture.

Whether my experience was institution dependent or not I cannot tell. But I will reiterate that connecting firmly with your agricultural base and seeing problems through the eyes of producers makes it far easier to identify research foci that are most likely to make a meaningful difference. You will also meet many dedicated people with very different perspectives from those of your research-driven colleagues!

CONCLUDING REMARKS

Understanding the complexity of interactions between plants and their pathogens has no end. Initial static pictures of particular aspects of individual associations and more holistic studies encompassing the demography, epidemiology, and genetics of individual interactions have increasingly moved to studies embracing the influence of time and space. These studies are uncovering aspects of the coevolutionary trajectories found in host–pathogen associations, but there is still much to be learned through a melding of field- and laboratory-based studies that utilize molecular technologies.

Although there are a number of studies that take a community view of the role pathogens play in ecosystems, this level of approach is one that desperately needs further lines of attack, as climatic change and continuing pressure on nonagricultural land will inevitably affect the fundamental dynamics of many host–pathogen associations. Increases or decreases in the frequency and intensity of pathogen activity will, in turn, have significant implications for the maintenance of biodiversity, an area of research in which plant pathology has much to offer.

Increasing interest by consumers in the origin of foods, the processes used in their production, and the sustainability of farming systems will continue to drive the need to review the ways in which crops are protected. Although some approaches raise challenging questions regarding their economic viability, it is essential that all strategies, whether they aim to control disease via genetic, chemical, or biological means, are applied with the potential of evolutionary change in mind.

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